1 **Sharing the burden? Earthworms and woodlice show seasonal complementarity in**
2 **peak abundances in soil in an oak-beech temperate woodland.**

3 Daniel Carpenter^a, Emma Sherlock^b, Kelly Inward^a, Kerry Carroway^a, Angela Lidgett^a,
4 Paul Eggleton^{b*}

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6 ^a Soil Biodiversity Group, Department of Life Sciences, Natural History Museum,
7 London, SW7 5BD, UK

8 ^b Aquatic Invertebrates Division, Department of Life Sciences, Natural History
9 Museum, London, SW7 5BD, UK

10 *Corresponding author: p.eggleton@nhm.ac.uk

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17

18 **Abstract**

19 Complementarity between functional analogues can confer resistance and resilience
20 on ecosystems in the face of environmental change. High biodiversity can lead to
21 increased ecosystem functionality through complementary effects. Earthworms,
22 woodlice and millipedes can have high densities in leaf litter and soils, but little is
23 known about their seasonal patterns. The two groups play important roles in the
24 breakdown and incorporation of organic matter into soils. Differences in peak
25 abundance could affect the rates of litter break down and incorporation in different
26 seasons. We sampled earthworms, woodlice and millipedes from leaf litter soil
27 every month for ten years in a New Forest woodland. We used non-parametric
28 regression to explore monthly and yearly variation in the abundance of decomposer
29 organisms and soil temperature and moisture. Earthworms have a distinct seasonal
30 peak in density different from woodlice and millipedes. Earthworm peak density is in
31 the winter and spring and is correlated with greatest soil moisture. Woodlice (and
32 millipede) have their peak density is in the summer and is correlated with the highest
33 soil temperatures. This means that earthworms, woodlice and millipedes have
34 complementary peaks in abundance. These two groups have similar functional roles
35 in litter decomposition and these data imply ecological complementarity in this
36 important ecological process. This effect is likely to be widespread in lowland
37 woodland in the UK and Europe, with only extreme temperatures and low pH
38 limiting the distribution. Increased summer drought as a result of climate change
39 may lead to changes in the relative abundance of these three groups and in

40 particular local extinctions of earthworms which will in turn affect litter
41 decomposition.

42

43 **Keywords** decomposers, earthworms, complementarity, millipedes, seasonal
44 patterns, woodlice

45

46 **1. Introduction**

47 A global decline in biodiversity, as a result of both climatic and human-influenced
48 environmental change, is fuelling a renewed focus on our understanding of the
49 relationships between species diversity and ecosystem function. Specifically, the
50 resilience of an ecosystem to change depends on its ability to maintain function
51 while species diversity declines (Yachi and Loreau, 1999). Ecological resilience
52 therefore depends on the relative levels of functional redundancy and
53 complementarity across species within an ecosystem.

54 Ecosystems are said to have functional redundancy when there are many species
55 doing the same or similar jobs (Loreau, 2004). This implies that local extinction
56 events could cause species to be lost from the system with no apparent loss in
57 function, as other species compensate by supplying the function lost through the
58 extinct species (e.g. Elser et al., 1995; Goheen et al., 2005). Functional redundancy
59 implies ecological analogy, where similar species have essentially the same
60 functional role.

61 Competition for resources between species, however, works against functional
62 redundancy as species usually must evolve different strategies to exploit the same
63 resource. This means that species tend to reach abundance equilibria based on the
64 different strategies that they employ to exploit a common resource. These
65 strategies are often where species use a different part of a common resource
66 (Wilson et al., 1999) or exploit the resource at different temporal or spatial scales
67 (Albrecht and Gotelli, 2001). In extensive heterogeneous environments (e.g. soil)
68 with a large number of generalist organisms (e.g. decomposers), competition is
69 generally reduced as species can avoid each other or use different parts of the same
70 resource. This allows coexistence between species with similar environmental
71 tolerances, which generally leads to high functional complementarity (Setälä et al.,
72 2005).

