

1 **Are earthworms really in decline? Representative data and rigorous models are needed to assess**
2 **large-scale, long-term trends in earthworm populations**

3

4 Keith, A.M.^{1,*}, Ashwood, F.², Boyd, R.³, Butt, K.R.⁴, Mason, K.¹, Seaton, F.M.¹, Schmidt, O.⁵

5 ¹ UK Centre for Ecology & Hydrology, Library Avenue, Bailrigg, Lancaster, LA1 4AP

6 ² School of Forestry, College of Engineering, University of Canterbury, Private Bag 4800, Christchurch
7 8140, New Zealand

8 ³ UK Centre for Ecology & Hydrology, Benson Lane, Maclean Building, Crowmarsh Gifford,
9 Wallingford, OX10 8BB

10 ⁴ Ecological Engineering, University of Lancashire, Preston, UK, PR1 2HE

11 ⁵ UCD School of Agriculture and Food Science, University College Dublin, Belfield, Dublin 4, Ireland.

12

13 *Corresponding author: A. M. Keith (ake@ceh.ac.uk)

14

15 **Abstract**

16 Declines in aboveground invertebrates have been reported widely but similar assessments
17 belowground are rare. A recent quantitative study aimed to address this gap, presenting findings
18 which suggested alarming long-term declines in earthworm abundance in the UK. Estimating
19 temporal trends in abundance from diverse sources of data presents many challenges and there is a
20 need for rigour toward inference. However, a comprehensive review of the published dataset
21 revealed numerous issues including extensive errors, omissions and various problematic aspects of
22 the data and modelling. For the present study, we have revised the published dataset, with data
23 from 70 of 91 original sources being corrected and/or amended, and augmented with data from
24 additional sources. Reanalysing the revised and augmented datasets and assessing the risk of bias
25 for estimating temporal trends, we demonstrate that the original conclusions are not robust and
26 that the large-scale declines suggested are not supported by the corrected data. The importance of
27 earthworms for soil functional processes and as a food source for animals is well established and
28 therefore significant declines would have critical ecological implications. It is conceivable that
29 earthworm populations in the UK may have declined to some extent in particular environmental
30 contexts, however sound conclusions on temporal trends must be based on correct and
31 representative data and rigorous analyses. We highlight factual errors, omissions and
32 methodological flaws in the original study and appeal to improve data collation, enhance meta-data
33 and encourage long-term monitoring to develop a sound understanding of trends in earthworm
34 populations and typical variability observed under different environmental contexts.

35

36 **1. Introduction**

37 Declines in populations and diversity have been reported widely for aboveground invertebrates [1-
38 4], but similar assessments for belowground invertebrates are rare. Earthworms dominate the
39 biomass of belowground invertebrates in temperate systems and the importance of earthworms for
40 functional processes in many soils has long been recognised (e.g., 5-6). There have been significant
41 international efforts to gather data on earthworms and associated environmental conditions toward
42 understanding the main drivers of community metrics and predictive mapping of these; in particular,
43 a European-scale earthworm mapping by Rutgers et al. [7] and global assessments by Johnston [8]
44 and Phillips et al. [9]. However, few long-term earthworm datasets with appropriate spatial and
45 temporal resolution exist that allow a robust assessment of long-term trends in species' populations
46 and overall abundance.

47 Combining different datasets is one approach that attempts to overcome the data limitation. A
48 recent study by Barnes et al. [10] collated selected historic data on earthworm abundance in the UK
49 from various published sources with sampling between 1928 and 2018, derived standardised
50 abundance values, and modelled these using Generalized Linear Mixed Models (GLMMs) to assess
51 temporal changes, in different habitats and accounting for other factors (e.g., sampling method,
52 depth of sampling). These authors reported the notable finding that earthworm abundance in the
53 UK may have undergone long-term decline by 1.6-2.1% per year (equivalent to a 33-41% decline
54 over 25 years) and that these were greatest in broadleaved woodlands (5.7% decline per annum and
55 77% over 25 years). If they were an accurate reflection of the situation, these are alarming statistics.
56 However, such approaches bringing together diverse datasets are not without their limitations and
57 problems for inference [11-12] and, therefore, rigour in data and model scrutiny is essential.

58 One key issue is that if the error changes over time then the estimated trend may be wrong. Another
59 significant issue in making descriptive inference from data collated from published studies and other
60 datasets is that they represent a non-probability sample which can lead to biased estimates [12].

61 This issue may be exacerbated when such data come from a small pool of sources with disparate
62 geographies, without sufficient representation of different driving variables. There is also a risk of
63 bias for temporal trends with potential for confounding space and time [11,13]. Furthermore, there
64 is a range of other risks collating data for meta-study analyses such as errors in data transcription,
65 overlapping or duplicated data, inadequate resolution of geographic location and inconsistency in
66 taxonomic resolution. Gaume and Desquilbet [14] highlighted these issues and others in a
67 comprehensive review of studies included in a database of invertebrate abundance and biomass,
68 used to analyse temporal trends.

69 The ambition to understand whether there are long-term temporal trends in earthworm populations
70 is welcome, and the effort to collate such data is a significant undertaking. However, evaluating the
71 dataset [15] and approach used to model earthworm abundance [10], we uncovered various
72 problems that undermine their conclusions. In the current study, we have revised the earthworm
73 dataset from [15] and reanalysed using the same modelling approach, then repeated this with an
74 augmented dataset including additional data from recent studies. We compare the outputs of the
75 original and new analyses and assess representativeness and context of data sources in the original
76 dataset. Furthermore, we discuss issues and considerations in collating such data, model
77 requirements to account for other processes and dependencies, and the remaining need for more
78 appropriate analyses with refined data.

79

80 **2. Methods**

81 ***2.1 Evaluation and revision of earthworm dataset***

82 The original dataset [15] contains data on earthworm and tipulid larvae abundance, standardised to
83 1 m², including 2210 rows with standardised earthworm abundance (59 rows have no value for
84 either earthworm or tipulid abundance). Accompanying data include start year, end year, broad
85 habitat (e.g., Farmland), fine habitat (e.g., Arable), location (typically a 10 km grid reference code),

86 broad method (e.g., Surface), fine method (e.g., Formalin), number of samples, area of a sample,
87 sample size (i.e., a product of the number of samples and area of a sample), sample diameter,
88 sample depth and season of sampling. We checked all these data against the cited, published data
89 sources, and associated literature, and produced a dataset containing original and revised data [16].
90 To add traceability, columns were also added in this for a row identifier (UniqueID), text description
91 of habitat (Habitat_described), location of data in source used to derive standardised earthworm
92 abundance (Data_location), and whether the data was derived via a biomass conversion equation
93 (Biomass_conversion). The revised dataset contains 1820 rows with standardised earthworm
94 abundance and associated data, including 51 new rows (Unique ID 2775-2825; [16]) with data that
95 had not been included but were found in studies from the original dataset. For various reasons (e.g.,
96 duplication of data across sources, inclusion of non-independent data, data only representing one or
97 several species), 547 rows from the original dataset were omitted. In our results section (3.1 and
98 3.2), we summarise the main issues that were found with the dataset used in Barnes et al. [10]. All
99 revisions, omissions and considerations are also documented by data source in Keith et al. [16].

100

101 ***2.2 Dataset augmentation, reanalyses and risk of bias assessment***

102 The literature search described in Barnes et al. [10], while acknowledged as not attempting to be a
103 full systematic review, appears to have evolved over time and the initial choice of journals for
104 manual searching was subjective. Aside from theses, using refined search strings with recognised
105 databases such as Web of Science should identify potential sources in the literature, including soil
106 ecology, agricultural and other ecological journals likely to contain earthworm data (e.g. [17]). Data
107 from several additional sources were added to the revised dataset, including data from known
108 recently published papers and datasets with coverage of farmland, grassland and woodland habitats
109 (see Table S3 in [16]); these resulted in an additional 236 rows (Unique ID 2826-3061; [16]).

110 Revised and revised+augmented (hereafter called augmented) earthworm datasets were reanalysed
111 using the same GLMM approach as Barnes et al. [10] for Model 1, 3 and 4. Briefly, Model 1 includes
112 Year as a continuous variable, Broad Habitat, Broad method, Season and Depth; Model 3 includes
113 the same as Model 1 with the addition of an interactive term between Year and Broad Habitat;
114 Model 4 includes the same as Model 3 with Fine Habitat replacing Broad Habitat. The original
115 dataset was analysed to ensure reported outputs could be replicated. These analyses were
116 conducted using the R package “glmmTMB” [18]. Point estimates, standard error and confidence
117 intervals were produced with the *emtrends* function in the R package “emmeans” [19]. All statistical
118 analyses were done in R (version 4.4.0; [20]).

119 We acknowledge that p-values and significance are not useful concepts in the presence of bias, since
120 point estimates are wrong. A qualitative assessment of the data was undertaken to establish risk of
121 bias in the modelled outputs. A key question is whether “the same portion of the focal domain has
122 been sampled over time”; if the answer is “no”, then variation in abundance over time could be
123 confounded by variation in space [11]. We mapped earthworm data by Location (i.e., 10 km grid
124 reference where available) across time periods to evaluate the extent to which shifts in time were
125 confounded by shifts in space.

