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Corresponding Author: Ms. Victoria J Burton,

Corresponding Author's Institution: Natural History Museum

First Author: Victoria J Burton

Order of Authors: Victoria J Burton; Paul Eggleton

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.

Cover Letter

Victoria Burton and Dr Paul Eggleton
Soil Biodiversity Group
Life Sciences Department
Natural History Museum
Cromwell Road
London
SW7 5BD
Tel: 020 7942 5000

29 December 2015

Dear Professor Tebbe

We hereby submit a manuscript entitled *Microhabitat heterogeneity enhances soil macrofauna and plant species diversity in an Ash – Field Maple woodland* by Victoria J. Burton and Dr Paul Eggleton to be considered for publication as an original article in the *European Journal of Soil Biology*. This is a revision of manuscript EJSOBI-D-14-00065, we thank the reviewers for their useful comments and apologise for the delay in revising this article. A detailed response to reviewers' comments is included with this submission.

This article derives from the first author's project submitted as part of requirements for the degree of Master of Science, Imperial College London. It explores the influence of small-scale habitat heterogeneity on the distribution of soil macrofauna and plants within a single woodland site. This replicates previously published work by the Soil Biodiversity Group at a spatial scale which has rarely been studied and we believe these findings will be of interest to the readers of your journal.

We declare that this manuscript is original, has not been published before and is not currently being considered for publication elsewhere. We also confirm there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. The manuscript has been read and approved by both named authors. We hope you find our manuscript suitable for publication and look forward to hearing from you.

Yours sincerely,

Victoria Burton (corresponding author)
Soil Biodiversity Group
Life Sciences Department
Natural History Museum
Email: v.burton@nhm.ac.uk

Dr Paul Eggleton
Researcher and Head
Soil Biodiversity Group
Life Sciences Department
Natural History Museum
Email: p.eggleton@nhm.ac.uk

***Detailed Response to Reviewers**

Victoria Burton and Dr Paul Eggleton
Soil Biodiversity Group
Life Sciences Department
Natural History Museum
Cromwell Road
London
SW7 5BD
Tel: 020 7942 5000

6th April 2016

Dear Professor Tebbe

Please find our revised manuscript EJSOBI-D-15-00429 *Microhabitat heterogeneity enhances soil macrofauna and plant species diversity in an Ash - Field Maple woodland*. Our responses to reviewers' comments follow.

Reviewer #1

line 63f: the abbreviation of hectar is ha (not HA), but please do not abbreviate it anyway.

The abbreviation for hectare has been expanded throughout the manuscript.

line 110ff: please give the depth in profile at which the temperature and moisture data were recorded.

Added to line 111.

lines 216 and 231: please help the reader in giving the full information here; instead of "envelope" write "the standard deviation envelopes of the species accumulation curves" ...

Amended as requested.

line 217: .. is much narrower than that for the additional ... ["than that" missing]

Amended.

line 238: ... only in stumps was this association significant [word position]

Amended.

line 247: where was plant species diversity high?? In both sites?

This was for the site overall site, which has now been clarified in line 249.

Reviewer #2:

This is an important area of study for terrestrial invertebrates and a large literature is accumulating which suggests that spatial variation is important. However, I feel that this manuscript requires significant revision if it is to be published. I have two main causes for concern. The first is that the paper assumes that the reader is familiar with the methodologies and terminologies used by this group of scientists. I am not and this caused me some difficulty. In addition the descriptions of the microhabitats were vague and require some tightening up.

> The manuscript has been revised so that methods and terminology is understandable to those unfamiliar with the research group's work. Microhabitat descriptions have been expanded (Table 1).

Secondly, given the elaborate nature of the analysis, the number of species and the number of environmental factors assessed the sample size seems very small (Lines 191 to 194). Is it possible to validly assess so many things using so few individuals? In fact, if there were only 757 individuals across 62 species, one has to assume that a large proportion were singletons. Surely this is not a large enough dataset to allow such analysis.

In this context, I don't believe the paper can be published in its current format and these questions would have to be addressed before it could be even reconsidered.

> We disagree with the reviewer here for a number of reasons. First, there is no clearly defined limit to sample sizes that are appropriate in ordination. Second, we do not believe that 757 specimens in 62 species is a "small" number, it is comparable to numerous other studies, particularly invertebrates. Third, the presence of a number of singletons is not a technical problem for the analysis, excluding them would be arbitrary. Fourth, some sort of multivariate approach is required here, as the essence of the paper is comparing composition in different samples. There are alternative ways to do this but we strongly believe that we have chosen the way that shows differences most clearly.

Is it expected that doi and dates on which PEER REVIEWED publications were assessed online should be included in reference list?

> The references have been reviewed with DOI now included for publications if known and date accessed for web references as per Guide for Authors.

Far too much emphasis is placed on function rather than patterns of biodiversity in introduction.

> The introduction has been revised to focus on patterns of biodiversity rather than function.

Line 81: How was the sufficient area decided upon?

> Area was considered sufficient if it was enough for a sample size of six $1m^2$ quadrats, this is now clarified in line 78.

The structure of Table 1 seems odd as it includes the site types as well as the microhabitat types under the heading microhabitat. Some of the descriptions also seem vague, e.g. path, seeps, power line. These could be quite extensive and contain several microhabitats in themselves.

> Table 1 structure has been revised and more detail included on the microhabitats.

Through the text there is discussion of additional and standard microhabitats and the additional ones are important in terms of species accumulation. THIS PAPER does not provide any information on what they are.

This is explained in section 2.2, lines 81 - 83.

How were the means in Table 2 for the woodland types arrived at? Are they means of the microhabitat values or something else?

Table 2 has been revised so only means of values in the microhabitats are included.

What, for example, does pH of stumps mean? How was it measured?

This is been clarified in Table 2 to read 'soil pH', measurement of pH is described in section 2.3.2, line 112.

Table 3 "indicator species associated WITH"

This has been amended.

Does the journal published colour figures?

Colour figures are to be published online only.

Line 97: Some details of methods should be provided as the paper should be understandable in its own right.

Details of methods have been expanded in section 2.3.

Lines 115-118: surely this is not acceptable if we assume spatial heterogeneity, as this study does.

The imputation method explicitly takes into account spatial heterogeneity, which was what was requested.

