Microhabitat heterogeneity enhances soil macrofauna and plant species diversity in an Ash - Field
Maple woodland

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Abstract

The high biodiversity of soil ecosystems is often attributed to their spatial heterogeneity at multiple scales, but studies on the small-scale spatial distribution of soil macrofauna are rare. This case study of an Ash-Field Maple woodland partially converted to conifer plantation investigates differences between species assemblages of soil and litter invertebrates, and plants, using multivariate ordination and indicator species analysis for eleven microhabitats.

Microhabitats representing the main body of uniform litter were compared with more localised microhabitats including dead wood and areas of wet soil. Species accumulation curves suggest that for this site it is more efficient to sample from varied microhabitats of limited spatial scale rather than the broad habitat areas when generating a species inventory. For comparative work sampling the main body of uniform litter is more appropriate, given that microhabitats vary from woodland to woodland and would make standardisation problematic.

Vegetation showed more distinctive microhabitat-specific species assemblages than soil and leaf litter invertebrates and was strongly associated with environmental variables. Microhabitats with distinct assemblages included dead wood habitats, which had a high proportion of saproxylic

species; a highly disturbed microhabitat with distinct plant and soil species characteristic of ruderal habitats and seeps with earthworm species rarely sampled in standard soil biodiversity surveys.

The leaf litter in the conifer plantation area was species poor and the biodiversity quantified was considerably enhanced by the sampling from the additional microhabitats - illustrating the importance of small-scale heterogeneity for increasing plant and soil macrofauna biodiversity at this site.

Keywords

Soil biodiversity; plant biodiversity; multivariate ordination; small-scale heterogeneity; woodland

1. Introduction

Soils are among the most important sources of ecosystem services, providing goods and functions beneficial to human populations, including supporting the majority of food production, regulating water quality and supply, buffering against floods and droughts and participating in carbon and nutrient cycling [1,2]. Soils have a high level of biodiversity, representing 23% of described organism diversity [3], in some ecosystems soil biodiversity may outnumber above ground biodiversity [2,4].

Spatial and temporal heterogeneity at multiple scales is a clear influence on soil biodiversity, with well-established differences in soil fauna from contrasting mull and mor forest soils [5] and habitat types [6,7]. On a smaller spatial scale tree species diversity has been found to influence earthworm density [8] and the presence of dead wood is positively correlated with soil arthropod abundance and diversity [9].

Previous studies [6,7] sampled the main microhabitat of uniform leaf litter and the soil beneath it, avoiding major sources of micro-heterogeneity such as dead wood and wet soil. This study investigates diversity patterns of soil macrofauna and plants at a smaller spatial scale, using Winkler

bag extraction of leaf litter, soil pits and plant quadrats within a single woodland to survey eleven microhabitats.

2. Materials and Methods

2.1 Site description

The surveys were carried out in two adjoining woodlands, Timber Copse and Greatmead Copse (50°43'46.59''N, -1°15'5.10''E), on the Isle of Wight, an island off the coast of Hampshire, southern England. The island is one of the most southerly parts of the UK and has a temperate climate (Köppen-Geiger classification Cfc) [10] with an annual mean maximum temperature of 14.5°C, and a minimum of 8.2°C, and with a mean annual precipitation of approximately 700mm (30 year average) [11]. The study site comprises 7.7 hectares of privately owned mixed coniferous and deciduous woodland, part of a 60 hectares complex of woodlands in the North East of the Island comprising the North-eastern Woods Isle of Wight Biodiversity Opportunity Area, which is also a Site of Importance for Nature Conservation [12]. The site is 20 m above sea level, bordered by deciduous woodland and pastureland with a small stream along the Western edge. The soils are fertile, seasonally waterlogged clays and loams [13] the underlying geology comprising Palaeogene clays, silts and sands of the Hamstead Beds and calcareous mudstones of the Bembridge Marls Formation [14]. The site is classified as ancient replanted woodland, defined as continuous woodland cover since at least 1600 AD but where the original native tree cover has been replaced by planting [15]. In this case the previous crop of oak (*Quercus* L.) was harvested in the 1950s with Timber Copse replanted with 3.9 hectares Western Red Cedar (*Thuja plicata* Donn ex D.Don 1824) and 0.3 hectares Norway Spruce (*Picea abies* (L.) H.Karst 1881) in 1964 (Forestry Commission, unpublished). Greatmead Copse was not replanted and has regenerated naturally with a community approximate to National Vegetation Classification (NVC) Woodland 8 *Fraxinus excelsior* - *Acer campestre* - *Mercurialis perennis* woodland [16].

2.2 Sampling regime

The study site comprises two broad habitats, 4.2 hectares of coniferous plantation (with some regrowth of deciduous species) (*con*) in Timber Copse and 3.5 hectares of deciduous woodland (*dec*) in Greatmead Copse. An initial survey identified 12 *microhabitats* which covered a sufficient area for a sample size of six 1m² quadrats, one of which (*streamside*) had no macrofauna, the 11 sampled are described in Table 1.

