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# Earthworm records and habitat associations in the British Isles

F. Ashwood <sup>a,b,\*</sup>, K.D. Brown <sup>a</sup>, E. Sherlock <sup>a,c</sup>, A.M. Keith <sup>a,d</sup>, J. Forster <sup>b</sup>, K.R. Butt <sup>a,e</sup>

<sup>a</sup> Earthworm Society of Britain, 42 Denham Lodge, Oxford Road, Uxbridge, UB9 4AB, UK

<sup>b</sup> Forest Research, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK

<sup>c</sup> Natural History Museum, Cromwell Road, London, SW7 5BD, UK

<sup>d</sup> UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster, LA1 4AP, UK

<sup>e</sup> Ecological Engineering, University of Central Lancashire, Preston, PR1 2HE, UK

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#### ABSTRACT

The National Earthworm Recording Scheme (NERS) is the most comprehensive national database of earthworm species occurrence records for the British Isles, and possibly for any individual country in the world. Utilising the NERS database, we sought to update the current knowledge of earthworm species occurrences in the UK, Ireland and Channel Islands; identify species-specific habitat and microhabitat associations; reveal any biases and complementarities between amateur naturalist and research-related earthworm record collection; and inform how future earthworm sampling can be better focussed to improve our knowledge of earthworm ecology. We found that the most commonly occurring earthworm species were present in farmland and woodland, and recovered via soil pit sampling, the most common habitat-sampling protocol combinations. However, several earthworm species showed specificity to alternative habitats (such as trees, wetlands, and compost), and association with microhabitat (non-soil) sampling. There were clear disparities between scientific researchers and amateur naturalist recorders in terms of habitat types visited and sampling protocols/microhabitats used in the collection of earthworm records. Most importantly, we found that earthworm species currently considered to be nationally 'rare' in the British Isles are significantly associated with the most under-represented habitat-protocol/ microhabitat combinations (forest deadwood and other microhabitats, in addition to scrubland, wetland and heathland habitats), and thus may not be rare, only under-sampled. We therefore encourage earthworm researchers and recorders to give greater attention to these situations, to gain new insights into these earthworm species' ecologies and distributions. Finally, we would like to promote the establishment of earthworm recording schemes in other countries, to enable national and global collaborative monitoring of earthworm responses to environmental change.

#### 1. Introduction

Despite their intrinsic value and recognised importance for many soil processes, soil invertebrates are largely overlooked in national and international biodiversity and conservation assessments [1,2]. Owing to their role as ecosystem engineers [3], in recent years earthworms have become *the* representative taxon for tackling questions on global soil invertebrate diversity and distribution assessment [4]. Given broad variations in sampling approaches and global distribution patterns, there is an urgent need for high-quality and systematic national long-term and large-scale datasets to determine soil invertebrate, and thus soil sustainability, responses to anthropogenic environmental changes [5,6]. Despite a rich heritage of earthworm research [7],

national distribution maps using earthworm species occurrence records were not produced for the UK & Ireland until 2012, and this was only for four species [8]. These first distribution maps were based on just 3941 records across all 28 species of earthworm known to occur in natural environments at the time, and included historical datasets used to generate fundamental publications on earthworm species' ecologies [9]. Due to a lack of consistent habitat information within this initial national database of earthworm species occurrence records, the authors determined that no analysis of earthworm rarity, distribution patterns or habitat preferences could be undertaken.

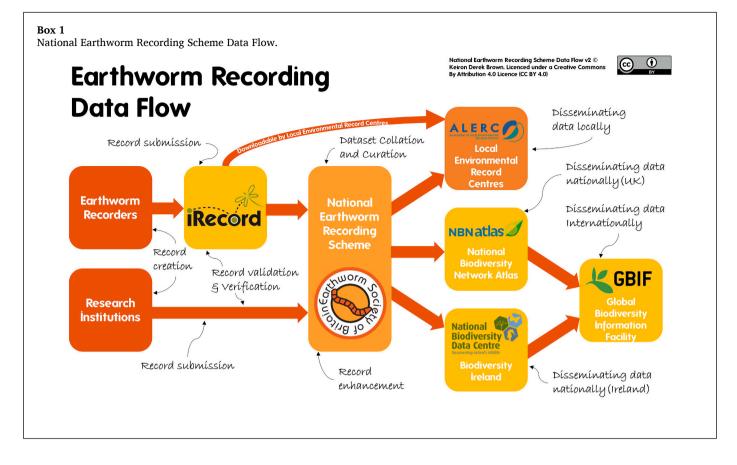
Subsequently, the largest and latest national earthworm survey of Great Britain was published in 2014, wherein 6,309 specimens were identified from 333 sites across England and Scotland [10]. From a

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<sup>\*</sup> Corresponding author. Earthworm Society of Britain, 42 Denham Lodge, Oxford Road, Uxbridge, UB9 4AB, UK. *E-mail address:* frank.ashwood@gmail.com (F. Ashwood).

