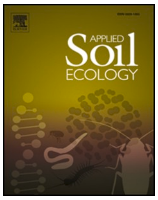
Applied Soil Ecology 215 (2025) 106471

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil



Oribatid mite taxa and composition associated with temperate habitats in Great Britain☆

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ARTICLE INFO

Keywords:
Oribatida
Soil biodiversity
Microhabitat
Indicator taxa
Gradient

ABSTRACT

Knowledge on the status of soil biodiversity and its variation across habitats is fundamentally important to soil monitoring. Oribatid mites are globally distributed, can be found in all terrestrial ecosystems and, being generally numerous and including various trophic traits, are important components in soil food webs for the ecosystem services they deliver. The Countryside Survey (CS) is an integrated monitoring programme in Great Britain, and here we analyse an existing dataset of oribatid mite records from soil invertebrate assessments of CS in 1998 that covered over 500 one-kilometre squares. Using vegetation-based classification (AVC) to represent broad habitat types, we tested differences in oribatid mite richness and community composition across these, and used indicator analysis to uncover taxa associations with habitats or habitat combinations. Furthermore, we explored links between species and soil properties using richness and prevalence across organic matter and pH gradients. Oribatid mite species richness and composition differed between habitat types. Lowland and Upland wooded habitats had highest species richness per core; richness was lower in the managed agricultural habitats (Crops & Weeds, Tall Grass & Herb, Fertile Grassland) and generally higher in wooded habitats and those typically with organic soils (Lowland Wooded, Upland Wooded, Moorland-Grass mosaic, Heath & Bog). Oribatid mite richness increased steeply to ~30 % organic matter. We list several species associated with AVCs that can potentially be used as indicators. These findings reinforce the link between oribatid mites, habitat, soil organic matter and pH, and provide a basis for mapping and further analyses.

1. Introduction

Soil fauna influence nutrient cycling, decomposition, water and carbon storage, and many of those functions that translate into ecosystem services such as food production, access to fresh water, and disease regulation (Anderson, 2009; FAO et al., 2020; Wall et al., 2012). While mites are some of the most abundant microarthropods in soils, corresponding to nearly two thirds of the soil arthropods on Earth (Rosenberg et al., 2023), their diversity and functionality remain poorly understood. Oribatid mites (Acari: Sarcoptiformes) are globally distributed and can be found in all terrestrial ecosystems (Behan-Pelletier and Lindo, 2023; Schatz, 2004), with their diversity increasing from boreal to temperate regions but not increasing further in the tropics (Maraun et al., 2007). They are important components in soil food webs (Barreto et al., 2024; Buchkowski et al., 2023; Lu et al., 2022), being generally numerous and including various trophic traits, and are often the dominant arthropod group in soils with high organic matter such as coniferous and broadleaf forest soils (Wallwork, 1983); for example, in temperate forests, 100–150 species can have collective densities exceeding 100,000 m^{-2} (Norton and Behan-Pelletier, 2009). They also occur in a wide variety of microhabitats (e.g., Barreto and Lindo, 2018; Wehner et al., 2016), which confers this group a great ecological indicator value (Ashwood et al., 2022; Behan-Pelletier, 1999; Lehmitz et al., 2020; do Prado et al., 2025).

As soil biodiversity is vulnerable to human disturbance, it is important to understand the role in ecosystem functioning and how they might respond to changes at various spatial scales to enable their future protection (Wall et al., 2010). The above-belowground relationship is

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☆ This article is part of a Special issue entitled: ‘Soil Biodiversity in Europe’ published in Applied Soil Ecology.
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https://doi.org/10.1016/j.apsoil.2025.106471
Received 24 March 2025; Received in revised form 11 September 2025; Accepted 12 September 2025

similarly important, as the distribution of soil fauna is largely influenced by the type of aboveground vegetation present, and plants rely on soil biodiversity to increase nutrient cycling and improve soil structure in terms of aeration and water retention (Bardgett, 2005). Knowledge on the status of soil biodiversity and its variation across habitats is therefore fundamentally important to soil monitoring. The Countryside Survey is a unique national monitoring scheme and inventory of the natural resources across England, Scotland and Wales, and was carried out in 1978, 1984, 1990, 1998, 2007 (and a rolling survey programme since 2019). Soil invertebrates were assessed at this national scale for the first time in the 1998 survey (Black et al., 2003; see Fig. 1); their inclusion was partially driven the need to develop indices of soil biological activity and diversity and the associated requirement for baseline data.

Fig. 1. Map outline of Great Britain, showing approximated locations of 10 km grid squares (black circles) containing locations sampled for invertebrates in Countryside Survey 1998.

In this paper we use an existing dataset of oribatid mite records from the Countryside Survey in Great Britain (GB) sampled in 1998/99 (Keith et al., 2018). Earlier work from this survey showed that Acari were the most frequently recorded group in 94 % of all soil samples (Black et al., 2003). Other more recent studies using Countryside Survey data have shown differences in total invertebrate abundance and richness of higher-order taxonomic groups between vegetation types (Keith et al., 2015), and the central role of organic matter in driving spatially aggregated oribatid mite composition and diversity metrics (Caruso et al., 2019). A more detailed assessment of available species-level data on oribatid mites could provide valuable understanding on their distribution and utility as indicators across different habitat types and their links with associated soil characteristics.

We investigated oribatid species records, alongside vegetation and soil data with three objectives: (i) to determine whether oribatid mite species richness and community composition differed between temperate habitats as defined by Aggregate Vegetation Class (AVC), (ii) to assess potential use of these taxa as indicators for these habitats and their combinations, and (iii) to explore relationships between oribatid mite richness and presence of indicator taxa with commonly measured soil properties (Organic matter content and pH). Additionally, we discuss future directions for these data in the context of key policy targets regarding land use change, emphasising the need for more data and mapping, more detailed understanding of habitat quality and to disentangle the functional role of oribatid mites in temperate habitats.