Line 123: What is being discussed in Krell? Do you mean described?

This line has been removed.

Lines 123-125: Not clear whether the fauna are extracted from stumps or just from the litter under the stumps. If stumps were sampled, were they broken up to facilitate extraction?

Only leaf litter was sampled, this has now been made explicit in line 120-122.

Lines 174-175: Was the analysis carried out in a stepwise fashion to identify the most important environmental variables?

Section 2.5.3 has been expanded to better explain the ordination analysis. All environmental variables were included in the model with Monte Carlo permutation tests used to compute significance for each variable.

While it is not really the purpose of this study, it would be interesting to discuss whether features such as temperature and moisture are proximate drivers or simply a consequence of vegetation type.

As the reviewer acknowledges this is a little outside the scope of this study.

We hope we have addressed the reviewers concerns sufficiently and look forward to hearing from you.

Yours sincerely,

Victoria Burton (corresponding author)
Soil Biodiversity Group
Life Sciences Department
Natural History Museum
Email: v.burton@nhm.ac.uk

Dr Paul Eggleton
Researcher and Head
Soil Biodiversity Group
Life Sciences Department
Natural History Museum
Email: p.eggleton@nhm.ac.uk

***Highlights (for review)**

- Plant and soil macrofauna in 11 microhabitats in temperate woodland were compared
- Winkler bags and hand sorting soil were used to extract invertebrates
- Plant species were more strongly associated with microhabitat differences than invertebrates
- Deadwood microhabitats had a distinct fauna of saproxylic leaf litter invertebrates
- The disturbed microhabitat was characterised by ruderal plant and earthworm species

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

Victoria J. Burton[ab]*, Paul Eggleton[a]

[a]Soil Biodiversity Group, Life Sciences Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

[b]Imperial College London, South Kensington Campus, London SW7 2AZ, UK

*corresponding author email v.burton@nhm.ac.uk

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].

75 *2.2 Sampling regime*

76 The study site comprises two broad habitats, 4.2 hectares of coniferous plantation (with some
77 regrowth of deciduous species) (*con*) in Timber Copse and 3.5 hectares of deciduous woodland (*dec*)
78 in Greatmead Copse. An initial survey identified 12 *microhabitats* which covered a sufficient area for
79 a sample size of six 1m^2 quadrats, one of which (*streamside*) had no macrofauna, the 11 sampled are
80 described in Table 1.

81

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

85

86 *2.3 Sampling methods*

87 Sampling was carried out during May 2013 over four sampling periods, each a week apart, with 6-7
88 replicate samples from each microhabitat. Each replicate consisted of a 1m^2 quadrat, which for the
89 deadwood microhabitats included a stump or log. All the stumps sampled were from trees felled in
90 the 1950s so were of uniform size and decay stage, logs were in decay class III [17] and were
91 selected on the basis of similar size (0.5-1.0 m length). Every effort was made to stratify sampling
92 spatially and temporally to minimise variability due to weather differences and temporal effects.

93

94 Environmental variables and a vegetation survey were carried out in each 1m^2 quadrat and
95 macrofauna were sampled using two methods: hand sorting of soil pits and Winkler bag extraction
96 of leaf litter. Pitfall trapping was not used since that sampling method is strongly biased towards
97 groups which actively move on the surface [18] and is therefore unsuitable for a small spatial scale
98 project, as it is likely to record arthropods originating from outside the microhabitat.

99

100 *2.3.1 Vegetation survey*

This was carried out in the same $1m^2$ 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 m^2 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 $1m^2$ 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 $1m^2$ quadrat was sieved using a $1cm^2$ 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 $1m^2$ 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

153 package [34] in R 3.1.0 [20] using the *multipatt* command (with func = ‘‘IndVal.g’’, all habitat
154 combinations considered). This function calculates an Indicator Value based on the predictive value
155 of a species for the microhabitat it was found in (specificity) and the probability of finding it a
156 different microhabitat (fidelity). A permutation test was run using nperm = 999 to test the statistical
157 significance of the calculated indicator values, species with an *IndVal.g* association index significant
158 at $P < 0.05$ are considered to be indicator species.
159
160 *2.5.2 Species accumulation curves*
161 Species accumulation curves were constructed for total, standard and additional microhabitats using
162 the *vegan* 2.2-1 package [35] in R 3.1.2 [20] using the *specaccum* command (with method=
163 “rarefaction”). This presents the accumulation of species as the number of individuals sampled
164 increases, visualising any extra diversity sampled using the additional microhabitats compared with
165 the standard ones.
166
167 *2.5.3 Ordinations*
168 Data for the vegetation survey, soil pit and leaf litter invertebrates were analysed separately using
169 CANOCO 5.02 [36] with all environmental variables included to provide the most complete model.
170 Constrained ordination was used with response data as log-transformed species and explanatory
171 variables as the environmental variables (temperature, pH and moisture) and microhabitats. The
172 significance of each ordination was tested using Monte Carlo permutation tests with 999
173 unrestricted permutations. Each permutation randomly re-shuffles the environmental variables
174 while the species data is fixed, producing a null hypothesis model. The value of the test statistic
175 (pseudo-F value) produced from the original data was compared with the distribution of the null
176 hypothesis model and a p-value for each environmental variable computed based on how often the
177 pseudo-F value of data is more extreme than obtained from the null hypothesis model [37].

178 The vegetation survey was in the form of presence-absence data so a unimodal method (Canonical
179 Correlation Analysis, CCA) was used as per CANOCO Advisor. The initial Detrended Correspondence
180 Analysis (DCA) automatically run by CANOCO Advisor found the gradient for the soil pit dataset to be
181 6.1 standard deviation (SD) units long so a unimodal method (CCA) was used to analyse the data. For
182 the leaf litter dataset the presence of samples with no target species meant that CCA was unsuitable
183 [37] so a linear method, Redundancy Analysis (RDA) was used. To ensure the uneven sampling effort
184 between the microhabitats did not influence the ordination results, analyses were re-run 20 times
185 with one of the unbalanced microhabitats (*moss* and *decstump*) removed at random. Comparison
186 with results of the complete dataset showed the effect of the additional samples to be very small.
187
188 Co-Correspondence Analysis (CoCA) was used to investigate the relationship between plant and
189 macrofauna communities as CCA was unsuitable due to the number of individual plant species being
190 much larger than the number of sites [38].
191
192 **3. Results**
193 Table 2 provides a summary of environmental variables for each microhabitat. A total of 1227
194 macrofauna individuals were sampled across all samples and methods, 62% were in the target
195 groups (80% of soil pits total, 52% of leaf litter total). Major non-target groups were true flies,
196 spiders and beetle larvae. Of the target groups 757 individuals in 62 species were identified,
197 comprising 26 beetle, nine centipede, five harvestmen, three ant, eight earthworm, four millipede
198 and five woodlice species. There were 45 species of ground flora, 11 understory and eight canopy
199 species across all samples. The vegetation dataset showed the strongest preponderance of indicator
200 species which was especially notable in the bluebell, power line and path microhabitats which had
201 three plant indicator species each (Table 3). The four indicator species in the leaf litter dataset were
202 in microhabitat groups containing deadwood and are all known saprophages. The soil pit method
203 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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Table 1 caption