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combination of historic data interrogation and new sampling of semi-natural habitats, the survey aimed to investigate the distribution and conservation status of British earthworms. Sheppard et al. [10] used local population size, geographical range and interpreted habitat specificity to cautiously classify nine earthworm species as Common, twelve as Rare, and six species as Extremely Rare. The authors also produced the first national ranked abundance and occurrence figures for British earthworm species. Whilst ground-breaking, this assessment was still based on limited species records, including nil-results for five entire species, and accordingly the authors called for greater national earthworm sampling to verify their conclusions regarding species occurrence, rarity, and habitat associations.

The National Earthworm Recording Scheme (NERS) was officially launched in 2014, with the aim of continuing the work of Carpenter et al. [8] and Sheppard et al. [10] to build a database of earthworm species occurrence records for the UK, Ireland and Channel Islands. Through the Earthworm Society of Britain and other partners, the NERS team trained and supported volunteer earthworm recorders (referred to henceforth as 'recorder') and collated data from research organisations and government agencies. In addition to collating records, the NERS team has actively worked to enhance the quality of the data by mining additional habitat and sampling protocol information associated with individual records. At the point of data analysis for this study (September 2022), the NERS database held 21,790 occurrence records for 30 earthworm species from 2683 sites [30-33]. Of these records, 6890 were generated by recorders and 14,900 were generated through scientific research projects (referred to as 'research'). As such, it is possible that the NERS database is currently the largest national dataset on earthworm distribution of any country in the world.

Utilising the NERS database, we sought to address the following aims: 1) Update the current knowledge of British earthworm species occurrences, 2) Identify species-specific habitat and microhabitat associations of British earthworms, 3) Reveal any biases and complementarities between recorder and research earthworm collection, and 4) Inform how future earthworm sampling can be better focussed to improve our knowledge of earthworm ecology in the British Isles.

## 2. Material and methods

# 2.1. Data verification for the national earthworm recording scheme (NERS)

The minimum data components required for earthworm species occurrence records to be accepted into the National Earthworm Recording Scheme datasets are a valid scientific species name, recorder name, a georeference and date (or date period). Data contributors are encouraged to also provide count, habitat, site name and sampling protocol data. To ensure accurate identification of earthworm specimens, several verification status assessment criteria are assessed before the records are added to the National Earthworm Recording Scheme datasets (Box 1). This includes voucher specimen availability, record impact on current knowledge base, photograph availability, determiner earthworm identification experience, features used for identification, identification resource used, specimen suitability and observation method used [11].

#### 2.2. Data exclusions and assumptions

From the 21,790 earthworm species occurrence records held within the NERS datasets at the time of this study, 7744 records were removed as they were deemed unsuitable for analysis within this study. This included all 5313 records from the Environment Agency's *Eiseniella tetraedra* Records (England) dataset, as during sampling only this species was recorded, and absence of other species cannot be assumed. We also

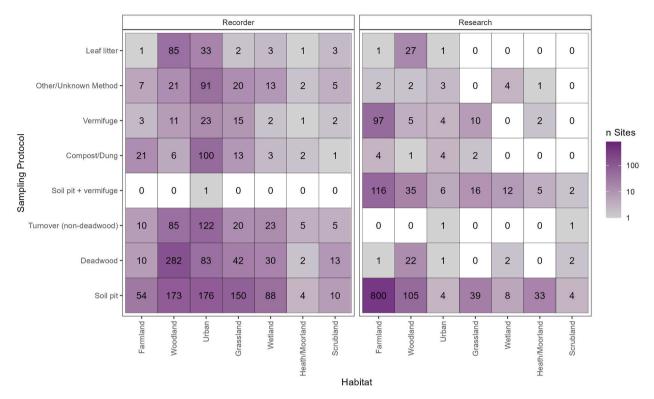


Fig. 1. Studies by habitat and sampling protocol in the NERS database, sub-divided by Recorder and Researcher (transparency of tile indicates number of sites represented).

omitted 2432 records where no habitat and/or sampling protocol data was provided by the data contributor. Thus, we analysed a total of 14,046 earthworm records for this study. Regarding the species *Aporrectodea caliginosa* and *Aporrectodea nocturna* (previously considered two morphs of the same species, *A. caliginosa*); whilst species determinations generated using the 2nd Edition of the 'Key to the Earthworms of the UK & Ireland' [12] are accurate to species level, any determinations made with earlier identification resources have been recorded as *A. caliginosa* 

*sensu lato* unless the morph was specifically recorded as *A. nocturna*. This is because *A. caliginosa* is taken to be the most common and widespread of the two species, however it should be noted that this approach may mean *A. nocturna* is underrepresented in the NERS dataset in historical records. Additionally, the composting earthworm species *Eisenia andrei* and *Eisenia fetida* are difficult to distinguish from each other morphologically [13] and thus were recorded as an aggregate under *E. fetida*.