2. Methods

2.1. *Oribatid dataset from Countryside Survey*

The Countryside Survey consists of equal numbers of 1 km × 1 km sampling squares randomly selected from a stratification of land classes (Firbank et al., 2003; Keith et al., 2015; Sheail and Bunce, 2003). Each 1 km × 1 km sampling square contains five randomly located 'X-plots', 200 m^2 vegetation sampling quadrats within which soil measurements and vegetation assessments are co-located. Based on plant species data, each X-plot was assigned an Aggregate Vegetation Class (AVC): a classification of plant communities representative of broad habitat type, with eight categories: (1) Crops & Weeds, (2) Tall Grass & herb, (3) Fertile Grassland, (4) Infertile Grassland, (5) Lowland wooded, (6) Upland wooded, (7) Moorland Grass mosaic, (8) Heath & Bog (Bunce et al., 1999, Supplementary Table S1). Soil cores were taken for measurement of soil properties, including organic matter content (via loss-on-ignition; 16 h at 375 °C) and pH (1:2 soil to water ratio by weight) (Emmett et al., 2008; Reynolds et al., 2013). Separate soil cores (1 per X-plot) were also taken for invertebrate extraction (4 cm diameter, 8 cm depth), with surface vegetation removed leaving the litter layer intact. Due to the extensive spatial distribution of Countryside Survey locations sampling was undertaken by multiple teams from late May through to October (see Supplementary Fig. S1). Cores were placed immediately in cool boxes and sent to the laboratory at the UK Centre for Ecology & Hydrology Lancaster for extraction of invertebrates. Soil invertebrates were extracted over five days using a dry Tullgren extraction method, preserving all specimens into 70 % ethanol. Invertebrates were identified and enumerated to broad taxa for a total of 1076 cores, including counts of acarids (Black et al., 2003; Emmett et al., 2010). Oribatid mites were further recorded and identified to species by Mr. Frank Monson (World Museum Liverpool), sometimes requiring specimen clearing using lactic acid at room temperature and mounting in glass cavity slides. An unpublished monograph of British oribatid mites (Luxton) was used for identification, with identifications checked against Weigmann (2006).

2.2. *Statistical methods*

We examined differences in the number of oribatid mite species per core between AVCs with a generalised linear model (GLM) and negative binomial with log link function in package *MASS* (Venables and Ripley, 2002). The significance of AVC was assessed using an analysis of deviance (likelihood ratio test). Post-hoc pairwise comparisons between AVCs used estimated marginal means with Tukey adjustment for multiple testing in package *emmeans* (Lenth, 2025). Additionally, we used a Generalised Additive Model (GAM) to assess non-linear relationships of species richness per core with organic matter content, soil pH, and their interaction, with the package *mgcv* (Wood, 2011). Tensor products were used to visualise the regression surface of species richness across organic matter content and pH gradients.

The Jaccard distance metric was used, following removal of singletons, to construct a sample-by-species dissimilarity matrix as the data contains presence of species but not abundance. Sample dissimilarity was visualised in two dimensions through Principal Coordinates Analysis (PCoA) using the cmdscale function in the *stats* package (R Development Core Team, 2022). To test for differences in community composition between AVCs, we performed a permutational multivariate analysis of variance (PermAnova, Anderson, 2001) on a Jaccard distance matrix in the *vegan* package (Oksanen et al., 2019). This non-parametric test uses a dissimilarity coefficient (distance between variables) to test the significance of multiple response variables with a permutational approach (Anderson, 2014).

To determine how oribatid species were associated with habitats or combinations of habitats, indicator species analysis (Dufrêne and Legendre, 1997) was implemented using the *indicspecies* package (De Cáceres and Legendre, 2009). This analysis is independent of species abundance and based on IndVal (the asymmetric indicator value index measure), an a priori partitioning of sites that measures the association between within-species presence and site group, looking for the groups with the highest association value. The IndVal is based on two qualities: Specificity (A), the proportion of the species occurrences restricted to a site (here: habitat type or AVC); and Fidelity (B), proportion of sites where the species occurs (here: habitat type or AVC). IndVal scores are the square-root of the product of A × B, and range from 0 to 1, whereby the highest value indicates that a species is primarily or exclusively observed at all sites belonging to a group. Groups were defined according to AVC. We used the multipatt function with AVC as a grouping factor to create a list of species associated to AVCs or combinations of AVCs.

All statistical analyses were performed in R v. 4.2.1 (R Development Core Team, 2022) and all plots of oribatid mite data generated with package *ggplot2* (Wickham, 2016).

3. Results

3.1. Prevalence and diversity of oribatid mites

Oribatid mites were recorded in 591 out of 1076 samples where acarids were present. The prevalence of oribatid mites (i.e. the percentage of samples where oribatid mites were recorded) differed between AVCs and was greater in wooded and semi-natural classes (Table 1). The dataset contains a total of 137 oribatid species across 40 families (Supplementary Table S2), with individual samples ranging in species richness (1 to 17 species) and number of families (1 to 12 families). Within AVCs, total species recorded also ranged from 16 to 88 species, and 11 to 32 families (Table 1). There was a significant effect of AVC on mean species richness per core ($\chi^2 = 158.36$, df = 7, $p < 0.001$; Fig. 2). Pairwise comparisons indicated that species richness in AVC1 was significantly lower than AVC4–8 (all $p < 0.001$), species richness in AVC2 was significantly lower than AVC5–8 (all $p < 0.001$), species richness in AVC3 was significantly lower than AVC4–8 (all $p < 0.003$), species richness in AVC4 was significantly lower than AVC5–7 ($p < 0.01$) and species richness in AVC6 was significantly higher than AVC8 ($p = 0.009$) (Fig. 2; statistics for individual pairwise comparisons in Supplementary Table S3). There were significant non-linear relationships between species richness per core and organic matter content ($\chi^2 = 20.9$; $p < 0.001$), pH ($\chi^2 = 24.4$; $p < 0.001$) and their interaction ($\chi^2 = 28.9$; $p < 0.001$). Species richness per core increased steeply up to ~30 % organic matter, was greater at both lower and higher pH, and the regression surface showed a distinct peak that represented Infertile Grassland and Lowland Wooded samples with high pH (Supplementary Fig. S2).