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 *Thuja plicata* and/or *Picea abies* 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 *Thuidium tamariscinum* (Hedw.) Schimp. 1852 and *Kindbergia praelonga* (Hedw.) Ochyra 1982
Path	conpath	3m wide, 350m long path through Timber Copse. Diverse and variable ground flora but little understory. *Fraxinus excelsior* L. and *Acer campestre* L. dominant in canopy.
Seeps (coniferous)	conseep	Very small, shallow water bodies flowing through conifer plantation
Stumps (coniferous)	constump	*Quercus* L. sp. stumps under conifer plantation
Bluebell woodland[S]	decblue	Woodland with *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. 1944 dominant ground flora
Ivy woodland[S]	decivy	Woodland with *Hedera helix* 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	*Quercus* L. sp. stumps in deciduous woodland

Table 2 caption

Table 2 Microhabitats surveyed with mean values for pH, moisture and temperature ± standard error of the mean [5] '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 caption

Table 3 Indicator species associated to fewer than four microhabitats using the *indicspecies* package in R Significance codes: '**' 0.01 '*' 0.05 [5] 'standard' microhabitats, all others are 'additional' microhabitats

Table 3

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

Table 4 caption

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 caption

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

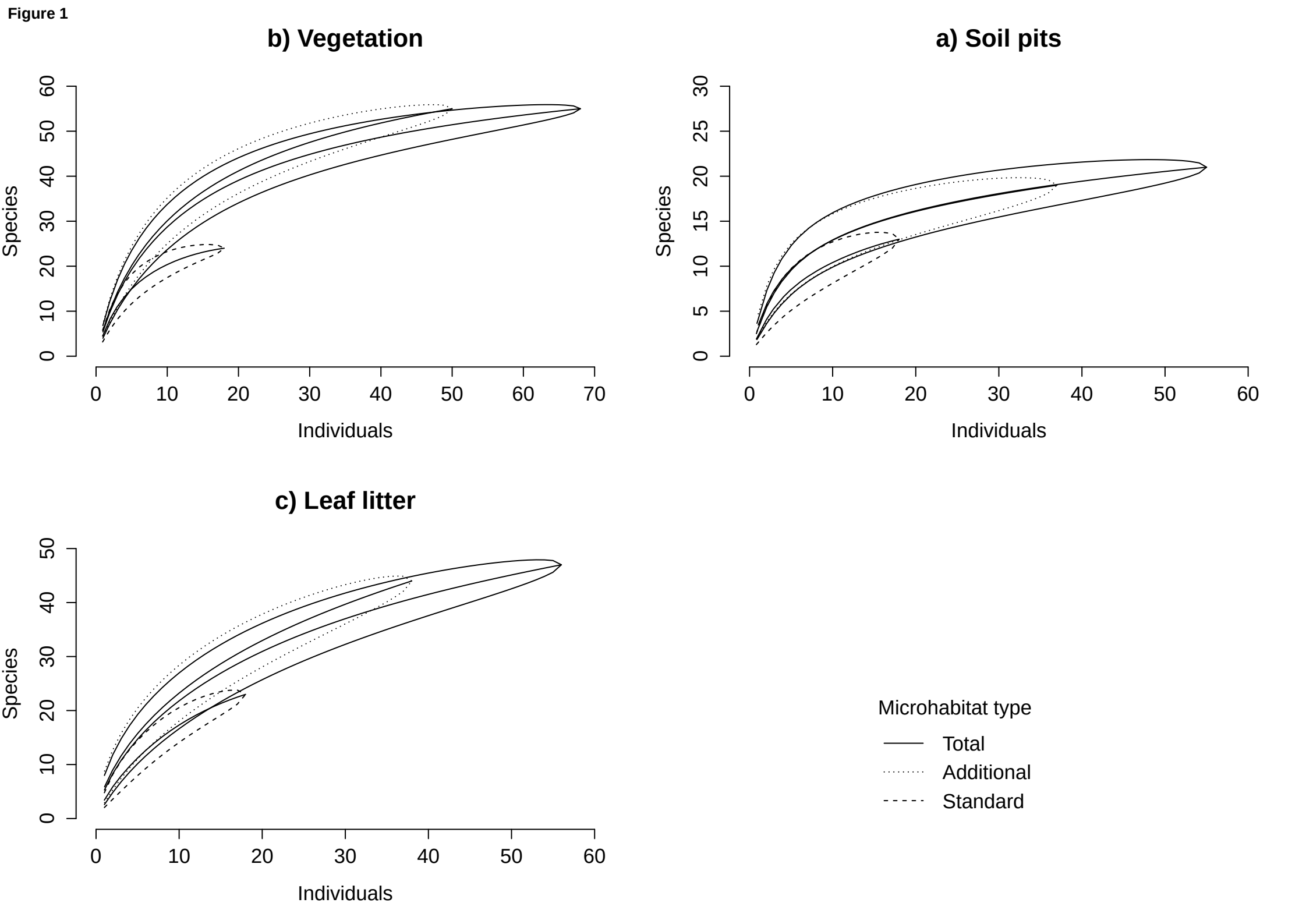

b) Vegetation
a) Soil pits
c) Leaf litter
Species
Individuals
Microhabitat type
Total
Additional
Standard