126 Assessed trends over time are likely to be biased if there are changes in the types of locations that
127 are sampled, with particularly high risk of bias if the locations that are sampled over time vary
128 considerably in the characteristics that will also affect earthworm abundance. Key drivers of
129 earthworm abundance include precipitation, soil chemistry, land cover and management practices
130 (e.g., 9, 21-22). Modelling change over time should account for key drivers to reduce bias;
131 unfortunately, few of the original data sources provide suitable data for this. Instead, we can assess
132 the risk of bias through examining the shifts in the spatial spread of the data over time as a proxy, in
133 addition to the relative changes in broad and fine habitat classifications. We can also consider the

134 potential role of specific studies in determining the overall trends, and whether those studies can be
135 seen as representative of the wider environment.

136

137 **3. Results**

138 **3.1 Data compilation errors**

139 *General errors and misclassification:* There are blank cells for standardised earthworm abundance in
140 59 rows across 7 sources, and cell calculation errors for 89 rows across 5 sources (with the original
141 dataset including formulas which return '#REF!' for sample size and/or area). The number of
142 replicates was incorrect for over 350 rows, while sample area was incorrect for over 250 rows. There
143 are various instances of habitat, season and method being misclassified when compared to
144 information in the original sources (see documented revisions in Keith et al. [16] for specific
145 examples).

146 *Miscalculation of standardised abundance:* Amongst sporadic errors there are several instances
147 where standardised abundance values are markedly different from that in the source, due to
148 miscalculations. These include: the data from study 108 are one-tenth of the correct values, i.e., a
149 calculation error of one magnitude (126 rows, Unique ID 2584-2709; [16]). In study 81, values did
150 not equate to those presented in the source and were also much lower (8 rows, Unique ID 2063-
151 2070; [16]). Data from study 109 are the median values per 20 cm × 20 cm soil pit rather than per 1
152 m², thus represent one twenty-fifth of the correct value (10 rows, Unique ID 2710-2719; [16]). On
153 the other hand, in study 20, the data represents twice the standardised abundance because, as
154 stated in the source, "density estimates from formalin sampling have been multiplied by two" (8
155 rows, Unique ID 429-436; [16]) and, in study 93, the standardised abundance values were inflated
156 because they were upscaled despite standardisation in the source (14 rows, Unique ID 2296-2309;
157 [16]). In study 51, the data were not standardised given the earthworm density and size of the
158 sampling unit reported (2 rows, Unique ID 1106-1107; [16]).

159 *Duplication of data:* There are two types of duplication in the dataset. First, there are several
160 instances where the same data has been derived from different published sources, predominantly
161 from a thesis and subsequent published paper (e.g., study 15 and 67; study 20 and 34) or from
162 different parts of the same source (for example, in thesis chapter and appendix in study 89). Second,
163 the dataset contains duplication through different aggregations of the same data; there are cases
164 where values are included for both individual timepoints/plots and values aggregated across
165 timepoints/plots (e.g., study 70; Unique ID 1455-1643; [16]), and cases where values included are
166 aggregated over space and aggregated over time (e.g., study 15; Unique ID 347-355; [16]).

167 *Exclusion of zero values:* Zero values are not included from several studies (e.g., study 13, 38, 42, 54,
168 75 and 88). In study 75, there are blank cells in 103 rows where earthworms were not recorded in a
169 sample, and abundance should therefore be zero.

170 *Data from selected species:* Standardised abundance data from single species or groups of species
171 are included. In study 38, some abundance data represent only *Aporrectodea caliginosa* and only
172 *Lumbricus rubellus* (4 rows, Unique ID 735-738; [16]). In study 49, the biomass data used to estimate
173 standardised abundance represents *Lumbricus* spp. In study 63, some abundance data represent
174 only *A. caliginosa* and only *Lumbricus terrestris* (8 rows, Unique ID 1283-1290; [16]). In study 66,
175 some abundance represents only *Aporrectodea rosea* (12 rows, Unique ID 1326-1337; [16]). In study
176 70, it appears that some abundance data are for *A. caliginosa* and *Allolobophora chlorotica* only (18
177 rows, Unique ID 1531-1546; [16]).

178

179 **3.2 Uncertainties and suitability of data**

180 *Conversion equations for predicting earthworm abundance:* Some earthworm abundance data (217
181 rows across 10 sources; [16]) are derived using predictive linear models (Equations 1 and 2 in [10],
182 with the graphs of the data and linear models presented in Figures S2 and S3 of the Supplementary
183 file). Equation 2, which predicts total earthworm abundance from wet biomass, is neither

184 statistically nor ecologically sound because it has an intercept at 85 earthworms m⁻². Very low (or
185 zero) biomass still results in at least 85 earthworms m⁻² so standardised abundance will be inflated.
186 The extreme of this is highlighted by several datapoints at or close to zero (e.g., study 42 and 103)
187 but included in the dataset at or close to 85 earthworms m⁻², following the biomass predictive
188 equation. While the r-squared value for Equation 2 is reasonable, there is considerable spread
189 around the linear model; this may be partly due to compositional differences in earthworm
190 communities and the fact that taxa differ substantially in their average biomass (e.g., *L. terrestris* will
191 tend to have a much greater biomass than *A. caliginosa*). Equation 1, which predicts total
192 earthworm abundance from abundance of adult earthworms, can suffer from similar inflation,
193 though it is possible for juveniles to be present in the absence of adults, so it may be appropriate in
194 particular instances. Furthermore, the published dataset does not indicate which data are derived
195 via these equations, and therefore the extent of this issue cannot be assessed, as published. Study
196 49 uses this biomass-to-abundance conversion for a total of 71 datapoints for broadleaved
197 woodlands (Unique ID 1020-1090; [16]). The biomass conversion equation is based on total
198 earthworm abundance but this source reports data from *Lumbricus* only and since this taxon has a
199 much larger average individual biomass, estimates of abundance will be inflated.

200 *Unsuitable methods to quantify earthworm abundance:* Several methods included are not
201 appropriate for estimating earthworm abundance. First, the use of counting earthworm cast density
202 ('Casts' as Fine Method; 44 rows in total) is not reliable, and this is not mentioned in Barnes et al.
203 [10]. Second, the use of Tullgren extraction is not an appropriate method for earthworm sampling,
204 as it is biased towards extraction of smaller organisms. For example, study 96 (Unique ID 2316-2351;
205 [16]) reports associated biomass values at less than 0.02 g dry weight per core which are likely
206 ascribed to only very small juvenile earthworms and enchytraeid worms (family Enchytraeidae).

207 *Uncertainty of higher-level taxonomic resolution:* Some studies that merely reported "Oligochaeta"
208 or "Haplotaxida" where standardised abundance was very high probably reported enchytraeid
209 worms. Again, study 96 (Unique ID 2316-2351; [16]), which used Tullgren extraction, reports

210 associated biomass values at less than 0.02 g dry weight per core which are likely ascribed to only
211 very small juvenile earthworms and enchytraeids. Study 87 (Unique ID 2222-2227; [16]) reported
212 some exceptionally high abundances of Oligochaetes in winter samples but it is not stated whether
213 these include both earthworms and enchytraeids – given the organic soil and high moisture in the
214 wetland reedbed habitats of this study, it seems very likely that these values include enchytraeids.

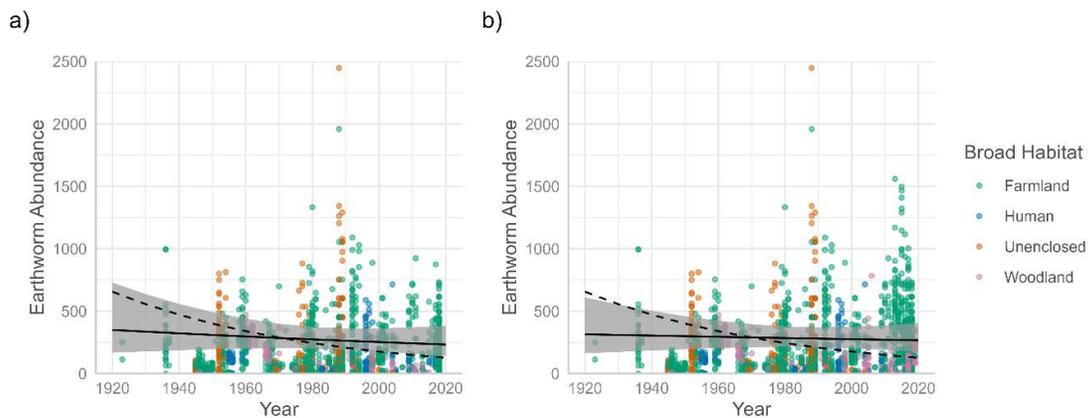
215 *Sampling in unrepresentative or extreme conditions:* Data are included from sampling under extreme
216 or experimental conditions or from specific microhabitats that may not be representative of habitat
217 conditions. Examples include: sampling timepoint after prolonged drought (Study 64); soils which
218 have been sterilised and placed back in plots (Study 85); heavily trampled (Study 50) or experimental
219 compaction treatment (Study 81); flooding by seawater following sea wall breaches (Study 55);
220 sampling in and under cow pats (Study 31 and 75; [16]).