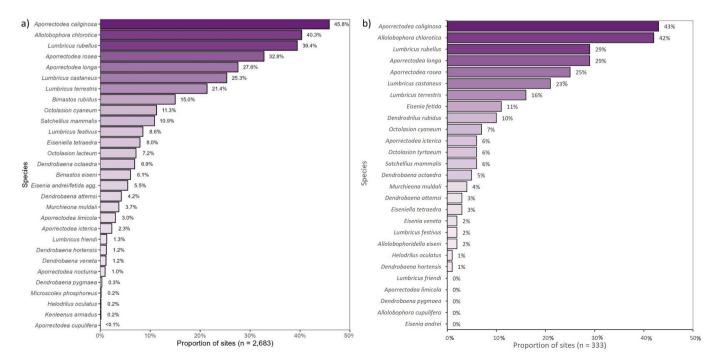


Fig. 2. a) Proportion of sites with earthworm species present in the NERS database; b) Proportion of sites with earthworm species present in Sheppard et al. [10].

#### 2.3. Site distributions in the NERS dataset

Gaps in the data sets are shown in Fig. 1. Farmland was the most sampled habitat in research records, with a total of 1021 sites, whilst woodland was the most sampled habitat by recorders, with 663 sites. Woodland, farmland and urban sites are reasonably well represented across both survey types, although research records show less diversity in sampling protocols (a clear lack of microhabitat surveying in leaf litter, compost/dung, or deadwood), and the recorder records show little use of the combined soil pit with vermifuge sampling technique (a chemical extractant liquid such as formalin or a mustard suspension that causes earthworms to surface from the soil). This is likely due the fact that recorders are encouraged to report those found via vermifuge and hand-sorting of soil separately where they use the combined method. Wetlands, heathlands, moorlands and scrubland sites are poorly represented across both data sets. It is important to note that Sampling Protocol, as defined by the NERS, includes certain microhabitats alongside traditional soil-based sampling methodologies. Thus, some combinations of the factors Habitat Type and Sampling Protocol are dependent on each other (e.g., Woodland and Leaf Litter), or unlikely to co-occur (e.g., Farmland and Deadwood) (Fig. 1).

#### 2.4. Statistical analysis

Analysis was conducted in R version 4.1.0 [14], with graphics produced using ggplot2 in R [15]. Datasets were cleaned, with all grid reference data converted to WGS84 lat/long data. It was taken that surveys were assessed for all earthworm species, such that a missing entry for a particular species meant this species was not found in the sample (i.e., for the absence/presence analysis, all unrecorded species were 0 values). Repeated measures (same location, same habitat, same sampling protocol, different years) were excluded from the data to ensure all sites were equally weighted in the absence/presence sample, with one unique species record per habitat type and sampling protocol randomly kept from each location. Correlations were assessed using Spearman's rho applied to proportional data. Species-specific estimated marginal means were calculated [16], and mean-corrected estimates plotted against relevant predictors to observe differences. Specific main effect and interaction proportions were calculated (e.g., the total proportion of all surveys in woodlands), and mean-corrected marginal means plotted against these proportions to observe any relationship between popularity of habitat/sampling protocol/survey types and occurrence of earthworm species.

