How high do Collembola climb? Studies of vertical migration in arboreal Collembola

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Abstract

Two studies were undertaken using inert fibrous pads as a non-destructive approach to sampling microarthropod communities on the bark of broadleaved trees. In the first study, pads were suspended at heights varying from 0–5m elevation in broad leaved trees in London to determine the vertical distribution of Collembola. In the second study, pads were attached to bark with excluders restricting arthropod ingress either from above or below to check directionality of movement. Collembola were found up to 5 m up trees, with clear vertical zonation in density and species composition. *Willowsia platani* (Nicolet, 1841) was the most height-associated species, but was only collected in summer. The second study suggested that *Willowsia platani* mainly climbed upwards, but none of the results were statistically significant.

1. Introduction

Although Collembola are considered as soil fauna, many species occur in trees both in 'suspended soil' (leaf litter accumulated in natural traps such as branch bases) and from the open bark surface (Bowden et al. 1976). These arboreal Collembola communities differ qualitatively from what is found in leaf litter at soil level, being generally dominated by a few specialist species that are uncommon in the soil (Hopkin 1997, Rogers & Kitching 1998, Lindow & Winchester 2006, Affeld et al. 2009, Rogers & Kitching 2011, Bolger et al. 2013). The flightless canopy fauna has traditionally been studied by destructive means, either as by-catch from insecticidal fogging (e.g. Shaw et al. 2007) or by collection of suspended soils by human climbers (e.g. Lindow & Winchester 2006, Rogers & Kitching 2011). Yoshida & Hijii (2006) and Bolger et al. (2013) obtained arboreal fauna by using human climbers to collect bark samples. The process by which tree canopies become populated by flightless fauna is under-studied, but presumably involves vertical migration up the tree bark. The most likely alternative is aeolian transport: Collembola are small enough to be blown by wind and have been recovered from aerial samples over 3000 m elevation (Freeman 1952, Gressit et al. 1960). Farrow & Greenslade (1992) noted unidirectional (upward) movement of > 10,000 *Cryptopygus* per hour up *Eucalyptus* trees in New South Wales, and suggested that this was to disperse on the wind. Blackith & Disney (1988) described vertical tree climbing in the springtail *Salina celebensis*, but in European studies, details of this hypothesised movement (e.g. vertical profile, phenology, directionality etc.) remain generally unclear. This is a difficult habitat to study for obvious reasons of access and safety (e.g. Bolger et al. 2013 hired professional climbers to collect sections of branches to be sampled).

Shaw (2013) introduced the use of domestic scouring pads as artificial habitats to quantify Collembola bark-surface communities. These have been used extensively by aquatic ecologists as ersatz substrata (e.g. King et al. 1990). They allow non-destructive collection of arboreal fauna and can be hoisted into otherwise inaccessible locations. Shaw (2013) recorded 33 species of Collembola

from arboreal surfaces in south-east England, and found that their densities did not seem to differ between pads made of plastic or of steel wool. The Collembola communities colonising these pads were shown to be a reasonable reflection of the arboreal community (being intermediate between those in suspended soil and vacuum-collected from the adjacent tree bark).

This use of inert pads is extended here to explore the vertical profile and migrational directionality of Collembola on bark-surfaces of mature trees in one strip of woodland. The studies sought answers to two questions: Firstly, whether inert pads can be used to quantify the changing density of arboreal Collembola with increasing elevation and season. Secondly, to explore whether they could be used to measure directionality in the vertical migration of Collembola on tree bark surfaces.

2. Methods

Site description: All work was undertaken on trees in the grounds of Whitelands College, London, UK, in a 200-year-old plantation of mixed broadleaved trees (oak *Quercus robur* L., lime *Tilia europea* L. and horse chestnut *Aesculus hippocastaneum* L.) centred on 51°26'58" N, 0°14'42" W (O.S. Grid reference TQ21938 73788). Twelve trees were used, of which all but four supported a dense epiphytic growth of ivy (*Hedera helix L.*).