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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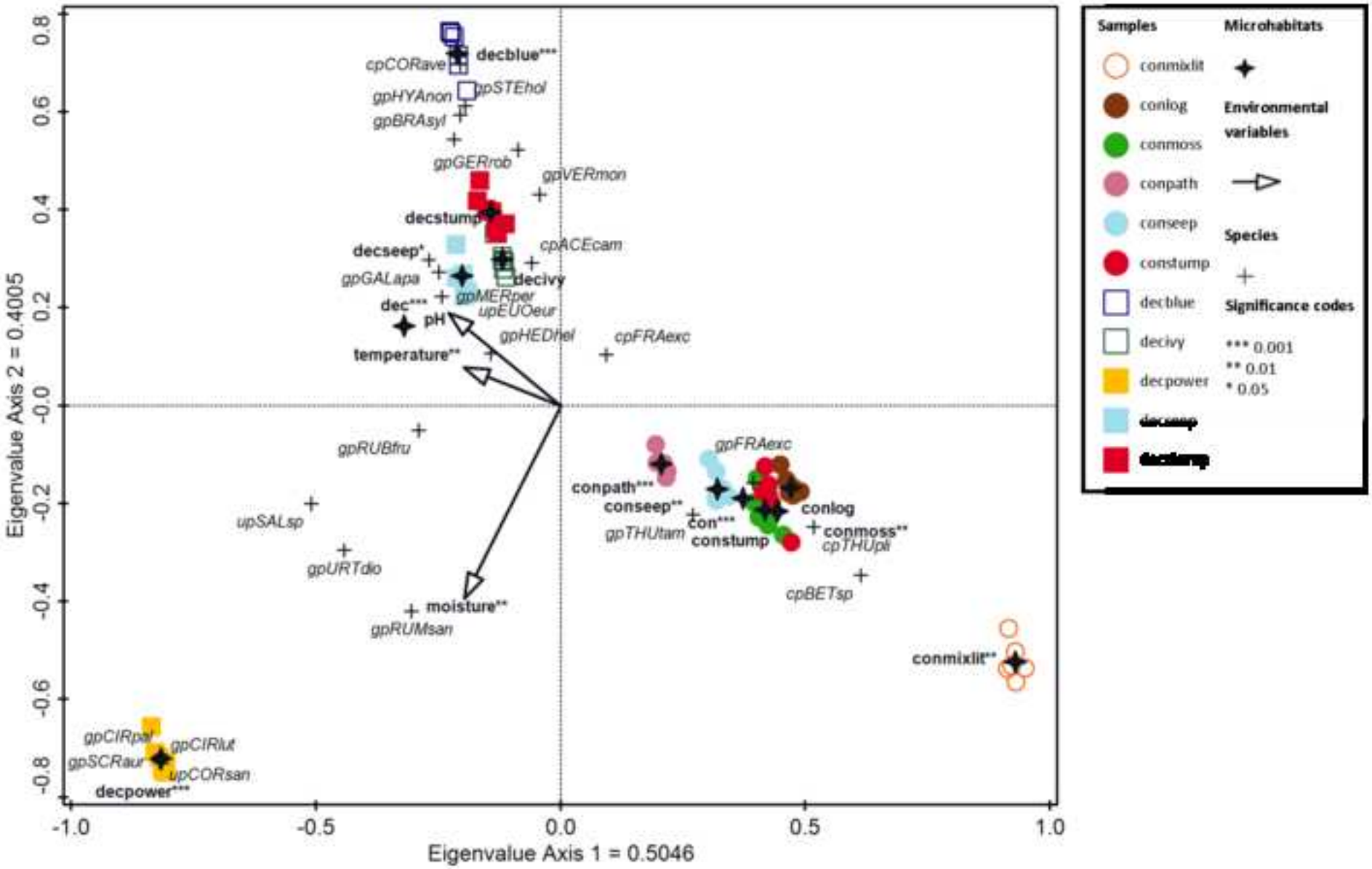


Figure 3 caption

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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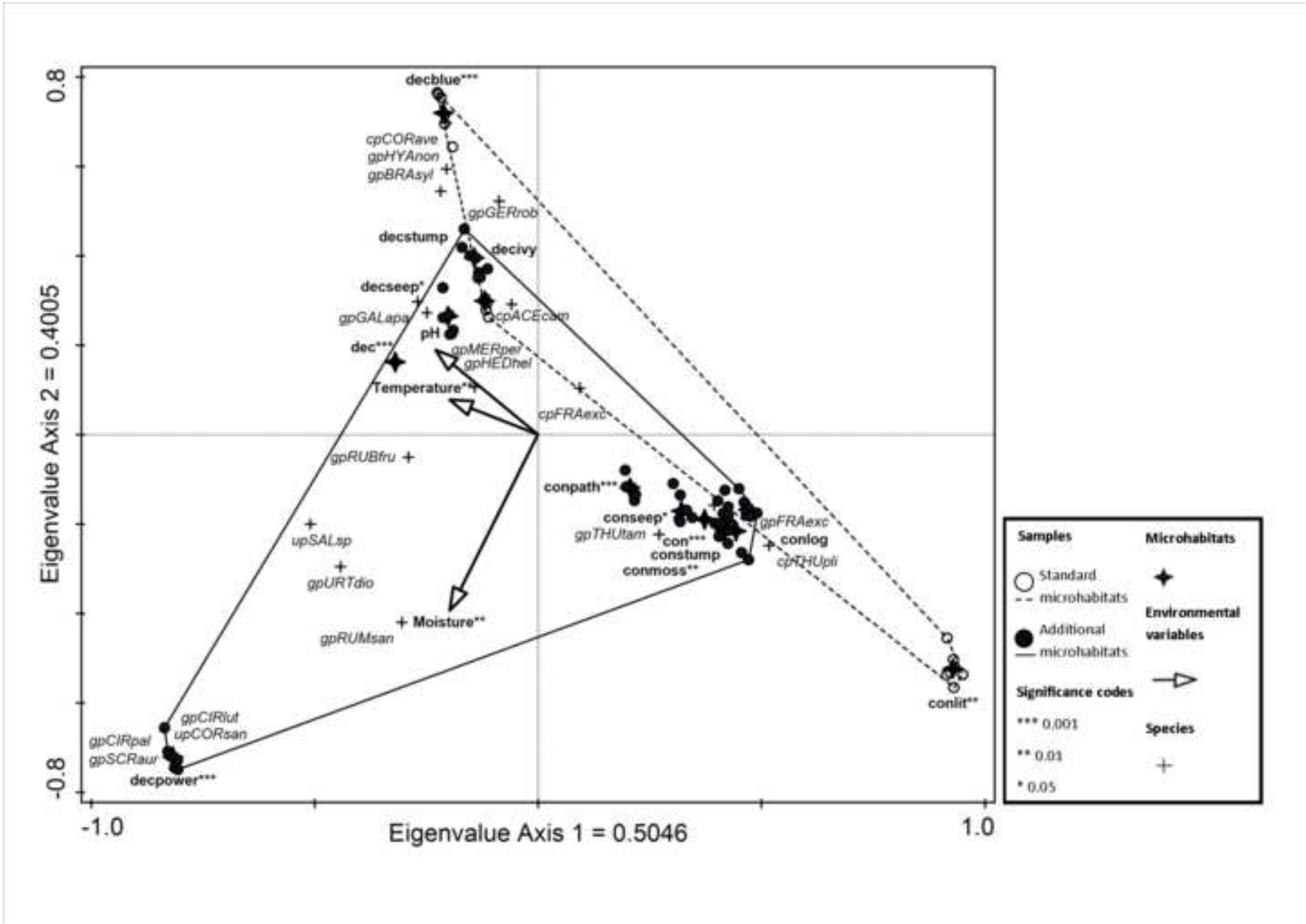