73

74 Complementary effects can enhance ecosystem functioning through an increase in
75 biodiversity (Loreau and Hector, 2001; Bracken and Stachowicz, 2006; Yachi and
76 Loreau, 2006); process rates are often greater with higher biodiversity than with
77 lower biodiversity. Complementarity also occurs when the combined function of
78 two or more species can provide enhanced mutualistic benefits to other species, for
79 example by reducing stress (Stachowicz and Whitlatch, 2005).

80

81 Decomposition is a vital biological process that breaks down dead organic matter,
82 incorporates it into the soil and releases plant nutrients. The process is

83 conventionally attributed predominantly to microbes, but it is increasingly obvious
84 that macrofauna have an important role (Wall et al., 2008; Gessner et al., 2010.).
85
86 Invertebrates in the decomposer guild have four main roles in the decomposition
87 process. First they increase the surface area of leaf litter by communitation (Anderson,
88 1988). Second, they are direct decomposers of substrates through (mostly) midgut
89 enzyme production (Hassall et al., 1987; Guggenberger et al., 1996; Le Bayon et al.,
90 2002). Third, they act as habitats for microbial decomposition (Hassall et al., 1987;
91 Pokarzhevskii et al., 1997; Jegou et al., 2001; Scullion et al., 2002; Drake and Horn,
92 2007). Fourth, many of the invertebrates are coprophages (Ullrich et al., 1992).

93
94 While much is known about the functional roles of these soil macrofauna groups,
95 there is less information concerning their seasonal patterns (Gerard, 1967; Baker et
96 al., 1993; Spurgeon and Hopkin, 1999; Tondoh, 2006). In temperate systems,
97 seasonal differences in soil temperature and soil moisture affect the abundance of
98 decomposer organisms (Riutta et al., 2012.), with peaks of abundance in a particular
99 season as a result of their environmental tolerances. Previous work has shown the
100 response of earthworms to seasonal and yearly changes in soil temperature and
101 moisture over a six year period (Eggleton et al., 2009). Decomposition rates may
102 well vary with season, due to differences in peak decomposer abundance, rates
103 being high with peak abundance and low when abundance is low. If the peak
104 abundance for the different decomposer groups coincides in a season, then rates of

105 decomposition are likely to be greatest in that season and concomitantly low at
106 times when abundances are low. Alternatively, if the peak abundance of
107 decomposer groups are complementary (i.e. one group has its peak when another
108 has low abundance) then decomposition rates may well be maintained throughout
109 the year. However, partitioning of the leaf litter resource could also account for
110 differences in seasonal abundances of different litter feeding taxa.

111

112 Here, we present data from a ten-year study of soil and leaf litter macrofauna from a
113 broadleaf wood in southern England. We explore the temporal patterns of the three
114 main decomposer taxa (earthworms, woodlice and millipedes) to uncover in which
115 season each taxon has its peak abundance and to estimate the extent to which these
116 peaks coincide or are complementary. We found that peak seasonal abundance for
117 earthworms was different to that of woodlice and millipedes.

118

119 **2. Materials and Methods**

120 **2.1 Site description and sampling methods**

121 Whitley Wood is an ancient semi-natural wood situated in the New Forest,
122 Hampshire, UK (Coordinates 50.849152, -1.5766458). It is classified broadly as a
123 W10 *Quercus robur* - *Pteridium aquilinum* - *Rubus fruticosus* woodland under the
124 National Vegetation Classification (NVC) (Rodwell, 1991). However, it has two co-
125 dominant tree species, oak (*Quercus robur*) and beech (*Fagus sylvatica*), and a varied
126 understorey of hawthorn (*Crataegus monogyna*) and field maple (*Acer campestre*).

127 The ground flora is patchy, but includes bracken (*Pteridium aquilinum*), bramble
128 (*Rubus fruticosus* agg), common dog violet (*Viola riviniana*) and wood spurge
129 (*Euphorbia amygdaloides*). The wood, like many of those in the New Forest, is
130 browsed by ponies (Tubbs, 2001). Soils at the study site are Planosols (FAO WRB)
131 and are seasonally wet, in places gleyed, indicating temporary waterlogging.