221 *Issues with habitat classifications:* The suitability of habitat classifications is not straightforward or
222 clearly linked to sample-level habitat attributes for some data. In study 1 (Unique ID 1-21; [16]) the
223 habitat is classified as Woodland-Scrub but the text description of the habitat in the source notes it
224 as an “*area of scrub-grassland...dense vegetative cover dominated by grasses...bramble...and willow-*
225 *herbs...interspersed with young oak trees...and thickets of hawthorn...blackthorn...and dogwood..*”
226 and we note the composition of the earthworm community is typical of grassland. This raises serious
227 doubts for definitively including these data as woodland and such nuance has critical implications
228 when few studies represent a time period for a habitat class. In study 90, the habitat is classified as
229 woodland (Unique ID 2272-2277; [16]) but the text describes these as an ‘Arable Orchard’ and a
230 ‘Grass Orchard’. The spacing and management of orchards suggests a woodland classification is not
231 clear and the UKHab classification [23] places ‘intensive orchards’ under Arable and horticulture.
232 Indeed, we note that the earthworm abundances of the arable orchard and grass orchard in this
233 study are typical of arable and pasture systems, respectively. There are also instances where the
234 historical context of a site and other factors are not considered. For example, in study 68
235 earthworms were sampled in a young Eucalyptus plantation on a reclaimed mining site with a sandy

236 loam texture, as well as the reference (former) land use being incorrectly classified as broadleaved
 237 woodland (Unique ID 1386-1387; [16]); such conditions, atypical of woodland, may be better
 238 classified as industrial. Furthermore, uplands/moorland have areas of limestone and rough
 239 grassland, and historically farmed land, which support larger earthworm populations and more
 240 species than the matrix of truly organic soils [24] suggesting a need for more granular classification.
 241

242 **3.3 Reanalyses of revised and augmented dataset**

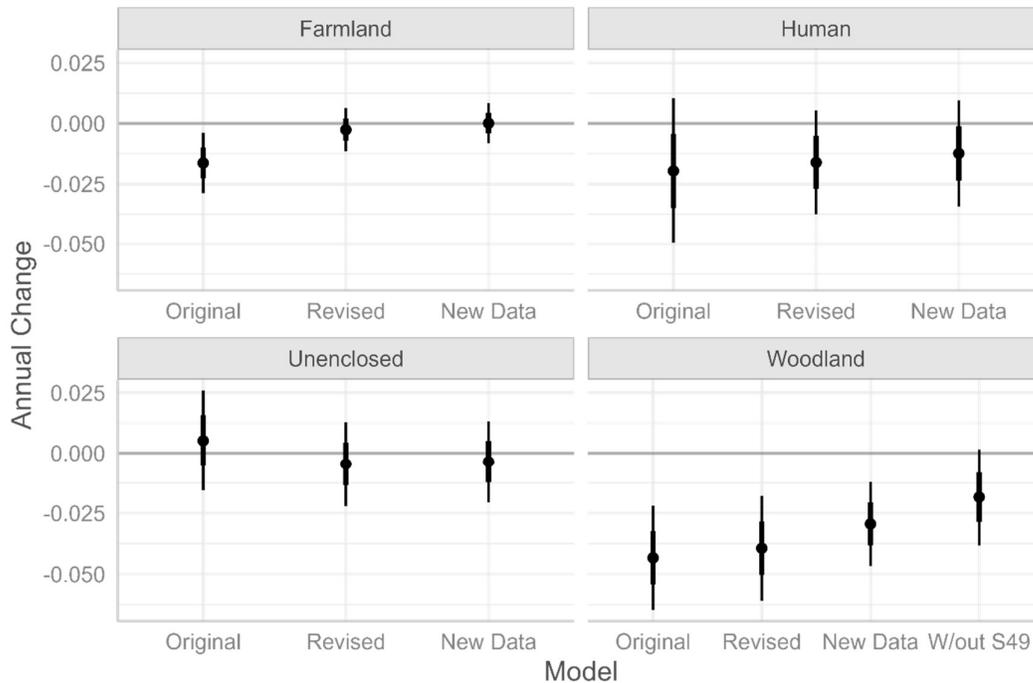
243 For the model of change over time across all habitat types (Model 1), compared to using the original
 244 dataset [15] where the effect of Year indicated a significant 1.6% decline per year (-0.016, $p = 0.006$),
 245 the effect of Year reduced toward zero and was non-significant using both the revised (-0.003, $p =$
 246 0.582) and augmented datasets (-0.001, $p = 0.843$) (Figure 1; Table S1). This was the same for
 247 unweighted and weighted models (Table S1).



248
 249 **Fig 1. The overall predicted change in standardised earthworm abundance per m² based on the**
 250 **revised dataset (a) and the revised plus augmented dataset (b).** Unweighted models only, mean
 251 estimate (black line) and 95% confidence interval (grey shading), with mean estimate from original
 252 dataset for comparison (dashed line).

253 For the unweighted model evaluating trends for specific Broad Habitats (Model 3), revising and
 254 augmenting the datasets reduced the estimated annual change (Figure 2). The Year \times Farmland

255 effect reduced toward zero and was non-significant using both the revised (-0.002 , $p = 0.581$) and
256 augmented datasets (-0.001 , $p = 0.911$) (Figure 2; Table S2). The Year \times Human effect remained
257 insignificant for revised (-0.013 , $p = 0.209$) and augmented datasets (-0.012 , $p = 0.269$) (Figure 2;
258 Table S2). The Year \times Unenclosed effect, significantly positive with the original dataset, became
259 slightly negative but non-significant using the revised (-0.002 , $p = 0.824$) and augmented datasets ($-$
260 0.004 , $p = 0.661$) (Figure 2; Table S2). The Year \times Woodland effect remained significant though was
261 less negative using the revised (-0.036 , $p = 0.011$) and augmented datasets (-0.029 , $p = 0.001$) than
262 the original dataset (Figure 2; Table S2). Data from study 49 (Lakhani & Satchell, 1970) represents
263 47% of broadleaved woodland data and issues with the data (see 3.2) and its representativeness
264 (see 3.4) have been identified. Therefore, we tested the sensitivity of this model by removing this
265 highly influential data set (study 49). Repeating Model 3 using the augmented dataset with study 49
266 removed, reduces the Year \times Woodland effect (-0.019 , $p = 0.06$) with the 95% confidence interval
267 including zero, i.e., no change over time (Figure 2). Weighted models gave no significant Year \times
268 Broad Habitat effects using either revised or augmented datasets (Table S2).
269



270

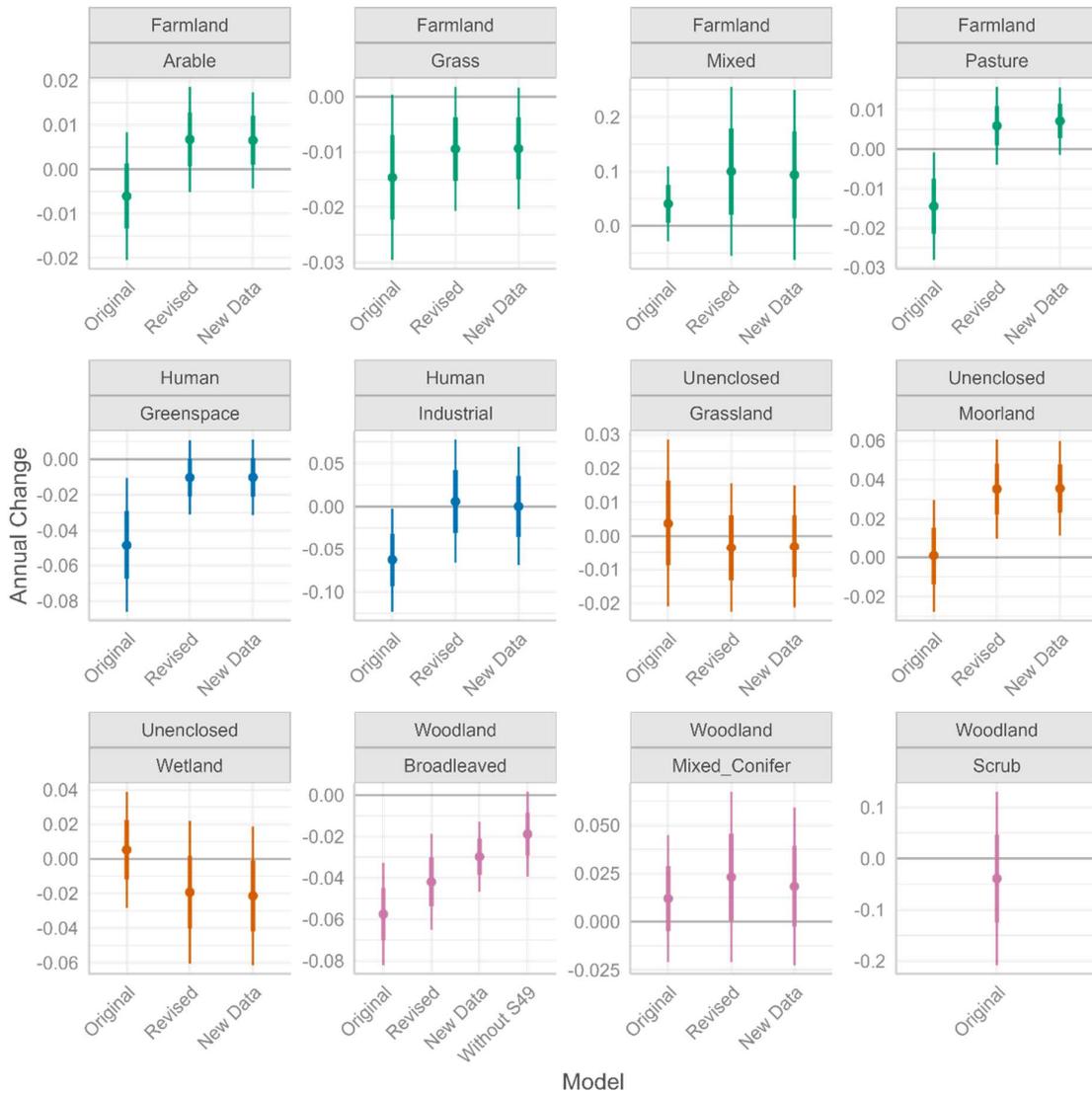
271 **Fig 2. The predicted annual change for each broad habitat category for the original, revised and**
 272 **augmented ('New Data') datasets, for unweighted models.** Model estimates are shown as the
 273 predicted mean (dot), the standard error (thick line) and the 95% confidence interval (thin line). The
 274 woodland broad habitat category also shows the effect of removing the influential study 49 (Lakhani
 275 and Satchell 1970, see Section 3.3 and 3.4).