Across all samples, the five most prevalent species were *Tectocepheus velatus* (131 records), *Malaconothrus monodactylus* (126 records), *Nanhermannia sellnicki* (108 records), *Oppiella* (*Oppiella*) *nova* (92 records) and *Punctoribates punctum* (73 records). There were 30 taxa recorded in only one AVC and 10 taxa recorded in only two AVCs (Supplementary Table S2).

3.2. Oribatid mite community composition

The PermAnova revealed significant compositional differences between AVCs ($F_{7,568} = 45.4$; $p = 0.001$; Fig. 3), where 35.9 % of the variation in oribatid mite community composition is explained by AVC. These results support clear oribatid mite community composition patterns associated to differences between habitat types. Distinctive communities are found for groups AVC1–3, corresponding to more intensively managed agricultural habitats (i.e., Crops & Weeds, Tall Grass & Herb, Fertile Grassland). The AVCs belonging to wooded habitats and those typically with organic soils (i.e., Lowland Wooded, Upland Wooded, Moorland Grass Mosaic, Heath & Bog) display greater overlap in similarities, reflected by the number of species shared by each community. The composition of Infertile Grass (AVC4) spans these previous two groupings (Fig. 3) and this likely reflects the varied nature of the habitat type, which can be represented in lowland and upland locations.

3.3. Indicator values

There were 55 oribatid species significantly associated with an individual AVC or sets of AVCs ($p < 0.05$) with IndVal statistics ranging from 0.187 to 0.548 (Table 2). A total of 20 oribatid mite species were associated with individual AVCs, including Fertile Grassland (2), Infertile Grassland (1), Lowland Wooded (11), Upland Wooded (4) and Heath & Bog (2), of which five were highly significant ($p = 0.001$; Table 2). Only one species, *Punctoribates punctum*, was associated with the two most disturbed habitats, Crops & Weeds (AVC1) and Tall Grass & Herb (AVC2), and this species had one of the overall highest indicator values.

Table 1
Descriptive sampling and oribatid mite community statistics for Aggregate Vegetation Classes (AVC). AVC1: Crops & Weeds, AVC2: Tall Grass & Herb; AVC3: Fertile Grassland; AVC4: Infertile Grassland; AVC5: Lowland Wooded; AVC6: Upland Wooded; AVC7: Moorland Grass mosaic; AVC8: Heath & Bog; prevalence represents the percentage of samples where oribatid mites were recorded.

	AVC1	AVC2	AVC3	AVC4	AVC5	AVC6	AVC7	AVC8
Number of samples (cores)	176	56	187	211	29	66	144	202
Prevalence in samples (%)	29.0	39.3	25.7	48.3	75.8	77.3	78.4	82.7
Total families recorded	12	11	16	30	32	27	29	27
Total species recorded	24	16	27	64	61	70	88	80
Total species records	78	37	84	311	123	274	492	632

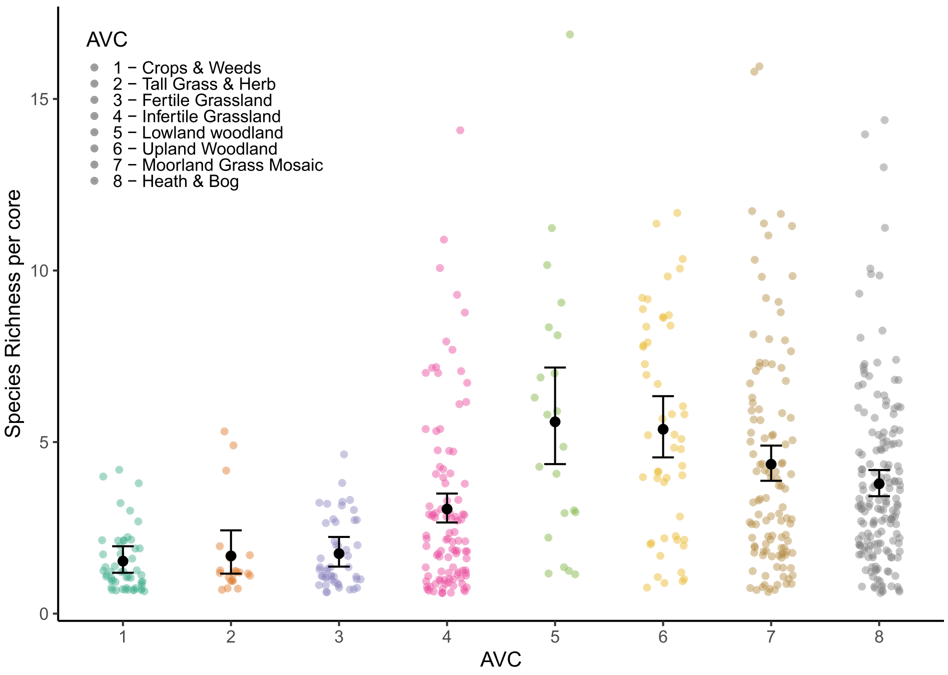

Fig. 2. Oribatid mite species richness per core in Aggregate Vegetation Classes (AVC). Black dots and error bars represent estimates and 95 % confidence intervals from GLM.