132

133 We sampled every month for ten years, from March 2002 to February 2012 in a 2 ha
134 area of the wood. Each month we placed a 100m transect line at random within the
135 2 ha area and sampled at fifteen points at 7 m intervals along the transect. At each
136 sampling point we used two methods to extract invertebrates from the leaf litter and
137 soil respectively. To extract invertebrates from leaf litter we placed sieved leaf litter
138 from a 1 m² quadrat into Winkler bags for three days (Krell et al., 2005). To sample
139 earthworms in the soil we dug four pits (15 cm x 15 cm x 10 cm [depth]) each next to
140 the middle of the four edges of the 1 m² quadrat that was used to extract leaf litter,
141 giving a total of 60 pits per transect. Adult earthworms, woodlice and millipedes
142 from these samples were identified to species.

143

144 We pooled data from each part of the transect (i.e. litter or soil separately) to give a
145 single species x abundance list for each transect (as in Eggleton et al., 2009). Our
146 sampling methods risk double counting all groups as the leaf litter scrapes inevitably
147 samples some soil and the soil pits will sample some leaf litter. We have employed
148 the simplifying assumption that the soil pits sample the earthworms almost

149 comprehensively (as even epigeic earthworms are found predominantly in the soil
150 and humus layers) and that sieving litter samples the woodlice and millipedes almost
151 comprehensively (as those two groups are generally leaf litter inhabitants only).

152

153 At each sampling point we also measured soil moisture using a using a SM200 soil
154 moisture probe attached to a HH2 meter (Delta T Devices, Cambridge, UK) and soil
155 temperature using a simple bi-metal thermometer.

156

157 **2.2 Data analysis**

158 We partitioned the variance in the abundances of the species into seasonal and year
159 components using non-parametric regression in the R package *sm* (Bowman and
160 Azzalini, 1997, as outlined in Eggleton et al., 2009 (as modified from Fergusson et al.,
161 2007). Full details are in the supporting information of Eggleton et al., 2009). Initial
162 bandwidth values for the partitioning analysis were obtained using
163 *sm.regression.autocor* as monthly points are likely to be autocorrelated.

164

165 Relationships between (log +1)-transformed abundances and soil moisture and soil
166 temperature were also examined using non-parametric regression. In all cases we
167 used the *sm.regression.autocor* function to estimate the optimum bandwidths for
168 smoothing and the used the *sm.regression* function to test for the presence of a
169 significant relationship, using the *model="no effect"* command. Where the null

170 hypothesis was rejected at the $p < 0.05$ level an additional test was undertaken to
 171 examine whether the relationship could be modelled as linear, using the
 172 `model="linear"` command.

173

174 3. Results

175 3.1 Decomposer data

176 Over the ten years of the project we sampled 5,279 adult earthworms in 15 species,
 177 15,156 adult woodlice in five species and 438 adult millipedes in 11 species (see
 178 Table 1 for details). The five most abundant species of earthworm account for nearly
 179 98% of the total earthworm abundance. For one of the five species of woodlice
 180 identified (*Haplophthalmus danicus* Budde-Lund, 1880), we only sampled one
 181 individual in the 120 sampling periods. The five most abundant millipede species
 182 account for nearly 93% of the total millipede abundance.

Table 1. Numbers of specimens counted for each species. Percentages are calculated as totals within each major clade. The woodlice and millipede data are all from litter samples and the earthworm data are all from soil pits.

Species	No. sampled
Earthworms	
<i>Dendrobaena octaedra</i>	2679 (50%)
<i>Allolobophora chlorotica</i>	1441 (27%)
<i>Dendrobaena attemsi</i>	458 (9%)
<i>Aporrectodea caliginosa</i>	373 (7%)
<i>Lumbricus rubellus</i>	290 (5%)
<i>Aporrectodea rosea</i>	71 (1%)
<i>Satchellius mammalis</i>	10 (<1%)
<i>Octolasion lacteum</i>	9 (<1%)
<i>Octolasion cyaneum</i>	7 (<1%)
<i>Dendrodrilus rubidus</i>	5 (<1%)