Microhabitats were classified into *standard* or *additional*. *Standard* microhabitats comprised the main body of uniform leaf litter and the soil beneath; *additional* microhabitats were those of small spatial extent – representing sources of micro-heterogeneity.

2.3 Sampling methods

Sampling was carried out during May 2013 over four sampling periods, each a week apart, with 6-7 replicate samples from each microhabitat. Each replicate consisted of a 1m² quadrat, which for the deadwood microhabitats included a stump or log. All the stumps sampled were from trees felled in the 1950s so were of uniform size and decay stage, logs were in decay class III [17] and were selected on the basis of similar size (0.5-1.0 m length). Every effort was made to stratify sampling spatially and temporally to minimise variability due to weather differences and temporal effects.

Environmental variables and a vegetation survey were carried out in each 1m² quadrat and macrofauna were sampled using two methods: hand sorting of soil pits and Winkler bag extraction of leaf litter. Pitfall trapping was not used since that sampling method is strongly biased towards groups which actively move on the surface [18] and is therefore unsuitable for a small spatial scale project, as it is likely to record arthropods originating from outside the microhabitat.

2.3.1 Vegetation survey

This was carried out in the same 1m² quadrat used for the macrofauna surveys; the presence or absence of plant species was recorded at ground level, the understory (up to 2 m height) and canopy (above 2 m height), assuming a three dimensional 1 m² quadrat extended up into the canopy. Species level identifications, including grasses, sedges and conspicuous mosses, were possible for most quadrats.

2.3.2 Environmental variables

Soil moisture was measured using a Delta-T Moisture meter with an attached SM200 moisture sensor (Delta-T Devices, Cambridge, England) recorded as % moisture filled space. Soil temperature was measured with a dial soil thermometer (Electronic Temperature Instruments Ltd., Worthing, England) and pH using an analogue Westminster Deluxe Soil pH Meter (West Meters Ltd., Manchester, England). Measurements were made at 10 cm depth with the probe placed in the centre of each 1m² quadrat, or in the case of logs and stumps as close to the wood as possible. Nearly half the soil temperature and pH measurements were not made due to equipment failure; values generated by random *k*-nearest-neighbour imputation were substituted in those cases using the *MissingDataGUI* 0.2-0 package [19] in R 3.1.0 [20].

2.3.3 Leaf litter

For each microhabitat, with the exception of seeps (where litter was absent), leaf litter and the loose uppermost topsoil from each 1m² quadrat was sieved using a 1cm² mesh and hung in Winkler bags for three days. The method was modified for logs and stumps with leaf litter being sieved from on, underneath and the area immediately adjacent to the wood to limit sampling to macrofauna living in close proximity to the wood rather than the surrounding leaf litter. Extracted invertebrates were preserved in 80% Industrial Methylated Spirits.

2.3.4 Soil pits

With the exception of stumps, where digging a pit was impossible, a 25 x 25 x 10 cm (deep) soil pit was dug in the centre of each 1m² quadrat and invertebrates hand sorted into 80% Industrial Methylated Spirits. For logs the pit was dug directly underneath after it had been rolled over and the leaf litter had been sieved.

2.4 Soil and litter macrofauna identification

Adult specimens were counted and identified to species in seven major clades. Ants were identified using Skinner [21], harvestmen with Hillyard [22], centipedes with Barber [23], millipedes with Blower [24], woodlice with Hopkin [25] and earthworms with Sherlock [26]. For beetles it was possible to identify true and broad-nosed weevils (Morris [27,28]), ground beetles (Luff [29]), leaf beetles (Hubble [30]), throscids (Telfer [31]) and rove beetles (except subfamilies Aleocharinae and Tachyporinae) (Lott and Anderson [32], Lott [32] and Tottenham [33]). Analyses were conducted on the combined datasets rather than sub-analyses of individual clades as this provides the most complete model for biodiversity [6] and avoids difficulties with analysing clades with only a few species.

2.5 Statistical analysis

A summary of the total number of species found across the study site was calculated by simply combining the data from each sampling method and calculating how many species from each taxonomic group were sampled in total. For statistical analysis the data from each sampling method (i.e. soil, litter and vegetation) were analysed separately since sampling effort is not directly comparable between the methods.

2.5.1 Indicator species

Indicator species analysis was performed to determine if any species were associated to a particular microhabitat or combination of microhabitats. This was executed using the *indicspecies* 1.6.7

package [34] in R 3.1.0 [20] using the *multipatt* command (with *func* = “*IndVal.g*”, all habitat combinations considered). This function calculates an Indicator Value based on the predictive value of a species for the microhabitat it was found in (specificity) and the probability of finding it a different microhabitat (fidelity). A permutation test was run using *nperm* = 999 to test the statistical significance of the calculated indicator values, species with an *IndVal.g* association index significant at $P < 0.05$ are considered to be indicator species.