276 For Model 4, unweighted models using both revised and augmented datasets altered the annual
 277 change trends for specific Fine Habitats (Figure 3). The Year × Arable effect remained insignificant
 278 using both the revised (0.007, $p = 0.253$) and augmented datasets (0.007, $p = 0.226$), though with
 279 marginal increases compared to marginal declines using the original model (Figure 3, Table S3).
 280 Similar was found for the annual change in pasture, with the Year x Pasture effect insignificant and
 281 closer to zero for revised (-0.001, $p = 0.872$) and augmented datasets (0.001, $p = 0.892$)(Figure 3,
 282 Table S3). Annual change in Grass and Mixed fine habitats remained slightly negative and slightly
 283 positive, respectively, with both revised and augmented datasets (Figure 3). Both Human
 284 habitats, with evidence of significant declines using the original dataset, had insignificant

285 interactions with Year and tended toward zero using both revised and augmented datasets (Figure 3,
286 Table S3). The Year × Moorland effect, compared to no change using the original dataset, showed a
287 significant increase with revised (0.028, $p = 0.038$) and augmented datasets (0.029, $p = 0.027$), and
288 with the overall annual change being greater (Figure 3, Table S3). For Mixed/Conifer Woodland,
289 trends were similar using original, revised or augmented datasets (Figure 3, Table S3). The Year ×
290 Broadleaved Woodland effect remained significant though was less negative using the revised (-
291 0.049, $p < 0.001$) and augmented datasets (-0.036, $p < 0.001$) than the original dataset (Figure 2;
292 Table S3). Again, as for the Broad Habitat analyses, repeating Model 3 using the augmented dataset
293 with study 49 removed, reduces the Year × Woodland effect (-0.025, $p = 0.022$) with the 95%
294 confidence interval of annual change including zero (Figure 3). Weighted models presented mostly
295 similar differences between fine habitat trends using original, revised and augmented datasets, with
296 the exception of the Year × Wetland effects which indicated large significant declines using revised
297 and augmented datasets (Table S3).

298

299



300

301 **Fig 3. The predicted annual change for each fine habitat category for the original, revised and**
 302 **augmented datasets, for unweighted models. Model estimates are shown as the predicted mean**
 303 **(dot), the standard error (thick line) and the 95% confidence interval (thin line). The broadleaved**
 304 **woodland habitat category also shows the effect of removing the influential study 49 [25]. Following**
 305 **reclassification of habitat types there were insufficient scrub woodland observations to run the new**
 306 **models, so no results are shown.**

307

308 As with the original dataset, there was consistently lower earthworm abundance under summer
309 sampling and chemical extractant sampling methods across all models using the revised and
310 augmented datasets, for both unweighted and weighted models (Table S1-3).

311

312 **3.4 Risk of bias and representativeness**

313 Shifts in the types of locations that are included within the models can be seen both across and
314 within habitats (Figure 4). There were no unenclosed habitats from the 21st century included within
315 the original Barnes et al. model. Within the farmland categories, the most numerous and therefore
316 the most influential on the overall model fit, there is a shift from being largely dominated by
317 sampling within Scotland pre-1960 to being dominated by sampling within the Midlands and Eastern
318 England later in the time series. The extreme in the original dataset is represented by the Scrub fine
319 habitat data coming from two studies separated by 14 years (1976-78, 1992), with one in South-East
320 England (Cambridgeshire, Unique ID 1-21 [16]) and one in North-East Scotland (Aberdeenshire,
321 Unique ID 678 & 683 [16]). Consequently, the importance of different driving factors that influence
322 earthworm abundance may change based on these confounded spatial and temporal differences

323 The sparsity within the early time series means that the modelled trends are vulnerable to being
324 strongly influenced by earlier studies. Similarly, where there are few data sources, the influence of
325 individual studies (and their environmental context) may be disproportional (Figure 5). This is
326 particularly evident within the broadleaved woodland habitats, which had 152 datapoints from 13
327 sources in the original analyses (126 datapoints across 13 sources in revised analyses). Almost half of
328 these datapoints (71 out of 152) came from one source - Lakhani and Satchell [25] who surveyed
329 three broadleaved woodlands in the early 1960s and, from weekly sampling, recorded biomass, with
330 Barnes et al. [10] deriving many estimates of relatively high earthworm abundances. However, this
331 study specifically focused upon limestone woodlands, a relatively rare broadleaved woodland type
332 within the UK. Limestone woodlands are expected to have higher earthworm abundances due to

333 their optimal soil pH and high-quality litter inputs. In contrast, study 68 (Unique ID 1383-1394 [16])
334 sampled woodland sites with low pH soils (3.9 at Gisburn, 4.1 at Rogate) in which lower earthworm
335 abundances would be expected. Therefore, the estimates of change within broadleaved woodland
336 are confounded by the presence of changes in habitat suitability (i.e., soil pH) across the time series.
337 As noted in section 3.2, there are also concerns about the appropriateness of the estimation of
338 earthworm abundance from the data in Lakhani and Satchell [25]. Removing Lakhani and Satchell's
339 study (Study 49) from the model presents 95% confidence intervals including zero for earthworm
340 abundance trends in the woodland broad habitat or broadleaved woodland fine habitat types
341 (section 3.3; Figures 2 and 3, respectively).

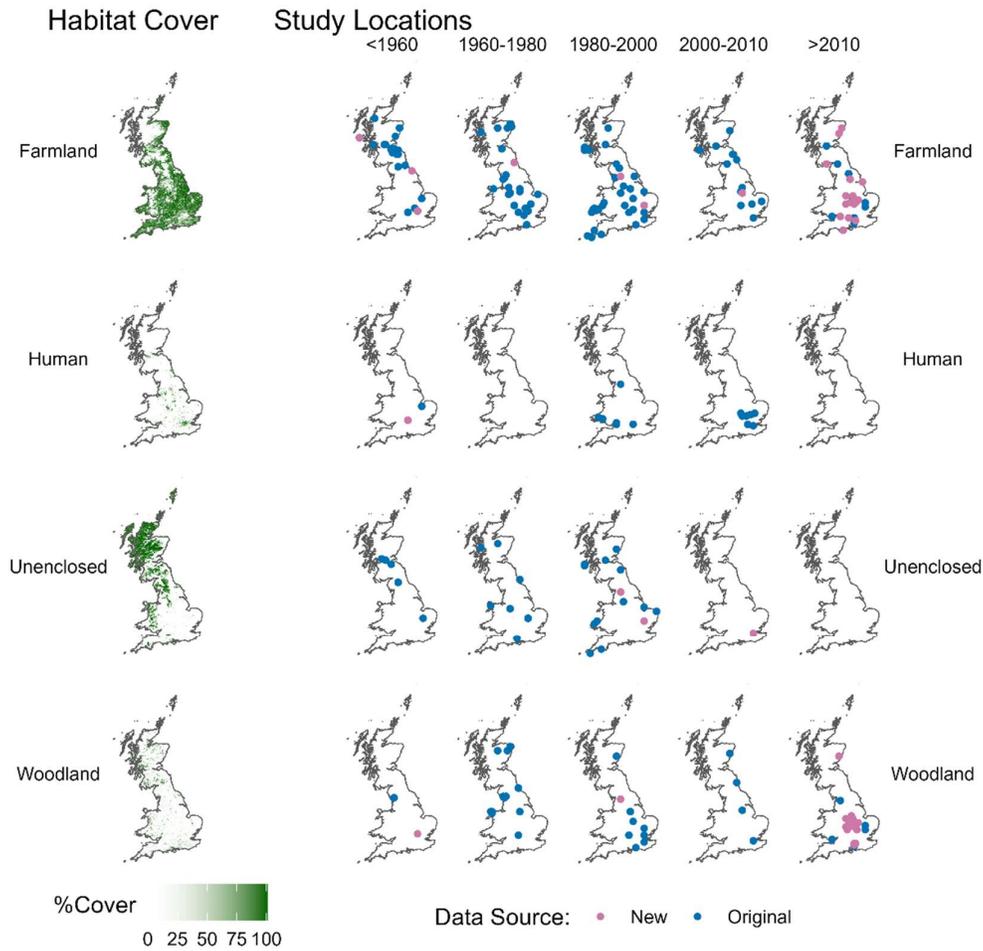
342 Similarly, diverse conditions may be found in other habitat classes with limited data. The Farmland-
343 Grass habitat classification (162 datapoints from 19 sources in the original analyses; 123 datapoints
344 across 19 sources in revised analyses) includes leys, margins, meadows, and set-aside; earthworm
345 abundance in leys and set-aside will depend on time since disturbance, with recently ploughed leys
346 having fewer earthworms.