<i>Aporrectodea longa</i>	2 (<1%)
<i>Dendrobaena hortensis</i>	2 (<1%)
<i>Dendrobaena pygmaea</i>	2 (<1%)
<i>Aporrectodea limicola</i>	1 (<1%)
<i>Eiseniella tetraedra</i>	1 (<1%)
Woodlice	
<i>Philoscia muscorum</i>	10013 (61%)
<i>Oniscus asellus</i>	2336 (14%)
<i>Trichoniscus pusillus</i>	1487 (9%)
<i>Porcellio scaber</i>	1319 (8%)
<i>Haplophthalmus danicus</i>	1 (<1%)
Millipedes	
<i>Glomeris marginata</i>	159 (36%)
<i>Polydesmus denticulatus</i>	90 (21%)
<i>Chordeuma sp</i>	74 (17%)
<i>Cylindroiulus punctatus</i>	48 (11%)
<i>Polydesmus sp</i>	35 (8%)
<i>Polydesmus coriaceus</i>	18 (4%)
<i>Chordeuma proximum</i>	10 (2%)
<i>Polyxenus lagurus</i>	1 (<1%)
<i>Ophiulus pilosus</i>	1 (<1%)
<i>Blaniulus guttulatus</i>	1 (<1%)
<i>Proteroiulus fuscus</i>	1 (<1%)

183

184

185

186 3.2 Temporal relationships

187 Species appear to have clear seasonal patterns, with abundance minima and maxima

188 in different seasons (Table 2); and different clades show different patterns.

189 Earthworms have their abundance maxima in the winter months (December –

190 February) and their abundance minima in the summer months (July and August) (Fig

- 191 1a). Woodlice and millipedes have similar patterns to each other but these differ
192 markedly from the earthworm pattern, with their abundance maxima in the summer

Table 2. Month of minimum and maximum abundances for each species of . The year response was tested against a null-hypothesis of no response at the $p>0.05$ level and that for a linear response at the $p<0.05$ level. H = estimated band width.

Species	Minimum	Maximum	Year
<i>Chordeuma</i> sp	February	August	No change ($h>10$)
<i>Glomeris marginata</i>	December	July	No change ($h>10$)
<i>Trichoniscus pusillus</i>	December	June	No change ($h>10$)
<i>Porcellio scaber</i>	January	July	Rising, linear ($h>10$)
<i>Oniscus asellus</i>	January	July	No change ($h>10$)
<i>Philoscia muscorum</i>	January	July	No change ($h=4.57$)
<i>Aporrectodea caliginosa</i>	July	December	Lower in yrs 1 & 2 ($h = 2.53$)
<i>Allolobophora chlorotica</i>	August	February	No change ($h>10$)
<i>Dendrobaena attemsi</i>	August	February	Rises to plateau ($h=2.53$)
<i>Dendrobaena octaedra</i>	August	February	No change ($h>10$)
All earthworms	August	February	No change ($h>10$)
All woodlice	February	August	No change ($h>10$)

193

194

195 Figure 1: Non-parametric regressions for earthworm (a) and woodlice (b) abundance,
196 with the variance partitioned into year and month.
197

Figure 1

198
199 months (June – August) and their abundance maxima in the winter months
200 (December to February) (Fig 1b). There appear to be no consistent yearly trends for
201 any species, except *Dendrobaena attemsi*, which shows a plateauing increase in
202 abundance over time, and *Porcellio scaber*, which shows a monotonic increase over
203 time.

204

205 3.3 Environmental (non-temporal) relationships

206 There is a strong (although not completely linear) negative relationship between soil
207 temperature and soil moisture, such that whenever the soil temperature is high then

208 soil moisture is low, and vice-a-versa (Fig 2). These conditions occur, of course,
209 particularly in the extremes of the seasons (August and February).

210
211 Figure 2: Relationship between temperature and moisture. (a) Non-parametric
212 regression with variance partitioned into month. (b) non-parametric regression of
213 temperature (black line) vs moisture (red line).
214

Figure 2

215
216
217 As a general pattern, then, earthworms and woodlice species have different and
218 opposite responses to temperature and moisture, while millipedes show a similar
219 pattern to woodlice. Earthworm abundance decreases with increasing temperature,
220 whereas woodlice abundance increases with increasing temperature (Fig 3a).

221

Figure 3: Non-parametric regressions of earthworms (black lines) and woodlice (redlines) log abundance against temperature (a) and moisture (b).