2.5.2 Species accumulation curves

Species accumulation curves were constructed for total, standard and additional microhabitats using the *vegan* 2.2-1 package [35] in R 3.1.2 [20] using the *specaccum* command (with *method*= “rarefaction”). This presents the accumulation of species as the number of individuals sampled increases, visualising any extra diversity sampled using the additional microhabitats compared with the standard ones.

2.5.3 Ordinations

Data for the vegetation survey, soil pit and leaf litter invertebrates were analysed separately using CANOCO 5.02 [36] with all environmental variables included to provide the most complete model. Constrained ordination was used with response data as log-transformed species and explanatory variables as the environmental variables (temperature, pH and moisture) and microhabitats. The significance of each ordination was tested using Monte Carlo permutation tests with 999 unrestricted permutations. Each permutation randomly re-shuffles the environmental variables while the species data is fixed, producing a null hypothesis model. The value of the test statistic (pseudo-F value) produced from the original data was compared with the distribution of the null hypothesis model and a p-value for each environmental variable computed based on how often the pseudo-F value of data is more extreme than obtained from the null hypothesis model [37].

The vegetation survey was in the form of presence-absence data so a unimodal method (Canonical Correlation Analysis, CCA) was used as per CANOCO Advisor. The initial Detrended Correspondence Analysis (DCA) automatically run by CANOCO Advisor found the gradient for the soil pit dataset to be 6.1 standard deviation (SD) units long so a unimodal method (CCA) was used to analyse the data. For the leaf litter dataset the presence of samples with no target species meant that CCA was unsuitable [37] so a linear method, Redundancy Analysis (RDA) was used. To ensure the uneven sampling effort between the microhabitats did not influence the ordination results, analyses were re-run 20 times with one of the unbalanced microhabitats (*moss* and *decstump*) removed at random. Comparison with results of the complete dataset showed the effect of the additional samples to be very small.

Co-Correspondence Analysis (CoCA) was used to investigate the relationship between plant and macrofauna communities as CCA was unsuitable due to the number of individual plant species being much larger than the number of sites [38].

3. Results

Table 2 provides a summary of environmental variables for each microhabitat. A total of 1227 macrofauna individuals were sampled across all samples and methods, 62% were in the target groups (80% of soil pits total, 52% of leaf litter total). Major non-target groups were true flies, spiders and beetle larvae. Of the target groups 757 individuals in 62 species were identified, comprising 26 beetle, nine centipede, five harvestmen, three ant, eight earthworm, four millipede and five woodlice species. There were 45 species of ground flora, 11 understory and eight canopy species across all samples. The vegetation dataset showed the strongest preponderance of indicator species which was especially notable in the bluebell, power line and path microhabitats which had three plant indicator species each (Table 3). The four indicator species in the leaf litter dataset were in microhabitat groups containing deadwood and are all known saprophages. The soil pit method also produced four indicator species, three earthworms and one centipede. For all three sampling

methods the accumulation curves (Figure 1) for the additional microhabitats are the steepest, accumulating species more rapidly than the standard microhabitats.

3.1 Ordinations

3.1.1 Vegetation

Explanatory variables accounted for 33.2% of variation with the CCA (Figure 2 and Figure S1) showing a clear split between plantation and deciduous habitats on axis 1 and 2, both variables having a highly significant association with species composition (Table 4). There were strong compositional differences between deciduous and plantation microhabitats in the vegetation dataset with the mixed litter microhabitat directly underneath the conifers particularly species poor. The power line samples were warm and wet with vegetation that was strikingly different from the rest of the woodland, with Water Figwort (*Scrophularia auriculata* L.), Marsh Thistle (*Cirsium palustre* (L.) Scop.), Enchanter's Nightshade (*Circaea lutetiana* L.), and Guelder Rose (*Viburnum opulus* L.) tightly clustered with the power line samples in the ordination (Figure 2), the last three being indicator species for that microhabitat. Soil temperature and moisture, and all but the three deadwood microhabitats were significantly associated with species composition (Table 4). The standard deviation envelopes of the canonical correspondence analysis of the standard microhabitats is much narrower than that of the additional microhabitats (Figure 3 and Figure S2). Co-correspondence analysis of the vegetation and macrofauna data sets showed no significant correlation between the axes (leaf litter first axis $P = 0.309$, all axes $P = 0.065$, soil pits first axis $P = 0.205$, all axes $P = 0.044$), indicating that the soil and litter macrofauna and vegetation communities cannot be predicted from one another and have different gradients, so are not responding in the same way to the environmental variables.