347 Including habitat type as a predictor in the model may account for some of the changes in relative
348 frequency of habitat types; however, it will not be capable of accounting for changes in the site
349 characteristics that influence earthworm abundance on top of the habitat type changes. The clear
350 shifts in spatial locations that occur over this time series indicate that any analysis of this data is at a
351 high risk of bias.

352

353

354



355

356 **Fig 4. The change in study locations over time within the four broad habitats (right), and the spread**

357 **of those habitats across Great Britain (left).** Broad habitat cover data for Great Britain is sourced from

358 the Land Cover Map 1990 [26]. Study locations are shown as the central point of the 10 km square, or

359 in the cases where only the 100 km square is known the central point of the 100 km square. Studies

360 whose locations are coarser than 100 km (i.e., estimates across England or Wales) are not included.

361 Studies that were included in Barnes et al. [10] are shown in blue, additional studies are shown in pink.

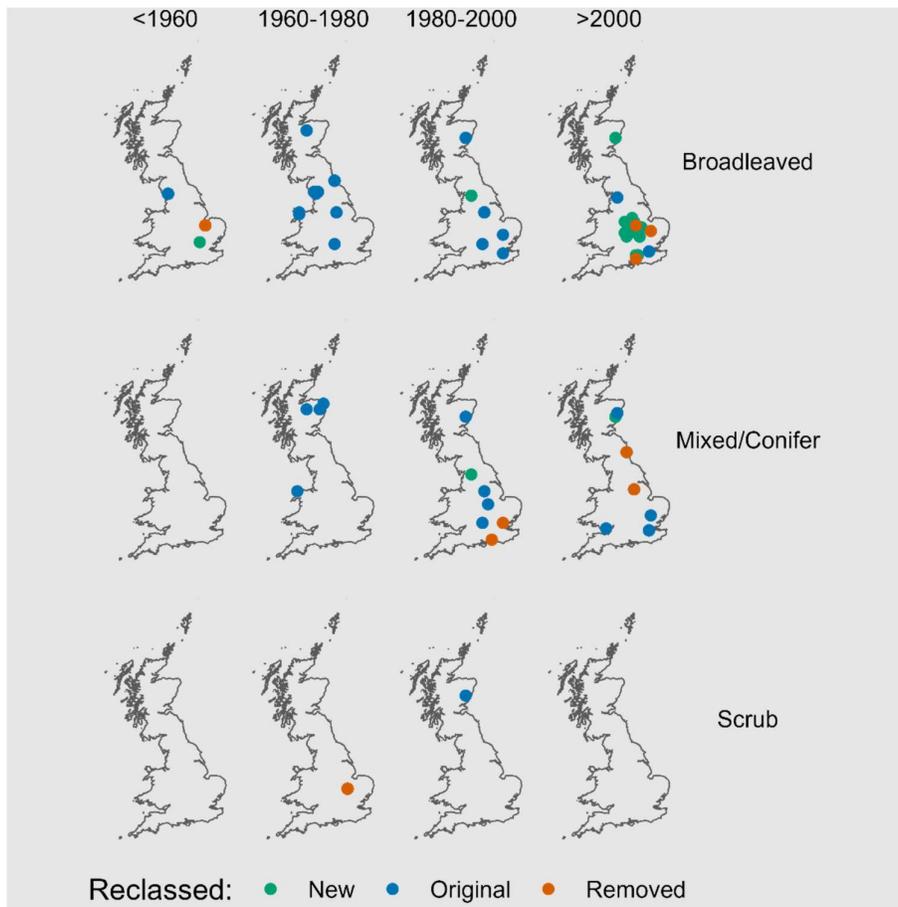
362 Broad habitat for each study is the reclassified version, which differs from the Barnes et al. [10]

363 classification for ten points.

364

365

366



367

368 **Fig 5. The locations of the sites across the woodland fine habitats over time.** Studies are included if
 369 they were originally in Barnes et al. [10] as woodland sites or if they represent sites added from
 370 additional literature (green). Sites that were originally included in Barnes et al. [10] are coloured by
 371 whether they remained the fine habitat designated by Barnes et al (blue) or whether we have
 372 reclassified them as different habitats (orange).

373

374 **4. Discussion**

375 **4.1 Clear challenges in derivation of meta-datasets**

376 The findings of the recent study by Barnes et al. [10] suggest alarming long-term declines in
 377 earthworm abundance in the UK. Subsequently, evidence of declines in earthworm populations was
 378 selected as an emerging issue in the horizon scan of conservation issues [27]. The study's findings
 379 have also attracted wide attention from public media outlets (e.g., 28-30). Given the importance of

380 earthworms for the dynamics of soil structure, hydrology and nutrient cycling, and as a major food
381 source for other animals, significant declines would have critical ecological implications. It is
382 therefore imperative that we have a sound understanding of trends in earthworm populations and
383 typical variability observed under different environmental contexts.

384 Review of the dataset used by Barnes et al. [10] led to data from 70 of 91 sources being corrected
385 and/or amended before reanalysis. Data compilation errors were extensive including basic and
386 general errors and misclassification, miscalculation of standardised earthworm abundance,
387 duplication of data, exclusion of zero values for earthworm abundance, and inclusion of data from
388 selected earthworm species (rather than total earthworm abundance). There were also additional
389 sources of uncertainty and problematic aspects of data suitability, including implausible conversion
390 equations for predicting standardised earthworm abundance from biomass, unsuitable methods to
391 quantify earthworm abundance, use of data at higher levels of taxonomic resolution (i.e.,
392 Haplotaxida, Oligochaeta), data from sampling in unrepresentative or extreme conditions, and issues
393 with habitat classifications. Furthermore, the ability to inspect and validate collated data is helped
394 by meta-data, but in the original dataset [15] there is no information associated with data to
395 determine where exactly in a source the values were extracted (e.g., table or figure numbers) or how
396 values are derived (calculations). This is a clear hurdle to re-use and re-analyses, and partly the
397 reason for the time taken to review and revise the original dataset.

398 Gaume and Desquilbet [14] undertook a similar review of the InsectChange database [31] which had
399 supported a meta-analysis reporting declines in the abundance of terrestrial insects. They found a
400 total of 553 issues, affecting 161 out of 165 datasets, with various types of problem including errors,
401 inconsistencies, methodological issues and information gaps. The review of Gaume and Desquilbet
402 [14] and the revised dataset in the present study demonstrate the practical challenges of initiatives
403 bringing together multiple datasets in a consistent framework. Collating diverse data from a
404 relatively small pool of sources that differ in space and time also comes with significant inferential
405 challenges, as noted in Barnes et al. [10]. Echoing the response of Thomas et al. [32] to the insect

406 decline findings of Sanchez-Bayo & Wyckhuys [2], there is a need for robust data and rigorous
407 analyses. The study by Barnes et al. [10] has highlighted a lack of systematic monitoring of
408 earthworm communities, at least in the UK, but without such data it is questionable to attempt to
409 decipher long-term trends in earthworm populations that may be taking place against the backdrop
410 of land management changes and fluctuating climate.

411

412 **4.2 No robust evidence of decline**

413 Leaving some of the debated modelling issues aside, our reanalysis of the revised and augmented
414 datasets using the same models generally highlights a lack of consistency with the original model
415 outputs. In particular, the estimates of annual change in earthworm abundance are close to zero and
416 non-significant with the revised or augmented datasets for the model of change over time across all
417 habitat types (Model 1). For the models evaluating trends for specific Broad Habitats (Model 3) and
418 Fine Habitats (Model 4), most remain around or tend toward zero with the revised or augmented
419 datasets. We acknowledge that the modelled outputs using revised and additional data here do not
420 provide a definitive conclusion, but they point toward a dynamic stability over time and they suggest
421 that the magnitude of the declines reported by Barnes et al. [10] appear to be grossly
422 overestimated. In an unrelated paper, Müller et al. [33] reanalysed 27 years of insect biomass data
423 from Germany, adding more recent insect biomass data and including sample-level climate data.
424 Insect biomass in the recent samples returned to that reported in the 1980s and they concluded that
425 “temporal variation in weather conditions explained most of the temporal changes in insect
426 biomass”. Accounting for the effects of recent and current climatic conditions may provide a more
427 realistic assessment of long-term trends in earthworm abundance, too.