Figure 3

The opposite trend is true with respect to moisture, where earthworm abundance increases with increasing moisture and woodlice abundance decreases with increasing moisture (Fig 3b). This means that the highs and lows of both groups coincide with the seasonal temperature/moisture highs and low.

4. Discussion

We have established that woodlice and earthworms show contrasting patterns in their seasonal minima and maxima across the woodland plot. Woodlice are most abundant when earthworms are least abundant, and vice versa. This seems to be a result of the different environmental tolerances of the two groups and their different responses to the same environmental factors.

236

237 Our data reflects earlier findings that soil moisture is the most important
 238 environmental factor affecting earthworm abundance (e.g. Gerard, 1967; Auserwald
 239 et al., 1996; Cannavacciuolo et al., 1998). Soil moisture content is highest during the
 240 winter months when earthworms are at their most abundant and this because
 241 earthworms are extremely sensitive to desiccation. During drought conditions
 242 earthworms either aestivate (Edwards and Bohlen, 1996) or survive as cocoons
 243 (Petersen et al., 2008). Few adults can survive low soil moisture conditions, so when
 244 soil moisture is lowest during the summer months, earthworm abundance and
 245 activity is lowest. Earthworm abundance is also inversely correlated with
 246 temperature, but earthworms appear to be responding to the interaction of
 247 temperature and moisture (Gerard, 1967). When the soil temperature is lowest, soil
 248 moisture content is highest and vice versa. Frost conditions can severely affect
 249 earthworm abundance as only some species of earthworm (or their cocoons) are
 250 frost tolerant (e.g. *Dendrobaena octaedra* (Holmstrup and Loeschcke, 2003)).
 251 However, soil temperature did not drop below 2° C during the study period
 252 (minimum soil temperature, 2° C, maximum soil temperature, 19° C), and so
 253 earthworms were presumably able to remain active during all of the winter when
 254 soil moisture is generally at its highest.

255

256 In contrast, woodlice were most abundant in the summer months. This is probably
 257 because woodlice are known to respond to photoperiod (McQueen and Steel, 1980)

258 and increase activity with increasing day length (Wieser, 1984). Daylight hours are
259 greatest in summer when it is warmest, hence the positive correlation between
260 abundance and increasing temperature. Day length is longest in June, shortly before
261 the peak of activity for woodlice in this study. During the winter months, when the
262 days are short, woodlice are therefore at their least active. Woodlice are well
263 adapted to survive low moisture conditions, but are still limited by moisture (Wieser,
264 1984; Warburg et al., 1984) but possibly at soil moisture levels lower than found in
265 this study.

266

267 Millipedes show similar patterns to woodlice, but their abundances are much lower
268 and so they probably do not play as great a role in decomposition in Whitley Wood.
269 Millipedes require calcium to build and repair their exoskeletons (Hopkin and Read,
270 1992). Soil pH in Whitley Wood is low (ca. 4.5) and calcium is likely to be limiting;
271 the geology of the New Forest is made up of clays, gravels and sands (Melville and
272 Freshney, 1982) and therefore there is likely to be only very small amounts of
273 available calcium (Marschner, 1991). Consequently, millipede abundances are
274 probably lower when compared with populations in woodlands growing on soils of
275 higher pH over chalk or limestone (Lee, 2006).

276

277 This study shows that in our study woodland earthworms and woodlice (and, to a
278 lesser extent, millipedes) have complementary seasonal patterns of density.
279 Earthworms are at their most abundant when woodlice are at their least abundant,

280 and vice versa. We propose two hypotheses that might explain the opposite
281 seasonal patterns of these two important groups of macrofauna decomposers.

282

283 First, is true complementarity. The differences in peak abundance are due to abiotic
284 rather than biotic factors; earthworms and woodlice do not appear to compete for
285 leaf litter as their periods of peak abundance do not coincide. Earthworms and
286 woodlice have similar ecological functions in the breaking down and incorporating of
287 organic matter into the soil. It is therefore quite possible that this density
288 complementarity means that rates of decomposition are maintained, at least
289 approximately, throughout the year as a result of this complementary effect.