3.1.2 Soil pits

Explanatory variables accounted for 30.7% of variation and the CCA (Figure 4) shows some overlap between the microhabitat types. The mixed litter microhabitat which was depauperate in the soil pit fauna compared to the other microhabitats appears as an outlier. Microhabitats found to have a significant association with species composition were the power line ($P = 0.008$) and seeps in the plantation area ($P = 0.019$), where most of the indicator species for this sampling method were found (Table 3). Temperature was the only abiotic variable found to have significant effect on soil pit fauna ($P = 0.023$) although the earthworms tend to be low on axis 1 in the wetter microhabitats and woodlice higher on the axis in the drier ones. The canonical correspondence analysis shows a larger standard deviation envelope for the additional than the standard microhabitats, although there was some overlap (Figure 5). There was no significant difference between deciduous and plantation woodland for the soil pit invertebrates.

3.1.3 Leaf litter

Explanatory variables accounted for 42.8% of variation, with most variation explained by the separation of dead wood microhabitats (logs and stumps) on axis 1 (Figure 6). These microhabitats are associated with the saproxylic weevil *Acalles ptinoides* (Marsham, 1802), most woodlice species and millipedes, although only in stumps was this association significant (Table 3). These deadwood microhabitats also largely accounted for the greatly expanded envelope for the additional microhabitats compared with the standard ones (Figure 7). Bluebells and power line microhabitats were the only others with significant association with species composition. Unlike the soil pit fauna and vegetation temperature was not found to have a significant effect but moisture did (Table 5). The leaf litter invertebrates showed fewer compositional differences between deciduous and plantation microhabitats than the plant communities.

4. Discussion

In common with many Ash - Field Maple woodlands (National Vegetation Classification W8) [39], overall plant species diversity for the site was high. Numbers of individuals and species of leaf litter invertebrates, particularly beetles, were fewer than in many woodlands previously sampled by the Natural History Museum Soil Biodiversity Group; although the results are comparable to other Ash - Field Maple woodlands (Soil Biodiversity Group, unpublished data). This is probably due to the relatively low litter depth in Ash - Field Maple woodlands [39], ash litter has a low phenol content and is fed on preferentially by earthworms [8], often being incorporated into the soil before spring.

4.1 Species composition between microhabitats

The ivy microhabitat had no significant species associations for any of the datasets and no strong indicator species; in contrast, the bluebell microhabitat had a considerable influence on vegetation. This may be because the ivy-dominated areas are characteristic of secondary regrowth [39] and therefore have a more variable species composition than the presumably longer-established bluebell flora. The centipede *Stigmatogaster subterraneus* (Shaw, 1789) was found to be an indicator species for the bluebell microhabitat but there is little published information on the ecology of the species so it is unknown whether this is a genuine association.

The litter underneath the conifers was extremely poor in both plant and soil pit invertebrate species, and the microhabitat was as an outlier in both ordinations. This microhabitat was very dry, which probably explains the lack of soil fauna; the only species close to the samples on the ordination was *Geophilus easoni* Arthur et al., 2001 - a centipede associated with heathland [6,23] and so probably particularly tolerant of desiccation. Vegetation is likely inhibited by the dense shade of the conifers, the only common inhabitant being ash *Fraxinus excelsior* L. seedlings, known to persist in shade [40]. The leaf litter invertebrates did not have a significantly different species composition from the other microhabitats, although the group mixed litter and deciduous stumps had the rove beetle *Micropeplus staphylinoides* (Marsham, 1802) as an indicator species, which is associated with decaying vegetation [33,41].

Although the presence of deadwood can influence floral composition in Ash-Field Maple woodland [39] there was no evidence of this occurring on the relatively small scale of this study, stump and log microhabitats having no significantly differentiated plant species composition. Soil pit invertebrates also did not differ in composition in the deadwood microhabitats but leaf litter invertebrates were strongly differentiated, with a striking separation between those microhabitats (all of which had low pH and moisture values) and the other microhabitats. Most of the species sampled are associated with these microhabitats on the ordination and unsurprisingly many of these are saproxylic. The weevil *Acalles ptinoides* (Marsham, 1802) emerged as an indicator species for stumps within the plantation and was surprisingly only found once in the deciduous woodland; despite being commonly found in other broadleaved woodlands (Soil Biodiversity Group unpublished data). This species is stated as feeding on, and developing in twigs and confined to primary woodland [42], but from these data it appears adults at least may be able to feed on larger pieces of decaying wood and are not confined to deciduous woodland. Myriapods were also associated with stumps on the ordination although none emerged as indicator species; *Cylindroiulus punctatus* (Leach, 1815) is particularly associated with decaying wood, as are the centipedes *Geophilus truncorum* Bergsoë & Meinert, 1886 and *Lithobius variegatus* Leach, 1813 [43]. Despite earthworms being more associated with areas of high pH and moisture content *Lumbricus rubellus* Hoffmeister, 1843, is correlated with stumps, this species exhibits tolerance to low pH and has a preference for areas with high organic content and has previously been noted as occurring within dead wood [44]. The strong influence of deadwood on isopods is well established [45,46] although in this study *Philoscia muscorum* (Scopoli, 1763) was an exception, as it has a preference for more open grassy areas [25].