	Aporrectodea caliginosa -	57%	10%	1%	1%	11%	4%	15%			
	Allolobophora chlorotica -	49%	11%	1%	1%	16%	6%	17%			
	Lumbricus rubellus -	41%	9%	3%	1%	10%	6%	28%			
	Aporrectodea rosea -	59%	11%	0%	1%	11%	4%	14%			
	Aporrectodea longa -	59%	10%	0%	1%	17%	3%	11%			
	Lumbricus castaneus -	41%	10%	1%	1%	18%	3%	26%			
	Lumbricus terrestris -	51%	11%	0%	1%	18%	3%	16%			
	Bimastos rubidus -	10%	7%	4%	1%	21%	5%	52%			
	Octolasion cyaneum -	49%	13%	1%	2%	12%	4%	18%			
	Satchellius mammalis -	44%	8%	0%	3%	13%	6%	26%	Pro	oportion	
	Lumbricus festivus -	65%	8%	0%	1%	14%	4%	7%		species	
	Eiseniella tetraedra -	28%	7%	1%	1%	9%	33%	21%		100%	
(0	Octolasion lacteum -	29%	9%	1%	1%	11%	16%	33%		10070	
Species	Dendrobaena octaedra -	8%	7%	5%	1%	6%	4%	68%		- 75%	
ec	Bimastos eiseni -	2%	6%	2%	3%	20%	3%	66%			
do	- Eisenia andrei/fetida agg	9%	6%	0%	1%	65%	4%	16%		50%	
0,	Dendrobaena attemsi -	1%	3%	3%	0%	10%	1%	82%			
	Murchieona muldali -	56%	6%	1%	2%	4%	6%	25%	_	25%	
	Aporrectodea limicola -	72%	2%	1%	1%	4%	13%	7%			
	Aporrectodea icterica -	12%	30%	0%	0%	41%	3%	14%		0%	
	Lumbricus friendi -	63%	5%	0%	0%	9%	19%	5%			
	Dendrobaena hortensis -	5%	5%	2%	5%	38%	0%	45%			
	Dendrobaena veneta -	11%	3%	0%	0%	63%	5%	18%			
	Aporrectodea nocturna -	16%	25%	0%	3%	41%	3%	12%			
	Dendrobaena pygmaea -	0%	9%	0%	0%	9%	18%	64%			
	Microscolex phosphoreus -	17%	0%	0%	0%	33%	0%	50%			
	Helodrilus oculatus -	0%	0%	0%	0%	0%	80%	20%			
	Keneenus armadas -	40%	20%	0%	0%	20%	0%	20%			
	Aporrectodea cupulifera -	100%	0%	0%	0%	0%	0%	0%			
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		(1	) p	pu	pu	) L	) p	) p			
		Farmland (1082)	Grassland (289)	Heath/Moorland (54)	Scrubland (41)	Urban (493)	Wetland (173)	Woodland (689)			
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Habitat Type (no. of sites)

Fig. 3. Proportion of each earthworm species per habitat type in the NERS database. Species ordered from most (top) to least (bottom) commonly occurring.

										-		
	Aporrectodea caliginosa -	75%	11%	2%	5%	3%	1%	1%	1%			
	Allolobophora chlorotica -	66%	10%	3%	8%	6%	3%	1%	2%			
	Lumbricus rubellus -	54%	9%	7%	15%	6%	4%	3%	2%			
	Aporrectodea rosea -	71%	12%	9%	3%	3%	1%	0%	1%			
	Aporrectodea longa -	62%	14%	11%	4%	4%	1%	1%	3%			
	Lumbricus castaneus -	46%	9%	7%	16%	10%	7%	4%	2%			
	Lumbricus terrestris -	48%	15%	16%	7%	6%	1%	1%	5%			
	Bimastos rubidus -	31%	7%	1%	31%	11%	8%	8%	4%			
	Octolasion cyaneum -	58%	11%	16%	4%	3%	2%	0%	5%			
	Satchellius mammalis -	32%	14%	18%	15%	8%	8%	4%	2%			
	Lumbricus festivus -	41%	22%	22%	5%	5%	1%	1%	3%		oportior	
	Eiseniella tetraedra -	42%	7%	14%	12%	12%	5%	2%	6%	of	species	5
	Octolasion lacteum -	55%	12%	10%	12%	5%	2%	1%	3%		100%	
es	Dendrobaena octaedra -	47%	4%	3%	28%	3%	10%	2%	3%		- 75%	
eci	Bimastos eiseni -	13%	2%	1%	57%	7%	8%	7%	5%		1370	
Species	Eisenia andrei/fetida agg	8%	3%	2%	21%	10%	5%	47%	4%	_	50%	
0)	Dendrobaena attemsi -	29%	1%	1%	46%	2%	12%	2%	6%			
	Murchieona muldali -	80%	13%	2%	2%	0%	1%	1%	2%		25%	
	Aporrectodea limicola -	39%	20%	36%	0%	2%	0%	0%	2%			
	Aporrectodea icterica -	76%	4%	3%	1%	1%	0%	0%	14%		0%	
	Lumbricus friendi -	12%	72%	12%	0%	0%	0%	2%	2%			
	Dendrobaena hortensis -	25%	0%	0%	28%	18%	10%	10%	10%			
	Dendrobaena veneta -	5%	3%	3%	13%	34%	3%	34%	5%			
	Aporrectodea nocturna -	75%	0%	9%	3%	6%	0%	0%	6%			
	Dendrobaena pygmaea -	45%	0%	9%	36%	0%	9%	0%	0%			
	Microscolex phosphoreus -	17%	50%	0%	17%	0%	0%	0%	17%			
	Helodrilus oculatus -	80%	0%	0%	0%	20%	0%	0%	0%			
	Keneenus armadas -	0%	100%	0%	0%	0%	0%	0%	0%			
	Aporrectodea cupulifera -	0%	100%	0%	0%	0%	0%	0%	0%			
		Soil pit (1585) -	Soil pit + vermifuge (183) -	Vermifuge (172) -	Deadwood (478) -	Turnover (non-deadwood) (267) -	b Leaf litter (156) -	Compost/Dung (149) -	Other/Unknown Method (166) -	_		
	Sampling Protocol (no. of sites)											

Fig. 4. Proportion of each earthworm species per sampling protocol in the NERS database. Species ordered from most (top) to least (bottom) commonly occurring.