290 However, the full extent of this ecological complementarity can only be assessed
291 through proper litter decomposition experiments with separate exclusions of both
292 groups.

293

294 A second possibility is resource partitioning by litter decomposition succession (Slade
295 and Riutta, 2012; Riutta et al., 2012). In this hypothesis, competition between
296 earthworms and woodlice results in seasonal partitioning of litter, with earthworms
297 being more abundance during leaf abscission than woodlice. Within UK woodlands
298 as a whole, leaf palatability of different species means that earthworms feed first on
299 ash (very palatable) and then oak (less palatable), but they feed poorly on beech
300 (unpalatable) (Quadros *et al.* 2014). Woodlice are unable to feed on ash as it has
301 been consumed by earthworms, but can feed on oak and beech. Therefore, the leaf

302 litter resource is partitioned according to leaf palatability. This could also be the
 303 result of past competition, through which selection pressure meant that the two
 304 groups partitioned the available litter resource seasonally. A combination of
 305 seasonal and litter succession would also explain patterns of seasonal abundance.
 306

307 Sampling and extraction methods may have biased our results. Winkler bags are an
 308 effective method for sampling macrofauna from leaf litter, but there are large
 309 differences in the extraction efficiency for different taxa; Krell et al. (2005) showed
 310 that even after seven weeks of litter drying in Winkler bags, woodlice were still
 311 recovered. The moisture content of the litter also affects how rapidly invertebrates
 312 are extracted by Winkler bags, with wet litter having increased extraction times
 313 compared with dry litter (NHM Soil Biodiversity Group, unpublished data). It is likely
 314 that extractions from dry litter would yield greater numbers of woodlice than wet
 315 litter over a three day period. One would expect then that woodlice abundances
 316 would be greater in August and September when the litter is driest (see Eggleton et
 317 al., 2009 for a discussion of patterns in moisture content). However, woodlice
 318 abundance peaks in June and July when the litter is still relatively wet and therefore
 319 the litter moisture content bias cannot be an adequate full explanation for these
 320 results.

321

322 Increasingly warm and dry summers as a result of climate change (Murphy et al.,
 323 2009) could see reductions in earthworm numbers due to adults and/or cocoons not

324 surviving the dry summer period (Holmstrup and Westh, 1995). This in turn could
 325 lead to a reduction in decomposition during the winter months due to lower
 326 earthworm densities. Some ecological compensation may occur with higher summer
 327 and winter woodlice abundances, with a corresponding increase in litter shredding.
 328 Woodlice incorporate litter into the soil (Hassall et al., 1987) but not to the same
 329 extent as earthworms, so litter incorporation may decrease. This in turn could lead
 330 to changes in soil structure accompanied by associated changes in soil fertility and
 331 pH (Riley et al., 2008). Dry soils particularly affect endogeic earthworms (Auserwald
 332 et al., 1996) and reductions in these species could affect soil structure and function.
 333 Reduced burrowing activity could lead to reduced porosity, aeration and drainage,
 334 fewer soil aggregates and less mixing of organic and mineral components of the soil
 335 (Lavelle, 1988).

336
 337 This study illustrates the value of long term ecological data sets for uncovering
 338 ecologically meaningful seasonal patterns. We have found evidence for functional
 339 complementarity in two key decomposer groups that have seasonal peak
 340 abundances at different times of the year. This complementarity seems to be due to
 341 opposite responses to two major drivers: soil moisture and day length. This effect is
 342 likely to be widespread in lowland woodland in the UK and Europe, with only
 343 extreme temperatures (i.e. freezing soils or prolonged drought) and low pH limiting
 344 the distribution.

345

346 Functional complementarity has been documented widely in various different
347 systems (e.g. Caradus et al., 1996; Stachowicz and Byrnes, 2004). Systems with high
348 species diversity and functional complementarity are more resilient in the face of
349 stress (e.g. invasion, changes in moisture and temperature) (Power, 2001). Function
350 in ecosystems can be maintained by the complementary effects of functionally
351 analogous species. It is increasingly important therefore that we understand the
352 complementary effects of species in the face of environmental change, to
353 understand which systems have in built resilience and which do not, and to focus
354 efforts on restoring resilience to those system that have the greatest need.

355

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