The coniferous seeps are distinct from the other microhabitats and unsurprisingly are associated with earthworms, which are moisture-sensitive [47]. Notably many of the commonest earthworms in this study were rare in previous studies e.g. *Eiseniella tetraedra* (Savigny, 1826), because of their preference for rarely-sampled wet soil microhabitats [47]. A different composition of plant species was associated with seeps, although not as markedly as for the soil fauna. Stinging nettle (*Urtica*

dioica L.) was an indicator species for the deciduous seeps/power line group of microhabitats suggesting these areas are particularly eutrophic [48] and may be subject to run-off from the neighbouring pastureland.

The power line microhabitat had a distinctive flora with species characteristic of moist and often disturbed sites [39], consistent with frequent disturbance from the coppicing in this area. There was also a significant association with soil fauna although the separation on the ordination was not as striking. The earthworm *Murchieona muldali* (Omodeo, 1956), was an indicator species for this microhabitat. It, like many of the plants, appears to be a ruderal species, having previously been found abundantly in field margins [26]. The power line had a less distinctive leaf litter invertebrate assemblage with the fewest species and individuals of all the microhabitats, probably because of the sparse litter in this microhabitat.

Comparison of standard and additional microhabitats

For all three sampling methods the additional microhabitats accumulated species more rapidly than the standard microhabitats alone, and in the case of the plants and leaf litter invertebrates, slightly more than the total dataset. This suggests that for generating a species inventory, at least for this woodland, it is more efficient to sample from varied microhabitats of limited spatial scale rather than the broad habitat areas. However they would be less suitable for comparative work as the 'standard' microhabitats are found in all woodlands while the number and types of 'additional' microhabitats varies from woodland to woodland and would make standardisation problematic. It also illustrates the importance of small scale heterogeneity for plant and soil macrofauna biodiversity, particularly for the plantation area where the poor diversity of the standard microhabitat (*mixed litter*) meant that biodiversity quantified was considerably enhanced by the sampling from the additional microhabitats. The sampled biodiversity of the deciduous woodland is also increased by the inclusion of microhabitats, largely due to the stumps which provide a habitat for leaf litter invertebrates within an environment with generally sparse leaf litter.

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446

Table 1 Descriptions of microhabitats surveyed. ^s ‘standard’ microhabitats, all others are ‘additional’ microhabitats

Table 1

Microhabitat	Code	Description
Mixed litter ^s	conmixlit	Mixed litter from under plantation of 50 year old plantation of <i>Thuja plicata</i> and/or <i>Picea abies</i> interspersed with regrowth of mixed broadleaf species
Logs	conlog	Leaf litter from under and periphery of logs within plantation
Moss	conmoss	Near continuous ground bryophyte layer, dominated by dominated by <i>Thuidium tamariscinum</i> (Hedw.) Schimp. 1852 and <i>Kindbergia praelonga</i> (Hedw.) Ochyra 1982
Path	conpath	3m wide, 350m long path through Timber Copse. Diverse and variable ground flora but little understorey. <i>Fraxinus excelsior</i> L. and <i>Acer campestre</i> L. dominant in canopy.
Seeps (coniferous)	conseep	Very small, shallow water bodies flowing through conifer plantation
Stumps (coniferous)	constump	<i>Quercus</i> L. sp. stumps under conifer plantation
Bluebell woodland ^s	decblue	Woodland with <i>Hyacinthoides non-scripta</i> (L.) Chouard ex Rothm. 1944 dominant ground flora
Ivy woodland ^s	decivy	Woodland with <i>Hedera helix</i> L. dominant ground flora

Power line	decpower	0.01 hectare area of deciduous woodland coppiced every 2-3 years due to presence of power line
Seeps	decseep	Very small, shallow water bodies flowing through deciduous woodland
Stumps	decstump	<i>Quercus</i> L. sp. stumps in deciduous woodland

Table 2 Microhabitats surveyed with mean values for pH, moisture and temperature $\pm$ standard error of the mean ^s ‘standard’ microhabitats, all others are ‘additional’ microhabitats

Table 2

Microhabitat	Code	Soil pH	Moisture (%)	Temperature (°C)
Coniferous woodland				
Mixed litter ^s	conmixlit	6.17±0.07	15.40±3.54	7.17±0.52
Logs	conlog	6.33±0.08	22.00±4.42	9.50±0.43
Moss	conmoss	6.00±0.11	38.62±6.34	6.63±0.68
Path	conpath	6.42±0.10	39.30±3.59	9.75±0.32
Seeps	conseep	6.19±0.12	44.75±4.15	7.13±0.90
Stumps	constump	6.42±0.17	16.20±4.69	8.13±0.57
Deciduous woodland				
Bluebell woodland ^s	decblue	6.19±0.24	23.00±1.69	9.50±0.13
Ivy woodland ^s	decivy	6.67±0.07	32.45±1.62	10.75±0.06
Power line	decpower	6.50±0.00	43.72±5.10	11.50±0.13
Seeps	decseep	6.17±0.09	37.23±2.74	10.00±0.26
Stumps	decstump	6.63±0.09	27.50±5.09	10.33±0.17