## 3. Results

# 3.1. Earthworm species occurrence

Fig. 2a shows the proportion of sampling sites (n = 2683) at which earthworm species were recorded. The most commonly occurring species (in over a third of all sites) were *A. caliginosa* (45.8%), *Allolobophora chlorotica* (40.3%), and *Lumbricus rubellus* (39.4%). The least commonly occurring species (each occurring in less than 1% of all sites) were *Dendrobaena pygmaea* (0.3%), *Microscolex phosphoreus* (0.2%), *Helodrilus oculatus* (0.2%), *Kenleenus armadas* (0.2%) and *Aporrectodea cupulifera* (<0.1%).

#### 3.2. Earthworm species habitat and microhabitat associations

In general, earthworm species were most likely to be found in woodland, grassland and farmland, and less likely to be found in heath/ moorland and scrubland (Fig. 3). The farmland habitat type possessed the greatest overall proportion of earthworm species, and yielded 9 of the top 10 most commonly occurring species, with a total species richness of 27 (out of 29). The greatest species richness, however, was in the woodland habitat type, which possessed 28 species. Species with proportionately greater occurrence in farmland habitats included *A. cupulifera* (100 % occurrence), *Aporrectodea limicola* (72 %), *Lumbricus festivus* (65 %), *Lumbricus friendi* (63 %), *Aporrectodea rosea* (59 %), *A. caliginosa* (57 %), and *Murchieona muldali* (56 %), amongst others (Fig. 3). Notably higher occurrences in

Aporrectodea caliginosa -	35%	65%	7
Allolobophora chlorotica -	43%	57%	
Lumbricus rubellus -	44%	56%	
Aporrectodea rosea -	32%	68%	
Aporrectodea longa -	34%	66%	
Lumbricus castaneus -	51%	49%	
Lumbricus terrestris -	38%	62%	
Bimastos rubidus -	65%	35%	
Octolasion cyaneum -	35%	65%	
Satchellius mammalis -	50%	50%	Duovoution
Lumbricus festivus -	29%	71%	Proportion
Eiseniella tetraedra -	58%	42%	of species
Octolasion lacteum -	54%	46%	100%
Dendrobaena octaedra -	45%	55%	75%
Dendrobaena octaedra - Bimastos eiseni - G Eisenia andrei/fetida agg	80%	20%	1070
Eisenia andrei/fetida agg	88%	12%	50%
Dendrobaena attemsi -	71%	29%	
Murchieona muldali -	30%	70%	- 25%
Aporrectodea limicola -	12%	88%	
Aporrectodea icterica -	84%	16%	0%
Lumbricus friendi -	12%	88%	
Dendrobaena hortensis -	80%	20%	
Dendrobaena veneta -	95%	5%	
Aporrectodea nocturna -	84%	16%	
Dendrobaena pygmaea -	64%	36%	
Microscolex phosphoreus -	17%	83%	
Helodrilus oculatus -	80%	20%	
Keneenus armadas -	0%	100%	
Aporrectodea cupulifera -	0%	100%	
	· · ·		
	421	265	
	(17	(12	
	Recorder (1421) -	Research (1265)	
	SOLG	eal	
	Sec	Res	
		(no. of sites)	
	Curvey Type		

Fig. 5. Proportion of each earthworm species per survey type in the NERS database. Species ordered from most (top) to least (bottom) commonly occurring.

woodland habitats were shown by the species *Dendrobaena attemsi* (82%), *Dendrobaena octaedra* (68%), *Bimastos eiseni* (66%), *D. pygmaea* (64%), *Bimastos rubidus* (52%) and *M. phosphoreus* (50%). Some earthworm species showed distinct associations with alternative habitat types to farmland and woodland: *H. oculatus* (80%) and *Eiseniella tetraedra* (33%) were associated with wetlands; whilst *Eisenia andrei/fetida* agg. (65%), *Aporrectodea icterica* (41%), *Dendrobaena veneta* (63%), *A. nocturna* (41%), and to a lesser extent *Dendrobaena hortensis* (38%) and *M. phosphoreus* (33%), showed strong associations with urban habitats. Grassland habitats yielded a wide range of species (26 in total), but they were notable for relatively high proportions of the species *A. icterica* (30%), *A. nocturna* (25%), and *K. armadas* (20%).