2.1. Study 1: Vertical profile

Domestic scouring pads (either stainless steel or plastic wool) were suspended from loops of cord at elevations from 0–5 m in broadleaved trees (Fig. 1). Twelve trees were used, six horse chestnuts, three limes and three oaks. They were rigged with a circular loop of cord passing over high branches (> 6 m) with loops tied at 1m intervals. Inert pads were fastened to these loops by string and lifted by pulling the loop of cord around so that pads ended up at 1, 2, 3, 4 and 5 m elevation, with a final pad against the tree base but touching the leaf litter, making 6 pads per tree evenly spaced from 0-5m. The pads were mainly plastic wool, 350 ml volume, but an initial run used stainless steel pads of the same volume. As far as possible, pads were left resting in contact with the tree bark. After a range of exposure times (2–8 weeks) all the pads off selected trees (6 pads each off 2 trees, making 12 pads per sampling date) were collected as gently as possible, returned to the laboratory

Study 1

Study 2

Figure 1. Photograph of pads suspended up a tree trunk (study 1), and of the directional excluder baffles in place on a tree trunk (study 2).

in a separate plastic bag and immediately placed into Tullgren funnels to extract fauna into 70 % ethanol (using two days under a 40W bulb). Two thirds of the records were from December 2014-January 2014 (N = 20 pads per height), the other third from May-July 2014 (N = 10 pads per height). The mean height for each species of Collembola was calculated as $\Sigma(N_i * h_i)/\Sigma N_i$ where h_i and N_i are the height and count for the ith record. (Hence a mean height of 0.0 means that all records were at ground level).

2.2. Study 2: Directionality

Groupings of 3 pads were pinned side by side to the bark at 1 m elevation on eight lime trees. Above or below these were fastened baffles cut from disposable dust masks, pinned and taped to the bark so that they surrounded the width of a pad, were flush against the bark but with an overhanging lip. The idea was that this physical exclusion should reduce access to the pads from one direction. In each group of three, one pad was blocked from above (so should mainly collect animals climbing up), one pad was blocked from below (to mainly collect animals climbing down), and one pad was attached to the bark but not covered (to collect from all directions equally – the control treatment). Data were available from seven trees over five dates (12 pads per tree except for one tree which only had 6 pads collected, leaving N = 54 pads).

2.3. Statistical Methods

Collembola densities were calculated as animals per litre (dividing animals per pad by the pad volume in litres) and are presented as mean +- se.

**Study 1**: Data were analysed in R3.0.2 using 'glm' (to fit Gaussian and Poisson distributions) and 'glm.nb' within the MASS package to fit negative binomial. The model generating the lowest AIC was used, which turned out to be the negative binomial. This was then used on a complete model (testing height, sampling date, season [summer or winter], tree type and pad type as dependant factors), which was then simplified by progressive removal of non-significant terms. This form of analysis produces an 'Analysis of Deviance' table instead of a standard ANOVA. A PCA was then run on Collembola counts for the commonest species (> 5 animals collected) after transformation by log(X+1) and using the correlation matrix (by setting 'scale = TRUE' within the R function 'princomp'). The axis scores were tested for significance by performing Pearson correlations and ANOVA as if they were primary data.

Study 2: To avoid pseudoreplication (Hurlbert 1984), repeated collections of data from each tree were condensed so that one tree became one unit of replication. To achieve this, a separate mean value of Collembola caught was calculated for each tree for each direction of the excluder baffle; this gives 3 numbers per tree (a mean for 'Up', one for 'Down', and one for 'Both/Control'). The null model is that these counts are all equal, hence the expected value of (Up – Down) will be zero. This statistic was tested using a one-sample t test. Similarly if the excluder baffles are not affecting numbers caught, the expected value of (Up + Down – 2* Both) will be zero, while if the excluders are impeding half the flux of Collembola along the trunk this value should tend to be negative. Again, this statistic was calculated and tested using a one-sample t test.