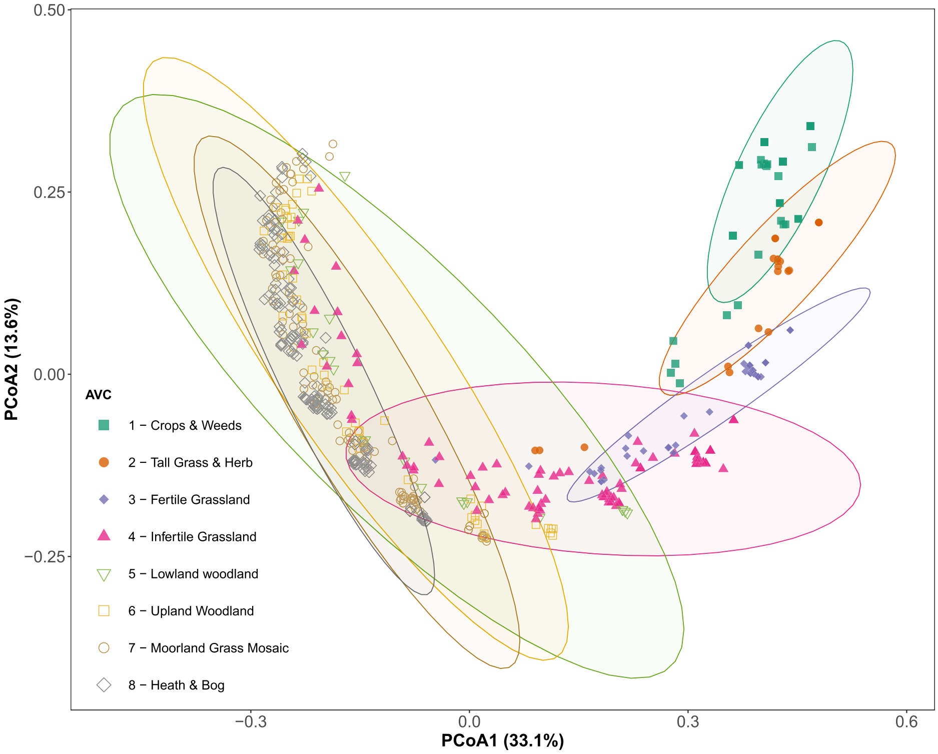

Fig. 3. Principal Coordinates Analysis (PCoA) of sample-by-species Jaccard dissimilarities by Aggregate Vegetation Classes (AVC). Ellipses represent 95 % confidence level.

However, *P. punctum* was recorded at lower prevalence across all AVCs, including 21 records from Infertile Grassland (AVC4; Supplementary Table S2). The oribatid mite species *Acrogalumna longipluma* and *Zachvatinibates quadrivertex* are associated with Fertile Grassland (AVC3) and *Nanhermannia nana* with Infertile Grassland (AVC4); however, these all have relatively low indicator values and numbers of records. Three species of those associated with Lowland Wooded (AVC5) had a highly significant indicator value (p = 0.001; *Atropacarus wandae*, *Eniochthonius minutissimus*, *Coronoquadroppia galaica*), with *A. wandae* having one of the highest indicator values (0.509). Upland Wooded (AVC6) had three species associated from the family Quadroppiidae (*Quadroppia* (*Quadroppia*) *maritalis*, *Quadroppia* (*Quadroppia*) *quadricarinata*,

Table 2

Oribatid mite species associations with Aggregate Vegetation Classes (AVCs) from IndVal analysis ($p < 0.05$).

Taxa	AVC1	AVC2	AVC3	AVC4	AVC5	AVC6	AVC7	AVC8	Stat	P	Total records
Malaconothrus monodactylus							×	×	0.548	0.001	126
Punctoribates punctum	×	×							0.544	0.001	73
Nanhermannia sellnicki					×	×	×	×	0.523	0.001	108
Atropacarus wandae					×				0.509	0.001	9
Tectocepheus velatus	×	×	×		×	×	×	×	0.499	0.001	131
Eniochthonius minutissimus					×				0.439	0.001	8
Quadroppia (*Quadroppia*) *maritalis*						×			0.435	0.001	36
Acrotritia duplicata					×	×			0.410	0.001	20
Minunthozetes semirufus		×		×			×		0.408	0.001	55
Oppiella (*Oppiella*) *nova*		×	×	×	×	×	×	×	0.406	0.034	92
Steganacarus (*Steganacarus*) *magnus*					×	×			0.395	0.001	19
Microppia minus		×	×	×	×				0.379	0.001	50
Ramusella clavipectinata	×		×	×	×				0.371	0.001	46
Liebstadia similis		×	×	×	×		×		0.359	0.016	67
Oppiella (*Rhinoppia*) *obsoleta*					×	×			0.358	0.002	48
Platynothrus peltifer			×	×	×	×	×	×	0.355	0.015	64
Scheloribates laevigatus		×	×	×	×				0.351	0.002	34
Suctobelbella subcornigera					×	×			0.342	0.001	30
Coronoquadroppia pseudocircumita						×			0.340	0.001	18
Banksinoma lanceolata			×		×	×	×	×	0.334	0.035	58
Carabodes willmanni						×		×	0.331	0.005	36
Phthiracarus affinis					×	×			0.324	0.003	22
Coronoquadroppia galaica					×				0.320	0.001	12
Berniniella sigma					×	×			0.316	0.004	15
Nothrus anauniensis					×	×			0.308	0.009	31
Pseudoprotoribates luxtoni					×				0.295	0.006	2
Mucronothrus nasalis								×	0.293	0.005	23
Tyrphonothrus sculptus								×	0.293	0.006	19
Dissorhina ornata					×		×		0.292	0.013	33
Oppiella (*Rhinoppia*) *subpectinata*					×	×	×		0.292	0.014	30
Suctobelbella falcata					×	×		×	0.291	0.005	29
Nanhermannia coronata							×	×	0.289	0.015	29
Ceratozetes gracilis		×		×	×	×	×		0.287	0.023	32
Suctobelbella similis					×	×	×	×	0.286	0.015	32
Chamobates schuetzi					×	×	×	×	0.285	0.015	29
Eupelops plicatus			×	×			×		0.284	0.021	29
Hypochthonius rufulus					×				0.283	0.005	13
Suctobelbella acutidens lobata					×	×			0.283	0.005	17
Phthiracarus globosus						×			0.278	0.007	9
Pilogalumna tenuiclava					×				0.267	0.009	4
Ctenobelba pectinigera					×				0.267	0.010	4
Multioppia neglecta			×	×	×				0.266	0.005	16
Sellnickochthonius zelawaiensis					×	×	×		0.264	0.006	17
Malaconothrus angulatus							×	×	0.260	0.015	19
Hermannia gibba					×	×			0.258	0.010	5
Euzetes nitens					×				0.256	0.012	4
Protoribates capucinus					×				0.255	0.007	5
Achipteria nitens					×				0.249	0.015	6
Nanhermannia nana				×					0.232	0.031	11
Carabodes labyrinthicus					×				0.230	0.032	3
Ophidiotrichus tecta					×	×			0.229	0.011	10
Quadroppia (*Quadroppia*) *quadricarinata*						×			0.223	0.030	9
Acrogalumna longipluma			×						0.202	0.012	2
Zachvatinibates quadrivertex			×						0.202	0.009	2
Damaeus (*Adamaeus*) *onustus*					×	×			0.200	0.014	3
Chamobates spp.							×		0.187	0.042	4