In terms of species recovery according to sampling protocol, all of the top 10 most frequently occurring earthworm species were mainly recovered via soil pit sampling, which was the most commonly used sampling protocol (Fig. 4). The addition of vermifuge (a chemical extractant liquid such as formalin or a mustard suspension that causes earthworms to surface from the soil) techniques to soil pit sampling was associated with greater occurrence of the species *K. armadas* and *A. cupulifera* (100 % of occurrences), *L. friendi* (72 %) and *M. phosphoreus* (50 %) than in soil pit sampling without vermifuge. Some species were

almost exclusively found in non-soil microhabitats such as deadwood and compost/dung. Species particularly associated with deadwood (>25 % occurrence) were *B. eiseni* (57 %), *D. attemsi* (46 %), *D. pygmaea* (36 %), *B. rubidus* (31 %), *D. octaedra* (28 %), and *D. hortensis* (28 %). Compost-associated species were *E. andrei/fetida* agg. (47 %) and *D. veneta* (34 %), whilst leaf litter microhabitats did not yield any notable species occurrences.

#### 3.3. Sampling trends in earthworm records

The five most common British earthworm species were all identified more often by researchers than recorders (Fig. 5). Conversely, the majority of the least common species (those associated with woodland, urban and wetland habitats and deadwood or compost/dung microhabitats) were reported more often by recorders than researchers. The remainder of species were split relatively evenly across both survey types.

Fig. 6 shows each species occurrence versus the main predictors (habitat, sampling protocol and survey type) alone and in combination, where species occurrence is plotted against the proportion of total studies for which the specific species occurrence was maximal. The

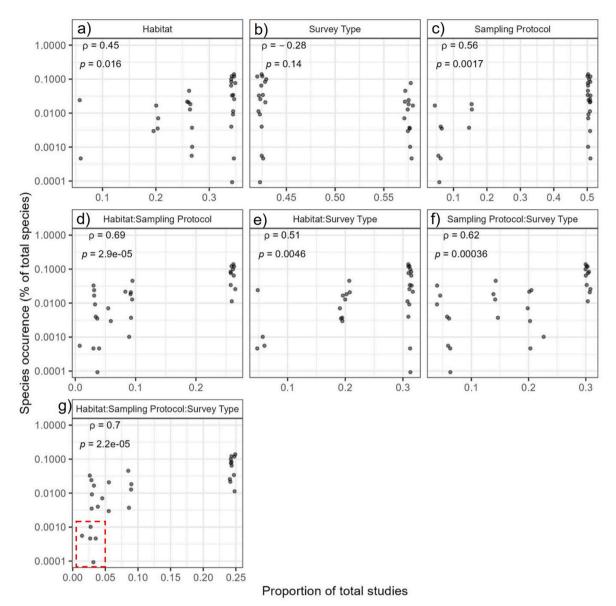


Fig. 6. Correlation between earthworm species occurrence in the NERS database and study type (a data point for each species per panel, with species occurrence plotted against the proportion of total studies for which the specific species occurrence was maximal). Five least common species:habitat:sampling protocol com-

strongest correlation was seen between the combined effect of habitat and sampling protocol (addition of survey type has a very small positive effect on correlation), and there were significant effects of habitat, survey type and sampling protocol, both as main effects and as speciesspecific effects. The five most common earthworm species (i.e., A. caliginosa, A. chlorotica, L. rubellus, A. rosea and A. longa) occurred in the most sampled habitat-protocol combinations of soil pit sampling on farmland (26 % of all studies) and woodland habitat types. Conversely and notably, the five least common earthworm species (D. pygmaea, H. oculatus, M. phosphoreus, K. armadas and A. cupulifera) occurred in the least commonly sampled habitat-protocol combinations (e.g., vermifuge sampling, deadwood, leaf litter and other microhabitat surveying on wetland and other habitats, p = 0.000022) (Fig. 6g, highlighted datapoints in red dashed box). Differences between survey type (research vs recorder) were predominantly driven by two rare species, A. cupulifera and K. armadas, which appeared only for research and not the recorder dataset.

binations highlighted in red box. Note the logarithmic scale on the Y-axis.

#### 4. Discussion

#### 4.1. Earthworm species occurrence

The last comprehensive national earthworm survey within the British Isles took place around a decade ago [10]. Data comprising 6,309 specimens were identified to species from 333 sites across England and Scotland representing 15 habitat types was interpreted alongside historical knowledge of species and their distributions across the entire British Isles [9]. Our dataset builds upon this greatly, with 14,046 records from 2683 sites across the entire British Isles. Using the NERS dataset, we addressed our first research aim to provide updated species occurrences, and directly compared these against the results of Sheppard et al. [10] to identify the impact of the additional data gathered from the NERS' public/amateur naturalist recorder engagement and research data collation activities. There have been some major advances in our understanding of earthworm distribution in the UK since the last national earthworm survey. Three new earthworm species have subsequently been added to the national species list, and in the NERS dataset