428 Earthworm activity, apparent abundance, and population dynamics are also known to be influenced
429 by the prevalent weather conditions through their effect on soil conditions, particularly moisture.

430 Earthworms are dependent on soil moisture with seasonal behaviours that avoid (moving to depth)

431 or resist (diapause) drier soil conditions in summer [34]. Several long-term studies of earthworm
432 populations have been published from single sites in the UK that highlight the dynamic impact of
433 climate on earthworm populations. For instance, through monthly sampling of earthworms over 6
434 years (March 2002 to February 2008) at a woodland site in southern England, Eggleton et al. [35]
435 demonstrated both seasonal fluctuations in measured abundances and longer-term trends reflecting
436 the prevalent climate. Butt et al. [36] monitored earthworms over two decades (1998 to 2019) in a
437 grassland in north-west England, presenting evidence of major earthworm declines in dry years such
438 as 2003, but an ability to recover. Recent European-scale modelling indicates that earthworm
439 species distributions may be impacted by changing climate over the next fifty years [37]. Expanded
440 distribution of some earthworm species under climatic changes have also been predicted in the UK
441 [38].

442 There is ample evidence that land use and management impact earthworm abundance, composition
443 and activity (e.g., 21, 39-41). Organic and upland soils, typically with acidic pH, have low earthworm
444 densities and tend to be dominated by fewer species (42-43). In agricultural soils, earthworm
445 communities are greatly influenced by land management practices; disturbance through tillage is a
446 key factor and cultivated systems tend to contain a relatively low abundance of earthworms (50–200
447 individuals m⁻²), depending on time since cultivation and crop type. Grassland or pasture systems
448 generally contain much greater abundances (300–600 individuals m⁻²)[44-46]. The expectation of
449 widespread declines in intensive agricultural soils in the UK (akin to findings on other invertebrates
450 e.g., [47]) does not appear to play out.

451

452 **4.3 Woodlands revisited**

453 Where declines were reported in Barnes et al [10] for particular habitats using existing data and
454 models, it appears unlikely that they are driven by any specific temporal factors but rather by the
455 particularities of the small set of sources from which data are derived. Indeed, Barnes et al. [10] raise

456 the caveat that ‘the accuracy of any habitat-specific trend produced is dependent on the assumption
457 that studies are equally representative of that habitat-type through time’. Focusing on the headline
458 decline in broadleaved woodland earthworms (77% over 25 years), it is clear this assumption is not
459 met. The study of Lakhani & Satchell [25] dominates the Woodland data with ~47% of broadleaved
460 woodland values in the original dataset. However, it is spatially restricted, temporally restricted,
461 temporally autocorrelated, and the estimation of earthworm abundance from the biomass of the
462 *Lumbricus* genus is dubious and problematic. It is also evident, visualising these data (Figure 5), that
463 shifts in space are confounded with shifts in time across the broadleaved woodland data.

464 Forest soils can have widely varying earthworm populations dependent on soil characteristics and
465 litter inputs (48-49), with clear effects of tree type and tree species (e.g., 48- 51), driven by
466 differences in litter quality and subsequent effects on soil characteristics. Additionally, there is
467 further nuance in the context of these studies that determine earthworm abundance, that are not
468 accounted for in coarse habitat classifications. In addition to the modelled variables (year, season,
469 sampling method, depth), differences between woodlands in soil pH, hydrology, previous land use,
470 and stand age all influence the status of earthworm communities.

471 Barnes et al. [10] note that “declines in woodland biodiversity [moths, birds] appear greatest in
472 south-East England and contrast with more positive trends in the north”. However, there are
473 exceptionally few earthworm data from woodlands in SE England so there is no way to support this
474 suggested climate-related mechanism, even though it is expected that geographical patterns of
475 changing climate should impact earthworm populations. Ascribing causal mechanisms to these data
476 is therefore highly speculative, and particularly given that estimation of causal effects requires much
477 stronger assumptions than correlations or descriptive parameters.

478

479

480 **4.4 Further considerations on data and modelling**

481 While data compilation errors and uncertainties have been largely addressed through revising the
482 dataset, there are further aspects of the data and modelling that may have a bearing on findings.
483 First, there is huge variation in the spatial extent of derived abundance values. Standardised
484 earthworm abundance values in the Barnes et al. [15] dataset are based on spatial scales ranging
485 from individual sampling plots to fields/parcels to multiple locations across a region to country-wide
486 (i.e., England). Combining data representing completely different spatial scales, and already
487 aggregations across those spatial scales, presents significant challenges. Values for standardised
488 earthworm abundance (i.e., means for habitat × method × season) represent vastly different sample
489 numbers, with contributing data being influenced by multiple varying environmental factors.
490 Weighting by sample area is not sufficient to address such differences in spatial extent because it
491 assumes that variability is equivalent across scales.

492 Another spatial issue is that the model uses a 10 km grid square reference code as a random term to
493 account for spatial dependence of data within the same 10 km grid square (152 datapoints from 5
494 sources use 'England' as the value for the random term). However, the model doesn't know their
495 relative positions in space, so it doesn't account for proximity of grid squares or wider geographical
496 separation of sampling locations. One example is provided by Study 49 [25], where two sites are
497 approximately 1 km apart but represented by different 10 km grid square reference codes. This
498 raises clear issues around spatial autocorrelation not being accounted for in the analyses. Other fine-
499 scale spatial and temporal data dependencies should also be accounted for. For instance, different
500 depths from the same sampling location should not be treated as independent datapoints, and
501 frequent within-study repeat site measurements (e.g., weekly sampling) should be addressed as
502 temporal autocorrelation.

503 There may also be an issue in assuming a depth of zero for chemical extractant methods. Chemical
504 extraction methods expel earthworms from the soil to the surface and in the dataset these have

505 been assigned a depth of zero. Hand-sorting samples earthworms from a known volume of soil
506 whereas chemical extraction methods sample earthworms from an unknown volume of soil, with
507 effective depth likely dependent on soil type/texture and moisture conditions. These methods also
508 have bias in the recovery of different ecological groups (e.g., 53).

509 Finally, Barnes et al. [10] used the year coefficient from GLMM for earthworm density to estimate
510 how it has changed over time. The model included habitat as a covariate, which raises some
511 questions. It appears that the authors included habitat to guard against the possibility that apparent
512 trends in abundance could in fact be explained by changes in which habitats were sampled over
513 time. This logic is sound, but it also applies to the many other variables that were presumably
514 sampled inconsistently over time (e.g. climate). If these other variables also affect earthworm
515 abundance, then failing to include them in the model will also bias the estimated year effect.
516 Another question concerns what is actually being estimated by the year effect. Including habitat in
517 the model means that the year effect represents the part of the trend not explained by changes in
518 habitat. This is not the total effect of year that the headline result of a 33-41% decline in abundance
519 implies.

520

521 **4.5 Data future**

522 Ristok et al. [54] flag one of the key messages from the first comprehensive soil biodiversity
523 assessment in Germany that “For evaluating the implications of environmental change, an
524 understanding of (long-term) temporal variation in soil biodiversity and ecosystem functions is
525 urgently required”. It is conceivable that earthworm populations in the UK may have declined to
526 some extent in particular environmental contexts arising through time (e.g., soils under intensive
527 agriculture with increasing droughts). However, evidence of large-scale and long-term declines (and
528 particularly conclusions of alarming earthworm declines) must be based on unbiased and consistent
529 data, and analyses that account for differences in driving variables.

530 There are benefits of striving to collate data at consistent and fine spatial scales (e.g., field) and
531 temporal scales (e.g., week or month). This can be lacking for historical studies and datasets where
532 this information may not be recorded and is not retrievable from linked sources. Inclusion of data
533 averaged over seasons or years, and over regions or countries, does not allow relevant temporal and
534 spatial context to be accounted for. Collating data from diverse studies and locations through time
535 presents multiple challenges for determining temporal ecological trends, some of which may be
536 insurmountable. As concluded by Dornelas et al. [55], the “Availability of long-term, large-scale,
537 high-resolution data is the single most important factor limiting progress in understanding temporal
538 patterns in biodiversity”. We would advocate the addition of ‘representative’ to this list.

539 We need systematic data from long-term and relatively frequent earthworm community
540 assessments across a representative network of sites to evidence widespread declines in habitats or
541 geographical specificity in trends for regions under different climates. Hohberg et al. [56] note that
542 “population trends for species remain largely unknown due to the lack of long-term, large-scale
543 monitoring programs”. In the UK, this type of approach was recently initiated in England in 2023 as
544 part of the England Ecosystem Survey and National Forest Inventory Plus projects [57]. In Germany,
545 though already relatively well studied, the National Soil Monitoring Centre is preparing
546 establishment of a long-term monitoring program [56]. There has also been a recent call for
547 international collaboration to enrich and extend earthworm time-series data [58]. We appeal to
548 improve data collation, enhance meta-data and encourage systematic long-term monitoring. Only
549 through robust data collection and rigorous modelling is it likely that we can provide a definitive
550 answer as to whether earthworm populations are in decline.