Table 3 Indicator species associated to fewer than four microhabitats using the *indicspecies* package in R
Significance codes: ‘***’ 0.01 ‘*’ 0.05 ^s ‘standard’ microhabitats, all others are ‘additional’ microhabitats

Table 3

Microhabitat(s)	Strata	Species
Mixed litter ^s + deciduous stumps	Winkler	<i>Micropeplus staphylinoides</i> *
Coniferous stumps	Winkler	<i>Acalles ptinoides</i> **
Coniferous seeps + ivy ^s	Soil pit	<i>Lumbricus rubellus</i> **
Coniferous seeps + path + bluebells	Soil pit	<i>Aporrectodea caliginosa</i> **
Logs + stumps	Winkler	<i>Oniscus asellus</i> **
Logs + stumps + moss + path	Winkler	<i>Trichoniscus pusillus</i> agg.**
Bluebells ^s	Soil pits	<i>Stigmatogaster subterraneus</i> **
	Vegetation	<i>Hyacinthoides non-scripta</i> **
		<i>Corylus avellana</i> (in canopy)**
		<i>Geranium robertianum</i> *
Power line	Soil pits	<i>Murchieona muldali</i> **
	Vegetation	<i>Circaea lutetiana</i> **
		<i>Cirsium palustre</i> **
		<i>Viburnum opulus</i> (in understory)**
Power line + path	Vegetation	<i>Rumex sanguineus</i> *
Power line + deciduous seeps	Vegetation	<i>Urtica dioica</i> **
Path	Vegetation	<i>Ajuga reptans</i> **
		<i>Viola riviniana/reichenbachiana</i> *
		<i>Filipendula ulmaria</i> *
Moss + path	Vegetation	<i>Thuidium tamariscinum</i> **

Table 4 Significant independent effects of individual explanatory variables (pH, temperature, moisture and microhabitat) on plant species distribution

Table 4

Environmental variables	Pseudo-F	P
Temperature	3.4	0.004
Moisture	2.0	0.003
Microhabitats		
Plantation	4.5	0.001
Mixed litter	2.1	0.004
Moss	1.9	0.012
Path	2.3	0.001
Seeps	1.6	0.052
Deciduous	4.5	0.001
Bluebells	2.7	0.001
Power line	4.6	0.001
Seeps	1.7	0.043

Table 5 Significant independent effects of individual explanatory variables (pH, temperature, moisture and microhabitat) on distribution of species extracted from leaf litter

Table 5

Environmental variables	Pseudo-F	P
Moisture	4.5	0.002
Microhabitats		
Plantation	3.4	0.013
Stumps	13.6	0.001
Deciduous	3.4	0.013
Bluebells	2.0	0.047
Power line	2.5	0.037
Stumps	2.5	0.034

Figure 1 caption

Figure 1 Species accumulation curves for total, standard and additional microhabitats for a) vegetation b) soil pits c) leaf litter, envelopes represent standard deviation

Figure 1

b) Vegetation

a) Soil pits

c) Leaf litter

Microhabitat type

- Total
- - - Additional
- . . . Standard

Figure 2 caption

Figure 2 CCA triplot of vegetation data. Habitat abbreviations as in Table 1. 24 best fitting species only included for clarity (see supplementary materials for complete figure) abbreviations as follows prefix *gp*-ground, *up*-understory, *cp*-canopy, *ACEcam*-*Acer campestre*, *BETsp*-*Betula* sp., *BRAsyl*-*Brachypodium sylvaticum*, *CIRlut*-*Circaea lutetiana*, *CIRpal*-*Cirsium palustre*, *CORave*-*Corylus avellana*, *CORSan*-*Cornus sanguinea*, *EUOeur*-*Euonymus europaea*, *FRAexc*-*Fraxinus excelsior*, *GALapa*-*Gallium aparine*, *GERrob*-*Geranium robertianum*, *HEDhel*- *Hedera helix*, *HYCscri*- *Hyacinthoides non-scripta*, *MERper*-*Mercurialis perennis*, *RUBfru*- *Rubus fruticosus* agg., *RUMsan*-*Rumex sanguineus*, *SALsp*- *Salix* sp., *SCRaur*- *Scrophularia auriculata*, *STEhol*- *Stellaria holostea*, *THUtam*-*Thuidium tamariscinum*, *THUpli*-*Thuja plicata*, *URTdio*-*Urtica dioica*, *VERmon*-*Veronica montana*