3. Results

3.1. Study 1

Collembola were collected from all heights up to and including 5 m and in the absence of epiphyte growth, but the numbers and species richness were greatest at ground level, declining sharply thereafter (Figs 2, 3). The springtail community was dominated by *Orchesella cincta* (Linnaeus, 1758)*, Entomobrya intermedia* Brook*, 1884, Entomobrya albocincta* (Templeton, 1835)*, Lepidocyrtus lanuginosus* (Gmelin, 1788) and *Willowsia platani* (Nicolet, 1841), although a total of 11 species was collected from at least 1 m above ground level. The species are listed in Tab. 1, along with their densities at
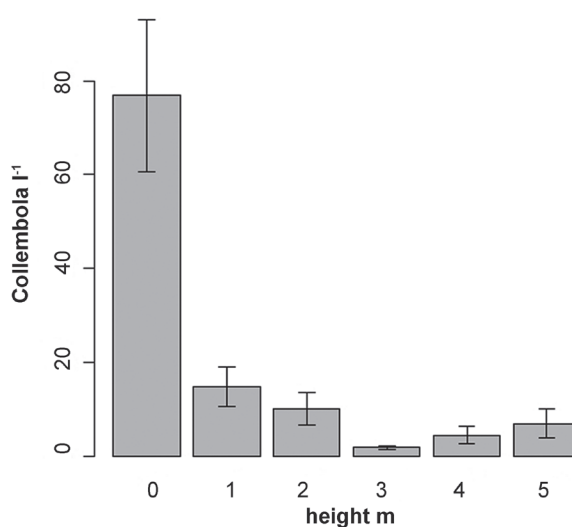
Figure 2. Mean Collembola density in pads (animals l[-1]) against elevation. Bars = 1 S.E.

different elevations and their mean height. While most species were largely found below 1 m, *Willowsia platani* had a mean elevation of 3.1 m and was almost solely collected from above 2 m.

There was a marked difference between summer and winter in the Collembola collected. Generally in winter the pads collected more animals (6.7 times, P < 0.001 by GLM) and had higher species richness (1.7 times,
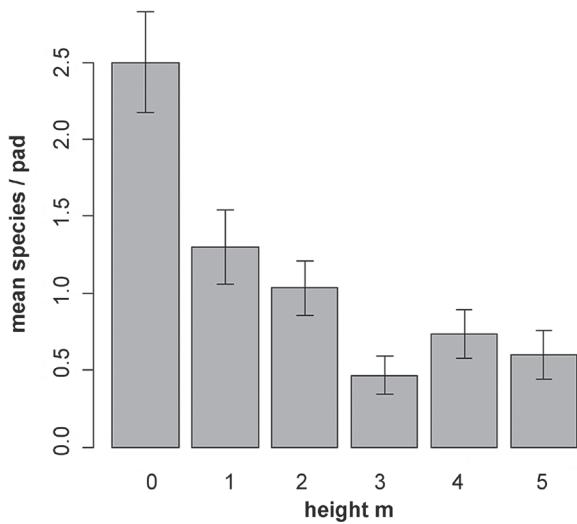

Figure 3. Mean species richness against elevation. Bars = 1 S.E.

p < 0.001 by GLM), though *W. platani*, *E. albocincta*, *L. lanuginosus* and *L. cyaneus* were found in greater numbers in summer (Tab. 1). In contrast, exposure time did not appear to affect total Collembola counts; the term 'sampling date' was non-significant in the GLM analysing total Collembola (deviance = 0.46; P = 0.5). The tree type and nature of the pads (steel or plastic) were removed from the model as non-significant.

The PCA showed that the dominant structure in the data (shown by the first principal axis) is the contrast between pads at ground level and those elevated to at least 1 m (Fig. 4). The summer-winter contrast appeared to separate out on the second principal axis. These were tested by univariate analyses of the axis scores: axis 1 scores correlated significantly with height (r = -0.46; P < 0.001 or $F_{1,178}$= 46.6; P < 0.001), but axis 2 scores did not differ with season ($F_{1,178}$ = 1.45; N.S.), which instead correlated in the first axis ($F_{1,178}$ = 22.3; P < 0.001).