551

552 **Acknowledgements**

553 We thank Miranda Prendergast-Miller and Mark Hodson for support and advice on additional
554 earthworm datasets.

555 **References**

- 556 [1] Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, et al. More than 75 percent
557 decline over 27 years in total flying insect biomass in protected areas. PLoS ONE. 2017;12:e0185809.
558 doi:10.1371/journal.pone.0185809
- 559 [2] Sánchez-Bayo F, Wyckhuys KAG. Worldwide decline of the entomofauna: A review of its drivers.
560 Biol Conserv. 2019;232:8-27. doi:10.1016/j.biocon.2019.01.020
- 561 [3] Seibold,S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, et al. Arthropod decline in
562 grasslands and forests is associated with landscape-level drivers. Nature. 2019;574:671–674.
563 doi:10.1038/s41586-019-1684-3
- 564 [4] Harvey JA, Tougeron K, Gols R, Heinen R, Abarca M, Abram PK, et al. Scientists’ warning on
565 climate change and insects. Ecol Monogr. 2023;93:e1553. doi:10.1002/ecm.1553
566 doi:10.1038/s41586-019-1684-3
- 567 [5] Blouin M, Hodson ME, Delgado EA, Baker, G, Brussard L, Butt KR, et al. A review of earthworm
568 impact on soil function and ecosystem services. Eur J Soil Sci. 2013;64:161–182.
569 doi:10.1111/ejss.12025
- 570 [6] Liu T, Chen X, Gong X, Lubbers IM, Jiang Y, Feng W, et al. Earthworms coordinate soil biota to
571 improve multiple ecosystem functions. Curr Biol. 2019;29(20):3420–9.e5.
572 doi:10.1016/j.cub.2019.08.045
- 573 [7] Rutgers M, Orgiazzi A, Gardi C, Römcke J, Jänsch S, Keith AM, et al. Mapping earthworm
574 communities in Europe. Appl Soil Ecol. 2016;97:98-111. doi:10.1016/j.apsoil.2015.08.015
- 575 [8] Johnston ASA. Land management modulates the environmental controls on global earthworm
576 communities. Global Ecology & Biogeography. 2019;28:1787-1995. doi:10.1111/geb.12992
- 577 [9] Philips HRP, Guerra CA, Bartz MLC, Briones MJI, Brown G, Crowther TW, et al. Global distribution
578 of earthworm diversity. Science. 2019;366(6464): 480-485. doi:10.1126/science.aax4851

579 [10] Barnes AE, Robinson RA, Pearce-Higgins JW. Collation of a century of soil invertebrate
580 abundance data suggests long-term declines in earthworms but not tipulids. PLoS One.
581 2023;18(4):e0282069. doi:10.1371/journal.pone.0282069

582 [11] Boyd RJ, Powney GD, Burns F, Danet A, Duchenne F, Grainger MJ, et al. ROBITT: a tool for
583 assessing the risk-of-bias in studies of temporal trends in ecology. Methods Ecol Evol. 2022;13:1497–
584 507. doi:10.1111/2041-210X.13857

585 [12] Boyd RJ, Stewart GB, Pescott OL. Descriptive inference using large, unrepresentative
586 nonprobability samples: an introduction for ecologists. Ecology. 2024;105:e4214.
587 doi:10.1002/ecy.4214

588 [13] Saunders ME. No Simple Answers for Insect Conservation: Media hype has missed the biggest
589 concern that ecologists and entomologists have about six-legged life: how little we know about it.
590 Am Sci. 2019;107:148. doi:10.1511/2019.107.3.148

591 [14] Gaume L, Desquilbet M. InsectChange: Comment. Peer Community Journal. 2024;4:e97.
592 doi:10.24072/pcjournal.469

593 [15] Barnes A, Robinson R, Pearce-Higgins J. Supplementary Material Data.xlsx. figshare. Dataset.
594 2022. doi:10.6084/m9.figshare.21428121.v1

595 [16] Keith AM, Ashwood F, Boyd R, Butt KR, Mason K, Seaton, FM, Schmidt O. Data from: Are
596 earthworms really in decline? Representative data and rigorous models are needed to assess large-
597 scale trends in earthworm populations [Data set]. 2025 September 23. Zenodo. Available from:
598 <https://doi.org/10.5281/zenodo.17183953>

599 [17] Mason KE, Ashwood F, Schmidt O, Cosby J, Keith AM. A compendium of earthworm data
600 sources and associated information from the UK and Ireland, 1891-2021 [Data set]. 2022 May 30.
601 NERC Environmental Information Data Centre. Available from: [https://doi.org/10.5285/1a1000a8-](https://doi.org/10.5285/1a1000a8-4e7e-4851-8784-94c7ba3e164f)
602 [4e7e-4851-8784-94c7ba3e164f](https://doi.org/10.5285/1a1000a8-4e7e-4851-8784-94c7ba3e164f)

603 [18] Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. glmmTMB
604 balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R
605 J. 2017;9:378–400. doi:10.32614/RJ-2017-066.

606 [19] Lenth R. Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version
607 1.11.2. <https://CRAN.R-project.org/package=emmeans>

608 [20] R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for
609 Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>

610 [21] Briones MJJ, Schmidt O. Conventional tillage decreases the abundance and biomass of
611 earthworms and alters their community structure in a global meta-analysis. Glob Change Biol.
612 2017;23:4396–419. doi:10.1111/gcb.13744.

613 [22] Lebron I, Feeney CJ, Reinsch S, Shokri N, Afshar MH, Lofts S, et al. Patterns and thresholds for
614 soil pH across Europe in relation to soil health and degradation. Catena. 2025;260:109454.
615 doi:10.1016/j.catena.2025.109454

616 [23] UKHab Ltd. 2023. UK Habitat Classification Version 2.0 (at <https://www.ukhab.org>)

617 [24] Svendsen JA. Studies on the earthworm fauna of Pennine moorland. PhD Thesis. Durham
618 University. 1955. Available from: <https://etheses.dur.ac.uk/9332/>

619 [25] Lakhani K, Satchell J. Production by *Lumbricus terrestris* (L.). J Anim Ecol. 1970; 39(2):473-492.

620 [26] Rowland CS, Marston CG, Morton RD, O'Neil AW. Land Cover Map 1990 (1km percentage
621 aggregate class, GB)[dataset]. 2020 Oct 9 [cited 2026 Mar 13]. In: NERC Environmental Information
622 Data Centre. Available from: <https://doi.org/10.5285/c7195a20-7943-4d5d-9f6e-c9fead472dde>

623 [27] Sutherland WJ, Bennett C, Brotherton PNM, Butchart SHM, Butterworth HM, Clarke SJ, et al. A
624 horizon scan of global biological conservation issues for 2024. Trends Ecol Evol. 2023;39:89-100.
625 doi:10.1016/j.tree.2023.11.001.

626 [28] Carrington D. Earthworms may have declined by a third in UK, study reveals. The Guardian. 2022
627 December 19 [Cited 2026 Mar 13]. Available from:

628 [https://www.theguardian.com/environment/2022/dec/19/earthworms-may-have-declined-by-a-](https://www.theguardian.com/environment/2022/dec/19/earthworms-may-have-declined-by-a-third-in-uk-study-reveals)
629 [third-in-uk-study-reveals](https://www.theguardian.com/environment/2022/dec/19/earthworms-may-have-declined-by-a-third-in-uk-study-reveals)
630 [https://www.theguardian.com/environment/2022/dec/19/earthworms-](https://www.theguardian.com/environment/2022/dec/19/earthworms-may-have-declined-by-a-third-in-uk-study-reveals)
[may-have-declined-by-a-third-in-uk-study-reveals](https://www.theguardian.com/environment/2022/dec/19/earthworms-may-have-declined-by-a-third-in-uk-study-reveals)

631 [29] Weston P. Vital for looking after the soil': fears as UK earthworm population declines. The
632 Guardian. 2024 April 8 [Cited 2026 Mar 13]. Available from:

633 <https://www.theguardian.com/environment/2024/apr/08/uk-earthworm-population-in-decline>

634 [30] Burgess K. Britain's earthworms are dying and we need to act now, say experts. The Times. 2024
635 May 28 [Cited 2024 December 17]. Available from: [https://www.thetimes.com/article/britains-](https://www.thetimes.com/article/britains-earthworms-are-dying-and-we-need-to-act-now-say-experts-hnl2dcmbd)
636 [earthworms-are-dying-and-we-need-to-act-now-say-experts-hnl2dcmbd](https://www.thetimes.com/article/britains-earthworms-are-dying-and-we-need-to-act-now-say-experts-hnl2dcmbd)

637 [31] van Klink R, Bowler DE, Comay O, Driessen MM, Ernest SKM, Gentile A, et al. InsectChange: a
638 global database of temporal changes in insect and arachnid assemblages. *Ecology*. 2021;102:e03354.
639 doi:10.1002/ecy.3354

640 [32] Thomas CD, Jones TH, Hartley SE. "Insectageddon": a call for more robust data and rigorous
641 analyses. *Glob Change Biol*. 2019;25:1891–2. doi:10.1111/gcb.14608.