Coronoquadroppia pseudocircumita), with these species also being recorded in other habitats, particularly Moorland Grass Mosaic (AVC7) and Bog & Heath (AVC8). Eleven species were associated with the combined wooded habitats, with four being highly significant (*Acrotritia duplicata*, *Steganacarus* (*Steganacarus*) *magnus*, *Oppiella* (*Rhinoppia*) *obsoleta*, *Suctobelbella subcornigera*) and, as with the previous significant taxa, were recorded in Moorland Grass Mosaic (AVC7) and Heath & Bog (AVC8). The two species associated with Heath & Bog (AVC8) were *Mucronothrus nasalis* and *Tyrphonothrus sculptus*, both having the same indicator value (0.293; Table 2) and a small number of records in Infertile Grassland (AVC4) and Moorland Grass Mosaic (AVC7). Those associated with both Moorland Grass Mosaic (AVC7) and Heath & Bog (AVC8) were *M. monodactylus*, with the highest indicator value (0.548), and *Malaconothrus angulatus*, with fewer records and a lower indicator value (0.26; Table 2). Both *Tectocepheus velatus* and *Oppiella* (*Oppiella*) *nova* were associated with seven and recorded in all AVCs (Table 2, Supplementary Table S2). The number of samples with recorded presence in each AVC is presented in Supplementary Table S2 for all oribatid species.

Oribatid mites generally had a lower prevalence in samples taken from soils with up to 15 % organic matter content (up to approximately 8 % carbon content), and in soils with pH greater than 5 (Fig. 4). The prevalence of all individual oribatid mite species across the gradient of organic matter content and pH are presented in Supplementary Figs. S3 and S4, respectively.

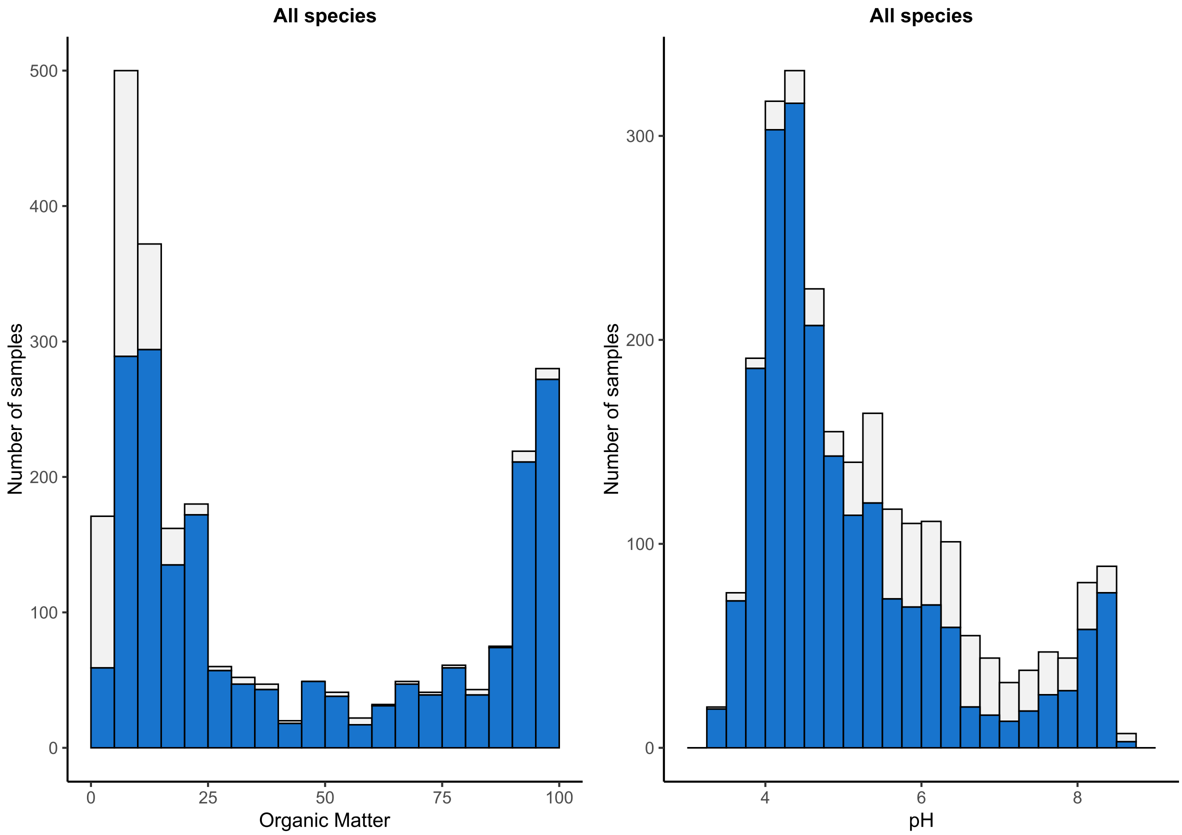

Fig. 4. Prevalence of all oribatid mites in invertebrate extractions across gradients of organic matter content (left) and pH (right). Light bars represent all samples with invertebrates extracted, overlaid dark bars represent extractions with oribatid mites recorded.