3.2. Study 2

A total of eight species were collected in Study 2 (Tab. 2). The densities of Collembola (total or by species) did not differ significantly between the different exclusion treatments (Fig. 5; the t statistic comparing 'up'
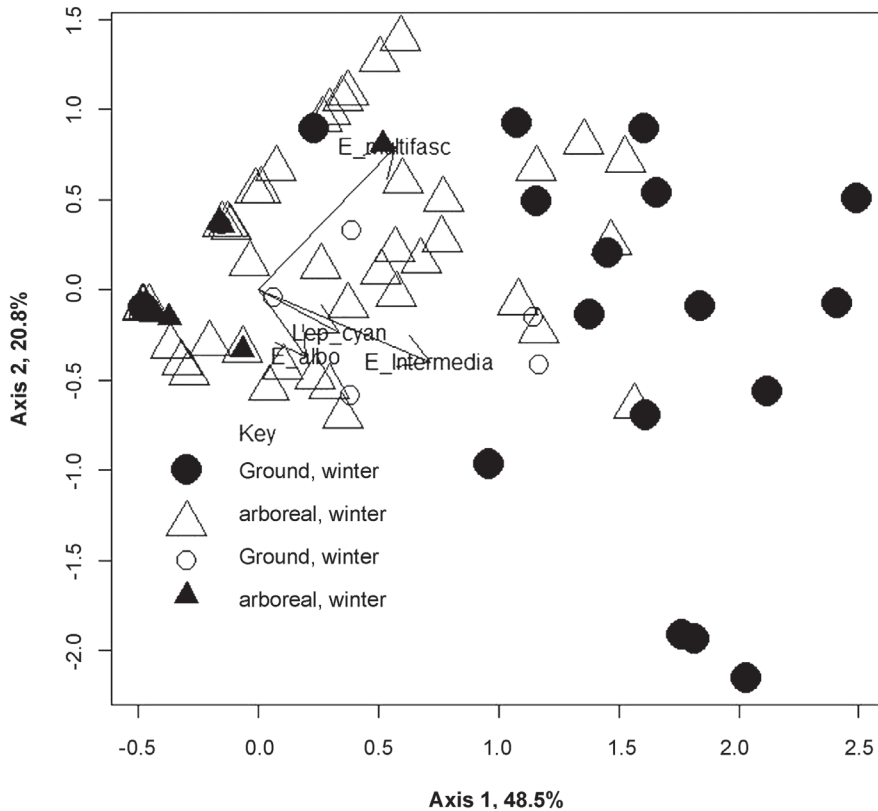

Figure 4. PCA of the main Collembola species (log transformed densities) overlain by elevation and season.

Table 1. Summary data from Study 1, listing the densities of each species of Collembola in inert pads as animals l⁻¹. The first three data columns (headed 'Ground level', '1 m'and '> 1 m') list densities at different elevations. The column 'mean height' gives the weighted mean height for each species. Statistical significance for the effect of 'height' in a general linear model using a negative binomial distribution is given along with mean height. The last columns list the mean density of each species in summer and winter, with the 'winter' column listing the significance of the 'season' term in the GLM. The final column 'N' shows how many animals were captured. If this total is < 10, no statistical tests were run as the sample size was deemed too small. ** P < 0.01; *** P < 0.001

Species	Ground level	1 m	> 1 m	Mean height	Summer	Winter	N
Dicyrtomina saundersi (Lubbock, 1862)	0.1	0.1	0	0.5	0	0.05	2
Entomobrya albocincta (Templeton, 1835)	1.2	1	0.25	1.3	1.2	0.3**	35
Entomobrya intermedia Brook 1884	16.1	5.4	3.7	1.6***	0.8	8.7***	393
Entomobrya marginata (Tullberg, 1871)	0.2	0	0	0	0	0.05	2
Entomobrya multifasciata (Tullberg 1871)	8.4	3.3	0.3	0.6***	0.2	3.2	140
Entomobrya nicoleti (Lubbock, 1867)	10.3	0.1	0.1	0.1***	1.1	2.1 NS	114
Isotomurus maculatus (Schäfer 1896)	0.2	0	0	0	0.05	0	2
Lepidocyrtus cyaneus Tullberg, 1871	1.3	0	0.01	0.6**	0.6	0.1**	17
Lepidocyrtus lanuginosus (Gmelin, 1788)	1.6	0.1	0.1	0.6***	0.4	0.3 NS	21
*Orchesella cincta (*Linnaeus 1758)	34.4	4.3	1.1	0.4***	0.4	10.6***	465
Orchesella villosa (Geoffrey, 1764)	0.1	0	0	0	0	0.02	1
Parisotoma notabilis Schäfer 1896	2.87	0.1	0	0.03***	0	0.7***	32
Willowsia platania (Nicolet, 1841)	0.1	0.4	0.2	3.1	0.6	0***	13
Xenylla maritima Tullberg, 1869	0	0	0.1	2.3	0.05	0.05	3