642 [33] Müller J, Hothorn T, Yuan Y, Sebold S, Mitesser O, Rothacher J. et al. Weather explains the
643 decline and rise of insect biomass over 34 years. *Nature*. 2024;628:349-354. doi:10.1038/s41586-
644 023-06402-z

645 [34] Edwards CA, Arancon NQ. Earthworm Life Histories and Biology. In: Edwards CA, Arancon NQ,
646 editors. *Biology and Ecology of Earthworms*. Springer, New York; 2022. pp. 81-108.

647 [35] Eggleton P, Inward K, Smith J, Jones DT, Sherlock E. A six year study of earthworm (Lumbricidae)
648 populations in pasture woodland in southern England shows their responses to soil temperature and
649 soil moisture. *Soil Biol Biochem*. 2009;41:1857-1865. doi:10.1016/j.soilbio.2009.06.007

- 650 [36] Butt KR, Gilbert JA, Kostecka J, Lowe CN, Quigg SM, Euteneuer P. Two decades of monitoring
651 earthworms in translocated grasslands at Manchester Airport. *Eur J Soil Biol.* 2022;113:103443.
652 doi:10.1016/j.ejsobi.2022.103433
- 653 [37] Zeiss R, Briones MJI, Mathieu J, Lomba A, Dahlke J, Heptner L-F, et al. Effects of climate on the
654 distribution and conservation of commonly observed European earthworms. *Conserv Biol.*
655 2024;38:e14187. doi:10.1111/cobi.14187
- 656 [38] Sherlock E, Coates M, Csuzdi CS. Modelling of climatic tolerances of three earthworm species:
657 *Satchellius mammalis*, *Lumbricus friendi* and *Lumbricus festivus* using Maximum Entropy Modeling.
658 *Opusc Zool (Budapest).* 2022;53:51–65.
- 659 [39] Spurgeon DJ, Keith AM, Schmidt O, Lammertsma DR, Faber JH. Land-use and land-management
660 change: relationship with earthworm and fungi communities and soil structural properties. *BMC*
661 *Ecol.* 2013;13:46. doi:10.1186/1472-6785-13-46
- 662 [40] Hodson, M.E., Corstanje, R., Jones, D.T., Witton, J., Burton, V.J., Sloan, T., Eggleton, P.
663 Earthworm distributions are not driven by measurable soil properties. Do they really indicate soil
664 quality? *PLoS One.* 2021;16:e0241945. doi:10.1371/journal.pone.0241945
- 665 [41] Ashwood F, Brown KD, Sherlock E, Keith AM, Forster J, Butt KR. Earthworm records and habitat
666 associations in the British Isles. *Eur J Soil Biol.* 2024;122:103642. doi:10.1016/j.ejsobi.2024.103642
- 667 [42] Scheu S, Albers D, Alphei J, Buryr R, Klages U, Migge S, et al. The soil fauna community in pure
668 and mixed stands of beech and spruce of different age: trophic structure and structuring forces.
669 *Oikos.* 2003;101(2):225–38. doi: 10.1034/j.1600-0706.2003.12131.x
- 670 [43] Butt KR, Lowe CN. Anthropogenic influences on earthworm distribution, Rum National Nature
671 Reserve, Scotland. *Eur J Soil Biol.* 2004;40:63–72. doi:10.1016/j.ejsobi.2004.04.001

- 672 [44] Rutgers M, Schouten AJ, Bloem J, Van Eekeren N, De Goede RGM, Jagersop Akkerhuis GAJM, et
673 al. Biological measurements in a nationwide soil monitoring network. *Eur J Soil Sci.* 2009;60:820-832.
674 doi:10.1016/j.apsoil.2015.08.015
- 675 [45] Schmidt O, Arroyo J, Bolger T, Boots B, Breen J, Clipson N, et al. CréBeo Soil Biodiversity Project
676 – Baseline data, response to pressures, functions and conservation of keystone micro- and macro-
677 organisms in Irish soils. STRIVE Report 67. Environmental Protection Agency, Ireland; 2011 Nov.
- 678 [46] Keith AM, Boots B, Hazard C, Niechoj R, Arroyo J, Bending GD, et al. Cross-taxa congruence,
679 indicators and environmental gradients in soils under agricultural and extensive land management.
680 *Eur J Soil Biol.* 2012; 49:55-62. doi:10.1016/j.ejsobi.2011.08.002
- 681 [47] Mancini F, Cooke R, Woodcock BA, Greenop A, Johnson AC, Isaac NJB. Invertebrate biodiversity
682 continues to decline in cropland. *Proc R Soc B Biol Sci.* 2023;290:20230897.
683 doi:10.1098/rspb.2023.0897
- 684 [48] Reich PB, Oleksyn J, Modrzyński J, Mrozinski P, Hobbie SE, Eissenstat DM et al. Linking litter
685 calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecol Letters.*
686 2005;8:811-818. doi:10.1111/j.1461-0248.2005.00779.x
- 687 [49] De Wandeler H, Bruelheide H, Dawud SM, Dănilă G, Domisch T, Finér L, et al. Tree identity
688 rather than tree diversity drives earthworm communities in European forests. *Pedobiologia.*
689 2018;67:16-25. doi:10.1016/j.pedobi.2018.01.003
- 690 [50] Neiryneck J, Mirtcheva S, Sioen G, Lust N. Impact of *Tilia platyphyllos* Scop., *Fraxinus excelsior* L.,
691 *Acer pseudoplatanus* L., *Quercus robur* L. and *Fagus sylvatica* L. on earthworm biomass and physico-
692 chemical properties of a loamy topsoil. *For Ecol Manag.* 2000;133:275-286. doi:10.1016/S0378-
693 1127(99)00240-6
- 694 [51] Schelfhout S, Mertens J, Verheyen K, Vesterdal L, Baeten L, Muys B, De Schrijver A. Tree species
695 identity shapes earthworm communities. *Forests.* 2017;8;85. doi:10.3390/f8030085

696 [52] Butt KR, Callaham MA Jr. Earthworms from soils developed after 80 years under tree
697 monocultures at Holt Down, Hampshire, UK. *Eur J Soil Biol.* 2023;119:103560.
698 doi:10.1016/j.ejsobi.2023.103560

699 [53] Chan K-Y, Munro K. Evaluating mustard extracts for earthworm sampling. *Pedobiologia.*
700 2001;45:272-278. doi:10.1078/0031-4056-00084

701 [54] Ristok C, Babin D, Bartowski B, Burkhard B, Filser J, Hohberg K, et al. Towards a comprehensive
702 assessment of soil biodiversity in Germany: status quo, challenges, and policy implications. *Soil Org.*
703 2025;97:143-157. doi:10.25674/446

704 [55] Dornelas M, Magurran AE, Buckland ST, Chao A, Chazdon RL, Colwell RK, et al. Quantifying
705 temporal change in biodiversity: challenges and opportunities. *Proc R Soc B Biol Sci.*
706 2013;280:20121931. doi:10.1098/rspb.2012.1931

707 [56] Hohberg K, Ristok C, Eisenhauer N, Tebbe CC, Scheu S. Status and trends in soil biodiversity – a
708 national survey of Germany. *Soil Org.* 2025;97:103-114. doi:10.25674/449

709 [57] Harrison, B., Doo, B., Harris, M., Hathaway-Jenkins, L., Schmidt, S. & Stone, R. 2024. 25 Year
710 Environment Plan Outcome Indicator E7: Healthy Soils – Progress Report. JNCC Report 763. JNCC,
711 Peterborough, ISSN 0963-8091. [https://hub.jncc.gov.uk/assets/afc17b55-b01c-49f4-8cae-
712 1c0ceb880c4c](https://hub.jncc.gov.uk/assets/afc17b55-b01c-49f4-8cae-1c0ceb880c4c).

713 [58] Ganault P, Ristok C, Phillips HR, Hedde M, Capowiez Y, Bottinelli N, et al. Soil BON Earthworm - A
714 global initiative on earthworm distribution, traits, and spatiotemporal diversity patterns. *Soil Org.*
715 2024;96(1). doi:10.25674/362

716

717 **Supporting information captions**

718

719 **S1 Table. Comparison of GLMM outputs for different datasets with Model 1.** Estimated
720 effects and significance for model terms using Original, Revised and Revised+Augmented
721 (=Augmented) datasets; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

722

723 **S2 Table. Comparison of GLMM outputs for different datasets with Model 3.** Estimated
724 effects and significance for model terms using Original, Revised and Revised+Augmented
725 (=Augmented) datasets; BH trend = Broad Habitat \times Year, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

726

727 **S3 Table. Comparison of GLMM outputs for different datasets with Model 4.** Estimated
728 effects and significance for model terms using Original, Revised and Revised+Augmented
729 (=Augmented) datasets; FH trend = Fine Habitat \times Year, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

730