Figure 4 caption

Figure 4 CCA triplot of soil pit data. Microhabitat abbreviations as in Table 1. Species abbreviations as follows: lSATmam-*Satchellius mammalis*, lEIStet-*Eiseniella tetraedra*, lDENrub-*Dendrodrilus rubidus*, lLUMrub-*Lumbricus rubellus*, lAPPcal- *Aporrectodea caliginosa*, lMURmul-*Murchieona muldali*, lALLchl-*Allolobophora chlorotica*, lAPPros- *Aporrectodea rosea*, iONIase-*Oniscus asellus*, iPHImus-*Philoscia muscorum*, iTRIpus-*Trichoniscus pusillus* agg., cSTIsub-*Stigmatogaster subterranea*, cGEOfla-*Geophilus flavus*, cLITvar-*Lithobius variegatus*, cLITmic-*Lithobius microps*, cGEOeas-*Geophilus easoni*, dGLOmar-*Glomerus marginata*, dTACnig-*Tachypodoiulus niger*, PTRmad-*Pterostichus madidus* var. *concinnus*, PTRstr-*Pterostichus strennus*, LATelo-*Lathrobium elongatum*

Figure 4

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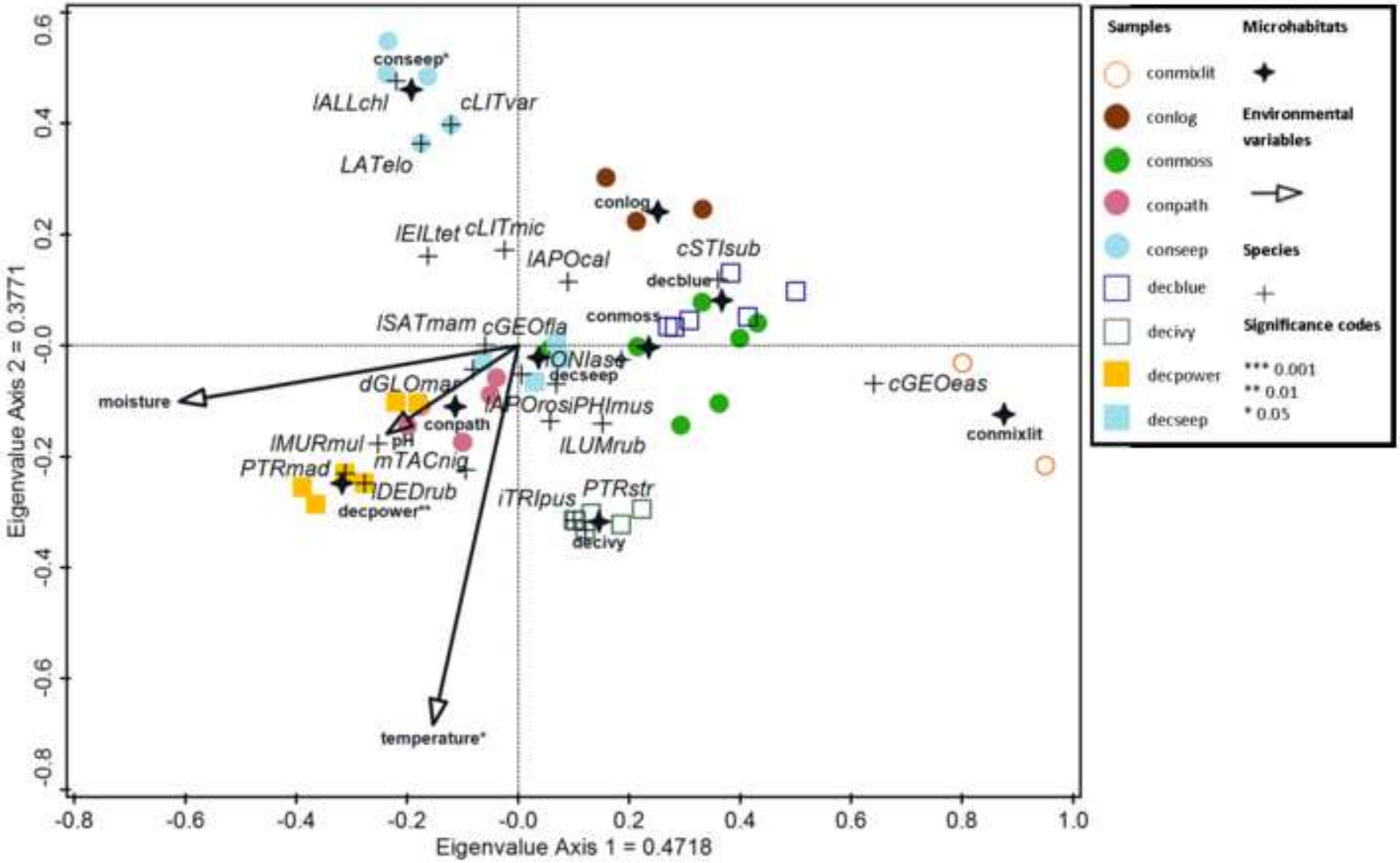