4. Discussion

The dataset of oribatid records from the Countryside Survey comes from the first systematic assessment of soil microarthropods across Great Britain. While the sampling was not designed with a focus on species-level characterisation of oribatid mites at a local scale, it has provided the ability to assess variability in oribatid species richness and community composition in different habitats (as defined by vegetation classes; AVCs) and across soil property gradients. These data enhance our fundamental understanding of the ecology and distribution of soil biodiversity across temperate habitats.

4.1. *Oribatid mite community metrics across temperate habitats*

This study highlights differences in oribatid mite prevalence, species richness and community composition across the habitat types. Oribatid mite prevalence, total family and species richness, and mean species per core were lower in the managed agricultural habitats (Crops & Weeds, Tall Grass & Herb, Fertile Grassland) and generally higher in wooded habitats and those typically with organic soils (Lowland Wooded, Upland Wooded, Moorland-Grass mosaic, Heath & Bog). Similar differences in oribatid mite community metrics across broad habitat types have been observed in Wales (George et al., 2017), Ireland (Arroyo et al., 2013) and at European level (Arroyo et al., 2005; Maraun and Scheu, 2000), and also elsewhere (Minor and Cianciolo, 2007; Lumley et al., 2023). It is likely these patterns are partly linked to levels of disturbance, with high disturbance (e.g., intensive agriculture) tending to reduce oribatid mite diversity and taxonomic closeness (Maraun et al., 2003; Tsiafouli et al., 2014). This comes as no surprise since land use intensification and associated management interventions are generally a catalyst for changes in ecosystem processes (de Vries et al., 2013), including a reduction of complexity in overall diversity and structure of agricultural soil food webs (Zhou et al., 2022). Land use type, particularly agricultural practices, can negatively impact soil properties such as moisture, organic matter content and pH, thus affecting oribatid diversity (Gergócs and Hufnagel, 2009). Silvicultural practices (e.g., site preparation, planting, harvesting) can also have detrimental effects on soil structure and organic matter, which in turn affects mesofauna density (Malmström et al., 2009; Rousseau et al., 2018) and diversity (Lindo and Visser, 2004; Rousseau et al., 2018). The magnitude of the effect of land use intensity, however, might vary between land uses and regions (Birkhofer et al., 2017).

In terms of sensitivity to disturbance, Maraun et al. (2003) found that Poronota, Enarthronota and Suctobelbidae were the most sensitive groups to mechanical disturbance, both in terms of natural disturbance (e.g., earthworm bioturbation) and anthropogenic, agricultural activities. This was mainly due to their K-strategy characteristics (producing fewer eggs with slow development), though differences in sensitivity between genera were also found. Within the superfamily Oppioidea, Suctobelbidae are more sensitive than Oppiidae, presumably due to the opportunistic feeding habits and parthenogenetic reproduction found in some Oppiidae species. Here, stress-tolerant species such as the ubiquitous *T. velatus* was found from disturbed environments (AVC1) to more natural habitats (AVC8), suggesting that it can be a bioindicator for stress gradient in ecosystems (Farská, 2015; Gulvik, 2007). Similarly, Maraun et al. (2003) found Desmonomata, and more specifically *Tectocepheus,* to be more tolerant to mid-level disturbance than any other group, believed to be due to their parthenogenetic reproduction. *Ramusella clavipectinata*, like *T. velatus*, is known to be tolerant to disturbance and here is associated with lowland mineral soils (AVC1, AVC3–5), but it was recorded in other habitats (Supplementary Table S2) and is known to show adaptability to different soil types (Murvanidze et al., 2013; Toschki et al., 2020).

Earlier results from the Countryside Survey show that Acari generally occurred at a higher frequency in the uplands and islands (> 95 %) in comparison to lowlands (89–93 %), and in more than 90 % of podzolic and peat soils (Black et al., 2003). Oribatid mite density is closely linked to soil type and habitat (Maraun and Scheu, 2000), and our results show how recorded oribatid communities are species poor in anthropogenic habitats (fewer than 30 species) when compared to more diverse communities associated with mull and moder soils characteristic of peaty and forested habitats (over 60 species). In managed plantation and woodland habitats with high soil organic matter, it is possible to find mite densities of up to or over 1 million per m^2 in podzol soil with raw humus, and a species richness of up to 62 species in a Finnish spruce forest with *Vaccinium myrtillus* (Hågvar, 2020). The overlap in communities from AVC5–8 in the first two axes of the PCoA suggests that soils with higher organic matter content house oribatid mite communities that are not completely distinct from each other. In fact, Barreto and Lindo (2024) suggest that peatlands (here in AVC8) may have a specific subset of species that are common to these ecosystems, but that in general species from drier ecosystems like forests (here AVC5–6) can be occasionally found in peatlands. The Countryside Survey data has also shown latitudinal gradients in oribatid species composition (aggregated at a 10 km × 10 km scale), with diversity increasing northwards and westwards in Great Britain associated with organic-rich soils such as peatlands which tend to be found in areas with colder winters and higher precipitation (Caruso et al., 2019).