Figure 2

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Figure 3 CCA triplot of vegetation data with maximum enclosing polygons for *standard* and *additional* microhabitats. Habitat abbreviations as in Table 1. 24 best fitting species only included for clarity (see supplementary materials for complete figure) abbreviations as follows prefix *gp*-ground, *up*-understory, *cp*-canopy, ACEcam-*Acer campestre*, BETsp-*Betula* sp., BRAsyl-*Brachypodium sylvaticum*, CIRlut-*Circaea lutetiana*, CIRpal-*Cirsium palustre*, CORave-*Corylus avellana*, CORSan-*Cornus sanguinea*, EUOeur-*Euonymus europaea*, FRAexc-*Fraxinus excelsior*, GALapa-*Gallium aparine*, GERrob-*Geranium robertianum*, HEDhel- *Hedera helix*, HYCscri- *Hyacinthoides non-scripta*, MERper-*Mercurialis perennis*, RUBfru- *Rubus fruticosus* agg., RUMsan-*Rumex sanguineus*, SALsp- *Salix* sp., SCRAur- *Scrophularia auriculata*, STEhol- *Stellaria holostea*, THUtam-*Thuidium tamariscinum*, THUpli-*Thuja plicata*, URTdio-*Urtica dioica*, VERmon-*Veronica montana*

Figure 3

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Figure 4 CCA triplot of soil pit data. Microhabitat abbreviations as in Table 1. Species abbreviations as follows: ISATmam-*Satchellius mammalis*, IEIStet-*Eiseniella tetraedra*, IDENrub-*Dendrodrilus rubidus*, ILUMrub-*Lumbricus rubellus*, IAPPcal- *Aporrectodea caliginosa*, IMURmul-*Murchieona muldali*, IALLchl-*Allolobophora chlorotica*, IAPPros- *Aporrectodea rosea*, iONlase-*Oniscus asellus*, iPHImus-*Philoscia muscorum*, iTRlpus-*Trichoniscus pusillus* agg., cSTlsub-*Stigmatogaster subterranea*, cGEOfla-*Geophilus flavus*, cLITvar-*Lithobius variegatus*, cLITmic-*Lithobius microps*, cGEOeas-*Geophilus easoni*, dGLOmar-*Glomerus marginata*, dTACnig-*Tachypodoiulus niger*, PTRmad-*Pterostichus madidus* var. *concinus*, PTRstr-*Pterostichus strennus*, LATelo-*Lathrobium elongatum*

Figure 4

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Figure 5 CCA triplot of soil pit data with maximum enclosing polygons for *standard* and *additional* microhabitats. Microhabitat abbreviations as in Table 1. Species abbreviations as follows : ISATmam-*Satchellius mammalis*, IEIStet-*Eiseniella tetraedra*, IDENrub-*Dendrodrilus rubidus*, ILUMrub-*Lumbricus rubellus*, IAPPcal-*Aporrectodea caliginosa*, IMURmul-*Murchieona muldali*, IALLchl-*Allolobophora chlorotica*, IAPPros-*Aporrectodea rosea*, iONlase-*Oniscus asellus*, iPHImus-*Philoscia muscorum*, iTRlpus-*Trichoniscus pusillus* agg., cSTlsub-*Stigmatogaster subterranea*, cGEOfla-*Geophilus flavus*, cLITvar-*Lithobius variegatus*, cLITmic-*Lithobius microps*, cGEOeas-*Geophilus easoni*, dGLOmar-*Glomerus marginata*, dTACnig-*Tachypodoiulus niger*, PTRmad-*Pterostichus madidus* var. *concinus*, PTRstr-*Pterostichus strennus*, LATelo-*Lathrobium elongatum*

Figure 5

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Figure 6 caption

Figure 6 RDA triplot of leaf litter data. Habitat abbreviations as in Table 1. Species abbreviations as follows (species occurring in a single sample removed for clarity): QUEcur- *Quedius curtipennis*, MIRsta- *Micropeplus staphylinoides*, STNimp- *Stenus impressus*, ANOtet- *Anotylus tetracarınatus*, ACApti- *Acalles ptinoides*, ACArob – *Acalles roboris*, BARpel- *Barypeithes pellucidus*, BARara- *Barypeithes araneiformis*, fMYRrug- *Myrmica ruginodis*, oANecam- *Anelasmocephalus cambridgei*, oPLAtri- *Platybunus triangularis*, ILUMrub- *Lumbricus rubellus*, ISATmam- *Satchellius mammalis*, dCYLpun- *Cylindroiulus punctatus*, dGLOmar- *Glomeris marginata*, cGEOtru- *Geophilus truncorum*, cLITvar- *Lithobius variegatus*, cGEOeas- *Geophilus easoni*, iTRIpus- *Trichoniscus pusillus* agg., iONlase- *Oniscus asellus*, iPHImus- *Philoscia muscorum*, iPORsca- *Porcellio scaber*, iHAPdan - *Haplophthalmus danicus*