Figure 5 caption

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 : lSATmam-*Satchellius mammalis*, lEIStet-*Eiseniella tetraedra*, lDENrub-*Dendrodrilus rubidus*, lLUMrub-*Lumbricus rubellus*, lAPPcal- *Aporrectodea caliginosa*, lMURmul-*Murchieona muldali*, lALLchl-*Allolobophora chlorotica*, lAPPros- *Aporrectodea rosea*, iONIase-*Oniscus asellus*, iPHImus-*Philoscia muscorum*, iTRIpus-*Trichoniscus pusillus* agg., cSTIsub-*Stigmatogaster subterranea*, cGEOfla-*Geophilus flavus*, cLITvar-*Lithobius variegatus*, cLITmic-*Lithobius microps*, cGEOeas-*Geophilus easoni*, dGLOmar-*Glomerus marginata*, dTACnig-*Tachypodoiulus niger*, PTRmad-*Pterostichus madidus* var. *concinnus*, PTRstr-*Pterostichus strennus*, LATelo-*Lathrobium elongatum*

Figure 5

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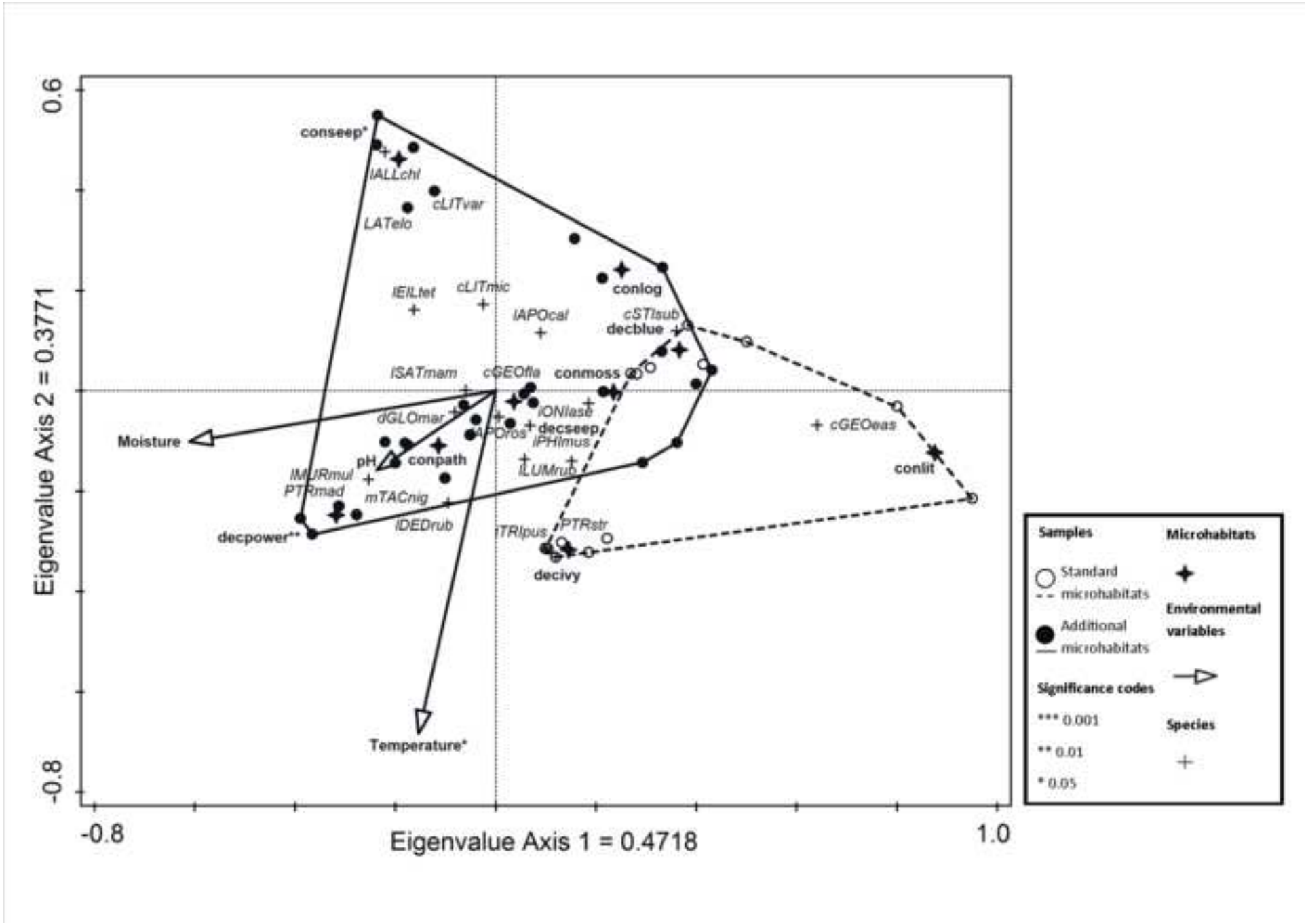


Figure 6 caption

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 tetracarinatus*, ACApti- *Acalles ptinoides*, ACArob – *Acalles roboris*, BARpel- *Barypeithes pellucidus*, BARara- *Barypeithes araneiformis*, fMYRrug- *Myrmica ruginodis*, oANEcam- *Anelasmocephalus cambridgei*, oPLAtri- *Platybunus triangularis*, lLUMrub- *Lumbricus rubellus*, lSATmam- *Satchellius mammalis*, dCYLpun- *Cylindroiulus punctatus*, dGLOmar- *Glomeris marginata*, cGEOtru- *Geophilus truncorum*, cLITvar- *Lithobius variegatus*, cGEOeas- *Geophilus easoni*, iTRIpus- *Trichoniscus pusillus* agg., iONIase- *Oniscus asellus*, iPHImus- *Philoscia muscorum*, iPORsca- *Porcellio scaber*, iHAPdan - *Haplophthalmus danicus*