4.2. Common and rare species

Here we list 137 species of oribatid mites for Great Britain, which represents 38 % of the species known for the region (Monson and Luxton, 2020) or 45 % of the species recorded for England (Luxton, 1996). Our recorded species richness is also lower than expected considering both the species-area relationship and species-latitude gradient present in Maraun et al. (2007).

One of the most common species in this study was the Desmonomata *T. velatus*, found in all AVCs (though with higher prevalence in organic soils AVC7 & AVC8); this is unsurprising with *T. velatus* being a parthenogenetic generalist species, distributed worldwide (Seniczak, 2020) and able to quickly colonise disturbed or early successional habitats (Ashwood et al., 2022; Norton and Behan-Pelletier, 2009). The other most common species was *Malaconothrus monodactylus,* recorded predominantly in Infertile Grassland, Moorland-Grass Mosaic, and Heath & Bog habitats. *Malaconothrus monodactylus* is associated with European alpine regions (Dirilgen et al., 2016), particularly bogs (Lehmitz, 2014); it is its hygrophilous nature that confers high prevalence in AVC7 & AVC8, being absent from the typically drier habitats (AVC2, AVC3 & AVC5). Two other species that were common in our dataset were *Nanhermannia sellnicki*, also with high prevalence in AVC7 & AVC8, and *Oppiella* (*Oppiella*) *nova* distributed across all AVCs. *Nanhermannia sellnicki* is a species usually found in drier habitats (Forsslund, 1958) and abundant in birch forests (Seniczak et al., 2023), which is not entirely in line with our results, although oribatid mites from drier habitats can be commonly found in wetter environments like bogs (Barreto and Lindo, 2024).

Organic soils in Heath & Bog (AVC8) housed unique species present in one or two samples such as: *Platynothrus punctatus*, a species recently redescribed and found in organic soils in Spain and Norway (Seniczak et al., 2022) but also North America (Behan-Pelletier and Lindo, 2019); *Camisia lapponica,* found in the interface between the base of the soil and the bedrock in Romania (Nae and Băncilă, 2017), *Sphagnum* mosses in Poland (Seniczak, 1991) and North America (Behan-Pelletier and Lindo, 2023); *C. solhoeyi,* found in Norway, Sweden, Poland and Austria (Colloff, 1993); *Cepheus latus* reported in Spain, Morocco and England (Bernini and Bernini, 1990), *Edwardzetes edwardsi* reported for England (Seyd, 1981) and Slovakia (Jászayová et al., 2022); *Liochthonius hystricinus*, found in North America (Behan-Pelletier and Lindo, 2023) and Korea (Bayartogtokh and Bae, 2023); *Phthiracarus montanus* reported for Spain (Pérez-Íñigo, 1969); *Serratopia* sp.; *Tyrphonothrus maior,* present in many *Sphagnum* locations worldwide (e.g., Barreto and Lindo, 2024; Minor et al., 2024; Seniczak et al., 2021) and *Zygoribatula exilis,* found in Greece (Gwiazdowicz et al., 2024) but also North America (Behan-Pelletier and Lindo, 2023).

Wooded habitats from AVC5&6 also had unique species present in only one or two samples including *L. sellnicki*, *Pseudoprotoribates luxtoni*, *Acrotritia ardua*, *Amerobelba decedens*, *Autogneta parva*, *Coronoquadroppia lesleyae*, *Hermanniella granulata*, *Liacarus* sp., *L. brevis*, *L. evansi*, *Machuella bilineata*, *Paratritia baloghi*, *Sellnickochthonius jacoti* and *Tritegeus bisulcatus*. Most of these species often occur in different managed habitats (e.g., Murvanidze et al., 2019) and natural habitats (e.g., Barreto and Lindo, 2021, 2024; Behan-Pelletier and Lindo, 2023).

4.3. Indicator taxa and links to soil properties

While we know that oribatid mite communities are influenced by land use and management (Behan-Pelletier, 1999; Birkhofer et al., 2017), and despite evidence for specialisation, species may show a high degree of adaptability in terms of soil type, vegetation, substrate and decomposition stage, allowing them to persist in different vegetation types and humus forms (Osler et al., 2006). It is therefore likely that many oribatid mite species are present and abundant across multiple habitat types. Indicator value analysis was undertaken to assess whether oribatid taxa were generally associated with particular habitats or sets of habitats.

A single species, *P. punctum*, was associated with Crops & Weeds and Tall Grass & Herb, indicating a tolerance of disturbance and a niche associated to the environment conditions in these habitat types; the distinctly greater prevalence of *P. punctum* at lower organic matter content values supported this (Supplementary Fig. S3). However, *P. punctum* has been found to be strongly associated to grass species and can become quite dominant in assemblages (Arroyo et al., 2015). Several other species, such as *Microppia minus* and *R. clavipectinata*, were more widely associated with agricultural habitat types, or possibly lowland mineral soils, with both being found across a wide range of soil pH and more prevalent at lower organic matter content (Supplementary Figs. S3 and S4); *M. minus* is a more generalist hygrophilous species often found in arable soils. The association of *Minunthozetes semirufus* with Tall Grass & Herb, Infertile Grassland and Moorland-Grass Mosaic habitat types indicates a link to unmanaged or extensively managed grass-dominated vegetation, and this was represented by a somewhat bimodal prevalence across soil pH and LOI gradients (Supplementary Figs. S3 and S4).