Figure 6

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Figure 7 RDA triplot of leaf litter data with maximum enclosing polygons for *standard* and *additional* microhabitats. Habitat abbreviations as in Table 1. Species abbreviations as follows (species occurring in a single sample removed for clarity): QUEcur- *Quedius curtipennis*, MIRsta- *Micropeplus staphylinoides*, STNimp- *Stenus impressus*, ANOtet- *Anotylus tetracarınatus*, ACApti- *Acalles ptinoides*, ACArob – *Acalles roboris*, BARpel- *Barypeithes pellucidus*, BARara- *Barypeithes araneiformis*, fMYRrug- *Myrmica ruginodis*, oANecam- *Anelasmoecephalus cambridgei*, oPLAtri- *Platybunus triangularis*, ILUMrub- *Lumbricus rubellus*, ISATmam- *Satchellius mammalis*, dCYLpun- *Cylindroiulus punctatus*, dGLOmar- *Glomeris marginata*, cGEOtru- *Geophilus truncorum*, cLITvar- *Lithobius variegatus*, cGEOeas- *Geophilus easoni*, iTRlpus- *Trichoniscus pusillus* agg., iONlase- *Oniscus asellus*, iPHImus- *Philoscia muscorum*, iPORsca- *Porcellio scaber*, iHAPdan - *Haplophthalmus danicus*

Figure S1 CCA triplot of vegetation data. Habitat abbreviations as in Table 2. Species abbreviations as follows (species occurring in a single sample removed for clarity): prefix gp-ground, up-understory, cp-canopy, ACEcam-Acer campestre, ADOmos-Adoxa moschatellina, ADJrep-Ajuga reptans, ANEnem-Anemone nemorosa, ARUmac-Arum maculatum, BETsp-Betula sp., BRAsyl-Brachypodium sylvaticum, CARsp-Cardamine sp ., CARpen-Carex pendula, CARsyl-Carex sylvatica, CIRlut-Circaea lutetiana, CIRpal-Cirsium palustre, CORave-Corylus avellana, CRAMon- Crataegus monogyna, EUOeur- Euonymus europaea, FICver- Ficaria verna, FILulm-Filipendula ulmaria, FRAexc- Fraxinus excelsior, GALapa- Gallium aparine, GERrob- Geranium robertianum, GEUurb- Geum urbanum, GLEhed- Glechoma hederacea, HEDhel- Hedera helix, HYCscri- Hyacinthoides non-scripta, KINpra- Kindbergia praelonga, gLONper- Lonicera periclymenum, MALsyl- Malus sylvestris, MERper-Mercurialis perennis, PICaib- Picea abies, PLAund- Plagiomnium undulatum, POTste- Potentilla sterilis, PRUspi- Prunus spinosa, QUEsp- Quercus sp., RANsp- Ranunculus sp., RUBfru- Rubus fruticosus agg., RUMsan- Rumex sanguineus, SALsp- Salix sp., SCRAur- Scrophularia auriculata, STEhol- Stellaria holostea, THUtam- Thuidium tamariscinum, THUpli- Thuja plicata, URTdio- Urtica dioica, VERmon- Veronica montana, VIBopu- Viburnum opulus, VIOsp, Viola riviniana/reichenbachiana

Figure S2 CCA triplot of vegetation data with maximum enclosing polygons for *standard* and *additional* microhabitats. Habitat abbreviations as in Table 2. Species abbreviations as follows (species occurring in a single sample removed for clarity): prefix gp-ground, up-understory, cp-canopy, ACEcam-Acer campestre, ADomos-Adoxa moschatellina, ADJrep-Ajuga reptans, ANEnem-Anemone nemorosa, ARUmac-Arum maculatum, BETsp-Betula sp., BRAsyl-Brachypodium sylvaticum, CARsp-Cardamine sp., CARpen-Carex pendula, CARsyl-Carex sylvatica, CIRlut-Circaea lutetiana, CIRpal-Cirsium palustre, CORave- Corylus avellana, CRAMon- Crataegus monogyna, EUOeur- Euonymus europaea, FICver- Ficaria verna, FILulm- Filipendula ulmaria, FRAexc- Fraxinus excelsior, GALapa- Gallium aparine, GERrob- Geranium robertianum, GEUurb- Geum urbanum, GLEhed- Glechoma hederacea, HEDhel- Hedera helix, HYCscri- Hyacinthoides non-scripta, KINpra- Kindbergia praelonga, gLONper- Lonicera periclymenum, MALsyl- Malus sylvestris, MERper- Mercurialis perennis, PICaib- Picea abies, PLAund- Plagiomnium undulatum, POTste- Potentilla sterilis, PRUspi- Prunus spinosa, QUEsp- Quercus sp., RANsp- Ranunculus sp., RUBfru- Rubus fruticosus agg., RUMsan- Rumex sanguineus, SALsp- Salix sp., SCRAur- Scrophularia auriculata, STEhol- Stellaria holostea, THUtam- Thuidium tamariscinum, THUpli- Thuja plicata, URTdio- Urtica dioica, VERmon- Veronica montana, VIBopu- Viburnum opulus, VIOsp, Viola riviniana/reichenbachiana

Supplementary Figure S2
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