Figure 6

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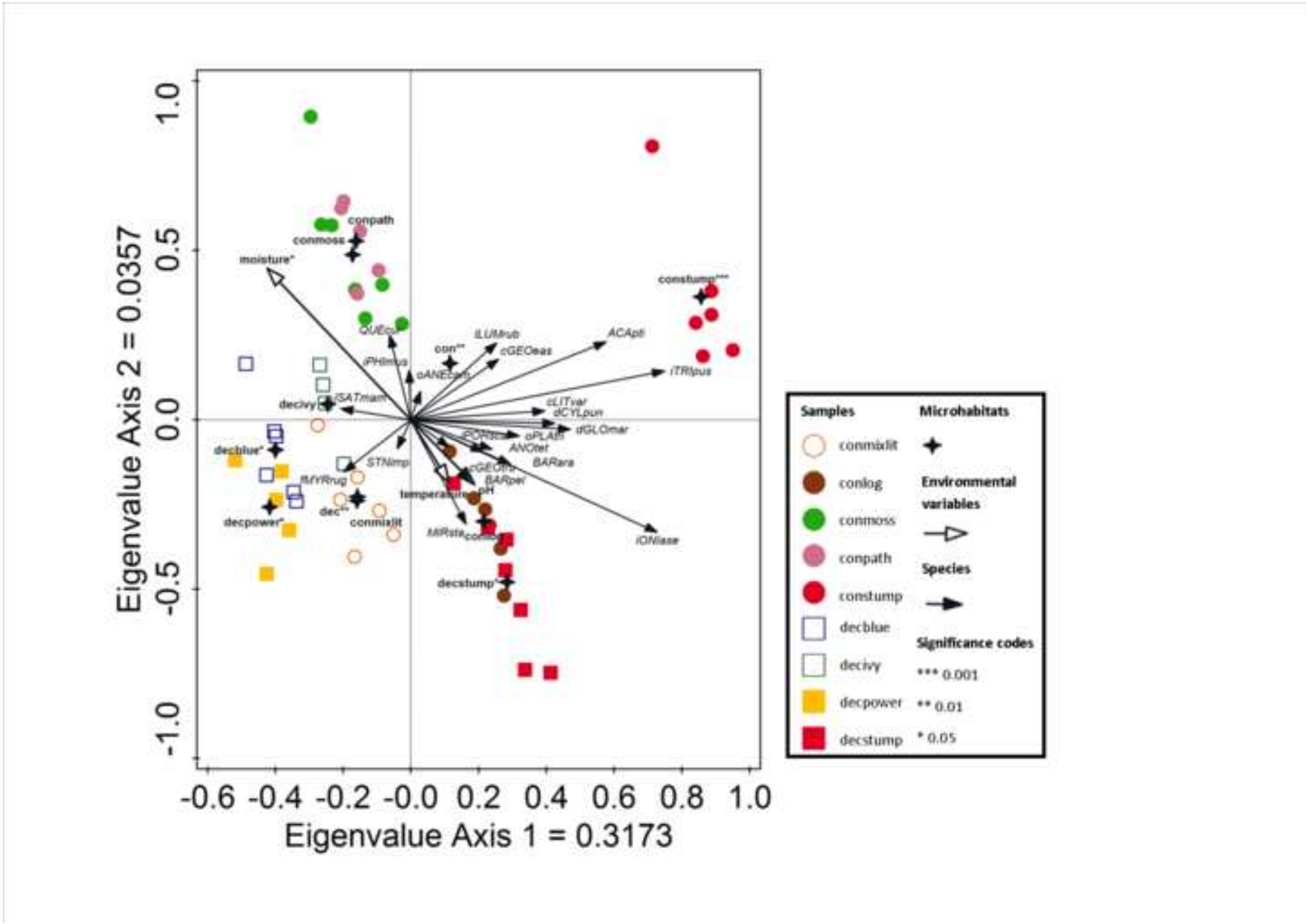
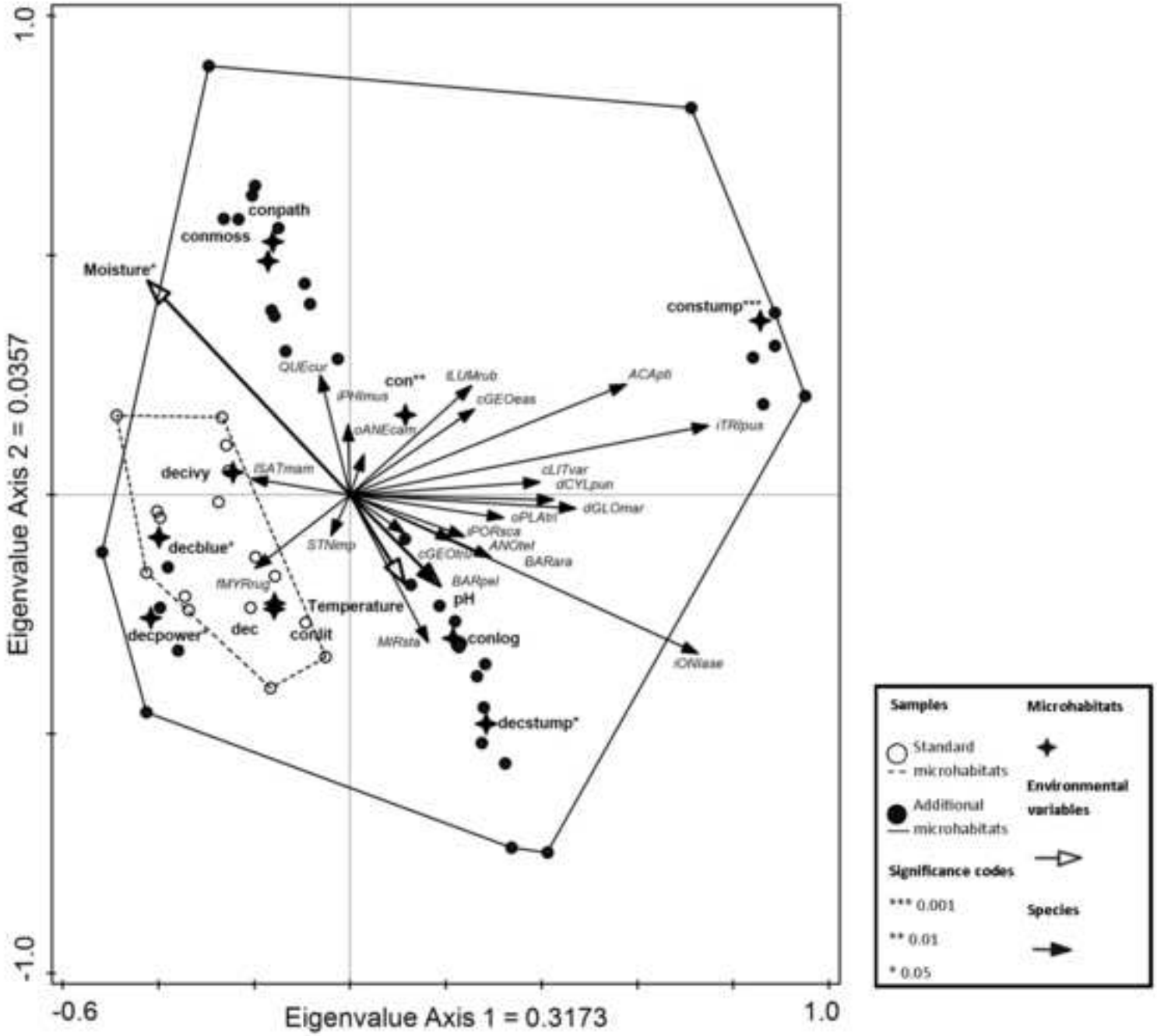