Stronger associations with wooded habitats were noted for several oribatid species, including *Atropacarus wandae*, *Eniochthonius minutissimus, Quadroppia (Quadroppia) maritalis*, *Acrotritia duplicata*, *Oppiella (Rhinoppia) obsoleta*, and *Steganacarus (Steganacarus) magnus*, though most of these taxa were recorded in other habitat types. *A. duplicata* had a greater prevalence in woodlands (AVC5&6), and has been found in Norway as a forest and tree-dwelling species (Seniczak et al., 2021) and dominating in deadwood (Skubała, 2016); *Acrotritia* juveniles can also practice endophagy (a particular case of saprophytic xylophagy) (Jacot, 1939). Similarly, *S. magnus* has been shown to play a role in decomposition processes in woodlands (Webb, 1991) and show strong fungivore preferences (Schneider and Maraun, 2005). *Eniochthonius minutissimus* is a fungivore in *Sphagnum* and forest litter/humus (Barreto and Lindo, 2021) that was associated in this study with Lowland Wooded (AVC5), though also recorded in Infertile Grassland (AVC4) and Moorland Grass Mosaic (AVC7). *Q. maritalis* was associated with Upland Wooded habitat (AVC6) but also had a large number of records from other organic soils (AVC7&8). The oribatid species with the highest IndVal statistic, *M. monodactylus*, was associated with Moorland-Grass Mosaic (AVC7) and Heath & Bog (AVC8) and this is reflected in the distinctively higher prevalence above ~75 % organic matter content (Supplementary Fig. S3); *M. monodactylus* was recorded in 29 % and 33 % of AVC7 and

AVC8 samples, respectively. *Nanhermannia sellnicki* had similarly high prevalence in the AVC7 and AVC8 habitat types at 23 % and 30 %, respectively. Strong links between these species and drier *Sphagnum* microhabitats has been shown in Barreto et al. (2023, 2024), and Barreto and Lindo (2021).

4.4. Study limitations

The sampling approach of the Countryside Survey was not aimed at exhaustively sampling oribatid mites (a single core was sampled from each plot), and the patterns of biodiversity may strongly depend on the available data and be influenced by sampling bias (Mumladze et al., 2017; Santos et al., 2008). Nonetheless, there is value in understanding if the sampling effort performed is sufficient to detect differences in oribatid communities due to changes in land use, which could differ per habitat (e.g., Minor and Cianciolo, 2007). In addition, the Countryside Survey oribatid mite data used here, although geographically complex, is from a single sampling event at each plot in 1998/99. Oribatid mites have been shown to change in population numbers seasonally (e.g., Pacek et al., 2020; Seniczak et al., 2019;), and seasonal variation has also been observed between different habitat types or microhabitats with regards to abundance, species richness and diversity (Gergócs et al., 2011).

The AVCs used in this study are, by definition, a clustering of 100 vegetation classes (Bunce et al., 1999), using TWINSPAN classification and DECORANA (Smart et al., 2016). We acknowledge that the AVC is a coarse type of classification and species-specific relationships between oribatid mites and plants have been demonstrated (Coulson et al., 2003; Noti et al., 1997; Santorufo et al., 2024). Here, vegetation data, associated with soil carbon and pH, has been used to explore patterns in oribatid communities across habitat types, but we also acknowledge other factors such as soil type (Minor and Cianciolo, 2007), litter type (Sylvain and Buddle, 2010), microhabitat (Barreto and Lindo, 2018), moisture (Minor et al., 2019) and land management (Behan-Pelletier, 1999) play an important role for oribatids communities.

4.5. Future directions

This study advances knowledge and understanding of the ecology and distribution of oribatid mites across temperate habitats in GB but also provides a good foundation to build on and to develop further research. Oribatid communities are strongly influenced by microhabitat variables such as litter quality, aboveground vegetation (Noti et al., 1997) and microclimate (soil moisture, temperature) (Gergócs et al., 2015; Lehmitz, 2014). Greater understanding could be gained from the oribatid species data in this study (and with synthesised oribatid data) if paired with more detailed information relating to land management and microhabitat. With oribatids spanning multiple trophic levels including decomposers, fungal feeders, scavengers and predators (Maraun et al., 2023; Schneider et al., 2004), linking oribatid mite data to existing specific knowledge on trophic status, trophic variation and process rates could also improve ability to quantify/model their role in soil functioning and the potential impacts of land management. In the UK, the National Biodiversity Atlas (https://nbnatlas.org/) contains hundreds of millions of species records, but only 200 records of Oribatida (excluding Astigmatina). Synthesising existing data for oribatid mites would provide basis for a more robust mapping of records to reveal distribution patterns of oribatid species across GB and present opportunities to feed into European and international initiatives.

One of the main drawbacks on soil biodiversity research is the lack of public knowledge with consequent absence of soil biodiversity in the political agenda (FAO et al., 2020; Farfan et al., 2024). Large initiatives such as the International Network on Soil Biodiversity (NETSOB – Eugenio et al., 2024), the Global Soil Biodiversity Initiative (GSBI) and the Soil Biodiversity Observation Network (Soil BON) recognize the need for studying soil biodiversity and including it in policies at the global level (Barreto et al., 2025). Greater public awareness, coupled with more detailed soil biodiversity data and mapping, as presented here, should support the establishment and delivery of key policy targets regarding soil biodiversity conservation and management.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106471.

CRediT authorship contribution statement

Ainoa Pravia: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization. **Carlos Barreto:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization. **Frank Ashwood:** Writing – review & editing, Conceptualization. **Aidan Keith:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization.

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.

Acknowledgements

We thank Forest Research statistician Toni Clarke for advice and troubleshooting with analyses, Frank Monson for the identification of oribatid mite species, and everyone involved in the fieldwork and laboratory processing of Countryside Survey samples in 1998/99. AK was supported by the Natural Environment Research Council (NERC) award number NE/Y006208/1, as part of the programme delivering National Capability.

Data availability

The data used are available via the Environmental Information Data Centre (https://eidc.ac.uk/): oribatid mites (Keith et al., 2018; https://doi.org/10.5285/05cae9ae-86c4-4a2f-a628-6c7fd0882459), plant species data used to produce aggregate vegetation classes (https://doi.org/10.5285/07896bb2-7078-468c-b56d-fb8b41d47065), soils data (Black et al., 2016; https://doi.org/10.5285/9d1eada2-3f8b-4a7b-a9b0-a7a04d05ff72).

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