there is now only a single species with zero occurrence data (Sparganophilus tamesis). This is compared to the five species for which Sheppard et al. [10] possessed no presence data, although they did note occurrence of those species in the literature for the purpose of assessing national rarity. Some species with very low occurrence were considered 'Very Rare' by Sheppard et al. [10], for example D. pygmaea, L. friendi, A. limicola, and E. andrei, and it was suggested that they may warrant classification as Vulnerable or Imperilled in conservation terms. However, these species have been subsequently found at several sites across the UK [17-20], and, following more comprehensive national earthworm sampling by recorders and researchers, the latter two have now been found at greater than 2 % of sites (E. andrei now being aggregated with E. fetida, due to difficulties in morphologically separating the two species [13]), in contrast to being recorded at zero per cent of sites by Sheppard et al. [10]. This serves to remind us of the importance of caution when assigning species conservation status to under-recorded taxa such as earthworms.

Sheppard et al. [10] calculated the percentage of independent sampling sites at which each species was recorded, to give an indication of the national occurrence of known earthworm species at the time (Fig. 1b). When applying this same method to our data, we saw that the overall species occurrence curve has clearly smoothed compared with that of Sheppard et al. [10], with the gaps between species narrowing and giving far fewer 'rare' species. Within the top five most common species, A. caliginosa and A. chlorotica still rank first and second respectively, however A. caliginosa has increased by  $\sim 3$  % and A. chlorotica has decreased by  $\sim 2$  %. Likewise, L. rubellus remains the third most common earthworm species, however its occurrence has increased by 10 % to be almost as nationally common as A. chlorotica. The species A. rosea has overtaken A. longa as the fourth most common species, having increased from 25 % to 32.8 % occurrence. Other notable changes in species occurrence since Sheppard et al. [10], include the species B. eiseni, O. cyaneum, S. mammalis, L. festivus and E. tetraedra all greatly increasing in occurrence, with L. festivus, for example, moving up from eighteenth to eleventh place and increasing from 2 % to 8.6 %occurrence. Notable decreases in occurrence include E. fetida dropping from eighth to sixteenth place (decreasing from 10 % to 5.5 % occurrence) despite aggregating it with E. andrei as previously described, and A. icterica moving down from eleventh to twentieth place (a decrease from 7 % to 2.3 % occurrence). Gathering comprehensive data on national species occurrence is important, as species commonality is the basis for widely used entry-level earthworm identification resources. For example, the OPAL Earthworm Guide [21] was produced as a resource for the OPAL Soil & Earthworm Survey and includes an identification key to the '12 most common' species of British earthworms, as determined using species occurrence data included in Sheppard et al. [10]. From our data, 25 % of the species in the UK's 'top twelve' have changed since the OPAL key was produced, and the gaps between most species' occurrences have narrowed greatly. Indeed, there is less than a 3-point difference in occurrence between the top 10 and top 15 species rankings, challenging the validity of using 'top X most common' approaches to designing earthworm identification resources; particularly considering the habitat-specificity demonstrated by several species within our dataset, as discussed below.

#### 4.2. Earthworm species habitat and microhabitat associations

The second research aim of this study was to identify any speciesspecific habitat and microhabitat associations of British earthworms. We found compelling evidence to support the classification of several British earthworm species as tree-associated or 'arboreal' [22], which are strongly associated with woodland habitats and deadwood microhabitats. In particular, the species *B. eiseni* and *D. attemsi* were far more commonly recovered in forest habitats, and from deadwood and leaf litter microhabitats. This corresponds well with contemporary earthworm studies across temperate forests in Europe, in which these two species have been primarily found during forest microhabitat surveys rather than in soil [17,23–26]. Since forest microhabitat sampling is not commonly carried out by earthworm research scientists [17], arboreal species such as these are almost certainly under-represented in the NERS and other soil-pit-survey-dominated earthworm datasets. In fact, only through novel microhabitat searching was *D. attemsi* recently added to the species list for Ireland, and its conservation status changed from 'rare' to 'moderately common' in Germany [25,26].

Species which appear to have strong association with urban habitats include the well-known, and commercially available, composting earthworms D. veneta and E. andrei/fetida agg. Our data supports the conclusions of Carpenter et al. [8] and Sheppard et al. [10], who identified that such species are likely to be far more common than is reflected in national distribution datasets, since they are likely to occur in domestic composting setups across the British Isles. Whilst relatively popular with recorders, urban habitats are almost completely unrepresented in research records, thus we lack sufficient records to draw conclusions about earthworm distributions in urban habitats. Our results showed clear wetland habitat association for the species H. oculatus and, to a certain extent, E. tetraedra; although the latter was almost as equally common in wet farmland and woodland soils as in wetland systems. Sheppard et al. [10] advocated greater future earthworm sampling in wetland and other semi-aquatic habitats to inform our ecological understanding of H. oculatus, E. tetraedra and A. limicola. Based on our results we support this, except perhaps in the case of A. limicola, which now appears to have greater association with agricultural land (albeit mostly in the wetter farmland soils of northwest England and southern Scotland [27]). Finally, whilst grassland habitats are relatively rich in earthworm species, they were particularly notable for yielding previously considered rare or non-existent species in Britain such as Kenleenus armadas [10]. This has been further confirmed since the analysis of our dataset, with the discovery in 2023 of Kenleenus armadas in a grassland in southeast England during a public earthworm surveying event (K. Brown, Pers Comm).