Figure 7 caption

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 tetracarinatus*, ACApti- *Acalles ptinoides*, ACArob – *Acalles roboris*, BARpel- *Barypeithes pellucidus*, BARara- *Barypeithes araneiformis*, fMYRrug- *Myrmica ruginodis*, oANEcam- *Anelasmocephalus cambridgei*, oPLAtri- *Platybunus triangularis*, lLUMrub- *Lumbricus rubellus*, lSATmam- *Satchellius mammalis*, dCYLpun- *Cylindroiulus punctatus*, dGLOmar- *Glomeris marginata*, cGEOtru- *Geophilus truncorum*, cLITvar- *Lithobius variegatus*, cGEOeas- *Geophilus easoni*, iTRIpus- *Trichoniscus pusillus* agg., iONIase- *Oniscus asellus*, iPHImus- *Philoscia muscorum*, iPORsca- *Porcellio scaber,* iHAPdan - *Haplophthalmus danicus*

Figure 7

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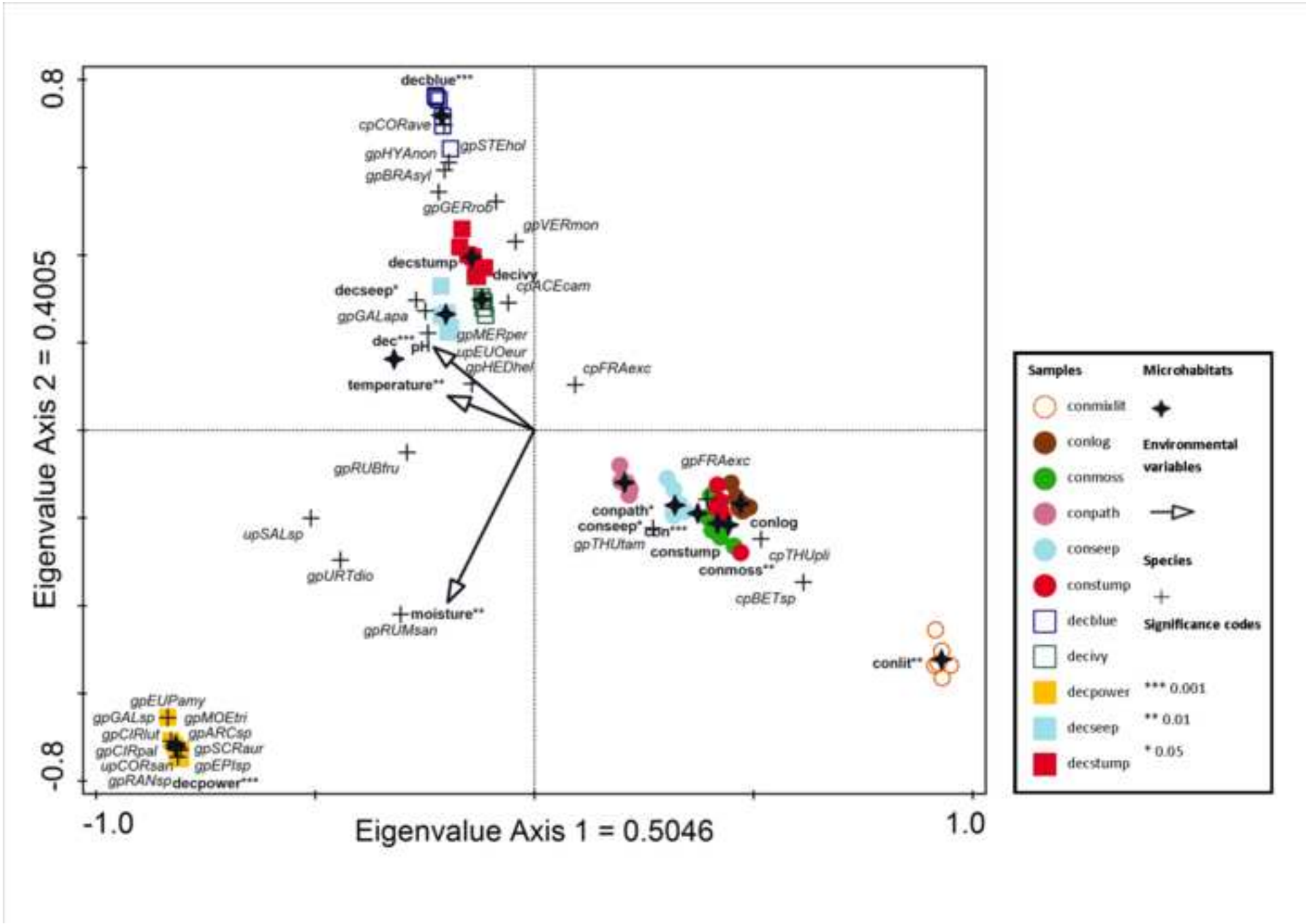


Supplementary Figure S1 caption

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*

Supplementary Figure S1

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Supplementary Figure S2 caption

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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