#### 4.3. Sampling trends in earthworm records

Our third aim was to reveal any sampling biases and complementarities between amateur naturalist ('recorder') and researcher earthworm records. Perhaps the most striking disparity we discovered was in the habitat types most visited by recorders and researchers. Most of the non-farmland and woodland records were contributed by recorders, especially for the urban, grassland and wetland habitat types. Similarly, recorders contributed most of the non-soil-based (microhabitat) earthworm species observations in our dataset. Given our finding of distinct species-specific associations with such habitats and microhabitats, it is clear that without earthworm recorders, we would know a great deal less about the national occurrence and ecologies of many British earthworm species.

Earthworm species previously considered to be 'rare' may be readily encountered during the sampling of uncommon habitats or microhabitats. For example, in an intensive and varied microhabitat survey of two broadleaf woodlands on the Isle of Wight, Burton & Eggleton [28] found that their wet woodland soil commonly yielded the species E. tetraedra. Schmidt et al. [26] placed D. attemsi on the species list for Ireland following the unusual research approach of surveying deadwood and other high organic microhabitats in woodlands. Similarly, Ashwood et al. [17] found that the nationally 'very rare' species D. pygmaea was locally abundant during litter turnover and deadwood surveying in an oak woodland in southeast England. Such occurrences raise the important question of whether certain earthworm species really are rare, or simply under-sampled. Through our analysis of the NERS dataset, we were able to assess species (micro)habitat preferences against national sampling patterns, to robustly address this question for the first time. In doing so, we addressed our fourth research aim, which was to inform how future earthworm sampling may be better focussed. We successfully

identified which habitat-protocol/microhabitat combinations are nationally over-represented (soil pit sampling on farmland and woodland) and those which are under-represented (most microhabitat types, and wetland, heath/moorland and scrubland habitats). This, combined with our finding that the 'rarest' species are significantly associated with under-represented habitat-protocol/microhabitat combinations, gives us a direction for focussing future earthworm sampling efforts. This is particularly the case for earthworm research scientists, who rarely look beyond soil-living earthworms in agricultural and forest systems, likely due to limitations in the scope of soil research funding [29]. However, thanks to the efforts of the National Earthworm Recording Scheme and its recorders, we are finally able to make a strong argument for investing resources into investigation of these previously underappreciated (micro)habitats, given their potential to generate unique earthworm ecological insights and inform the conservation status of our most poorly understood earthworm species.

## 5. Conclusions

By analysing the British National Earthworm Recording Scheme dataset, we found several disparities between scientific researchers and recorders (e.g., amateur naturalists) in terms of habitat types visited and sampling methods used in the collection of earthworm records. We also identified species-specific habitat associations for many earthworm species. Most importantly, we found that earthworm species currently considered to be nationally 'rare' in the UK, Ireland and Channel Islands are significantly associated with the most under-represented habitatsampling method combinations, and thus these may in fact not be rare, instead simply under-sampled. We suggest that earthworm researchers and recorders give greater attention to forest deadwood and other microhabitats, in addition to scrubland, wetland and heathlands in future earthworm sampling campaigns, due to the high likelihood of generating unique earthworm ecological and distribution insights. To conclude, this study has demonstrated the value of the National Earthworm Recording Scheme datasets for the UK, Ireland and Channel Islands for improving our knowledge of national earthworm ecology and species occurrence, and we encourage the establishment of similar schemes in other countries. A global collaborative network of national earthworm recording schemes would go a long way towards answering fundamental questions about earthworm species distributions, declines, introductions and invasions, as well as providing high-quality datasets to better predict earthworm responses to the increasing anthropogenic pressures of climate and land-use change.

#### CRediT authorship contribution statement

F. Ashwood: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. K.D. Brown: Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Data curation, Conceptualization. E. Sherlock: Writing – review & editing, Validation, Data curation. A.M. Keith: Writing – review & editing, Data curation. J. Forster: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. K.R. Butt: Writing – review & editing, Methodology, Data curation.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# Data availability

The data used are openly and freely available via the National Biodiversity Network (NBN) Atlas and Biodiversity Ireland

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejsobi.2024.103642.

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