Table 2. Collembola species recorded from pads in study 2, along with their average densities (animals l⁻¹).

species	density l⁻¹
Entomobrya albocincta (Templeton, 1835)	3.2
Entomobrya intermedia Brook 1884	0.9
Entomobrya nicoleti (Lubbock, 1867)	0.05
Lepidocyrtus cyaneus Tullberg, 1871	0.2
Lepidocyrtus lanuginosus (Gmelin, 1788)	0.9
Orchesella cincta (Linnaeus 1758)	0.1
Willowsia platania (Nicolet, 1841)	0.7
Vertagopus arboreus (Linnaeus. 1758)	0.05
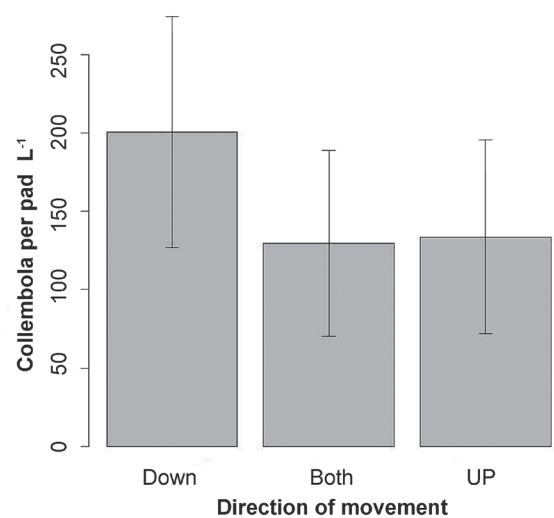
Figure 5. Mean Collembola densities (Ind. l⁻¹) in directional pads (**U** – Up only, **D** – Down only, **B** – Both directions). Bars = 1 S.E. The differences were not significant.

against 'down' was 0.2 and the t statistic comparing 'both directions' with 'one direction excluded' was 0.1 (both P > 0.05). It is worth noting that *W. platani* (which showed the greatest association with height) was recovered from control and 'upward movement' pads, but not found in any 'downward movement' pads.

4. Discussion

This small study gives some new insight into the bark-surface fauna in southern UK, although since the data all come from one woodland strip, the results cannot be regarded as general principles. The main result is that at least 11 species of Collembola have been proven to occur on tree bark as of a height of at least 1 metre (Tab. 1). In addition, *E. marginata* has previously been collected by the author only from tree bark above 1 m, so its mean elevation of 0 m here is presumably an artefact of small sample size. The clearest evidence for habitual climbing was for *W. platani*, which was only once collected at ground level and was not found in 'downward moving' pads. Although not statistically significant, this would be consistent with the model that this species typically climbs up trees, but with occasional falls to the forest floor. Its dense coating of scales (to restrict evaporation), and an apparent lack of downward migration, also agree with this being a largely arboreal species. A second useful result is that an exposure time of 2 weeks is sufficient for colonisation of the pads to take place (as shown by the lack of significance in the 'sampling date' term of the GLM).

Noordijk & Berg (2002) studied the collembolan of the bark fauna of plane trees (*Platanus* spp.) across the Netherlands, and described *W. platani* as a typical member of the corticolous fauna. Their collembolan community was generally very similar to the species listed in Tab. 1, except that *E. intermedia* was replaced by its close relative *E. nivalis*. They also recorded the same other *Entomobrya* species: *E. albocincta* (very common), *E. multifasciata* (uncommon) and *E. marginata* (uncommon). Other species recorded commonly in Noordikk & Berg's and our study are *Xenylla maritima* and *O. cincta*, although the latter was noted as mainly climbing within 12 hours of rainfall. Although *Vertagopus arboreus* is thought of as a classic arboreal species (Bowden et al. 1976, Hopkin 2007), it was not recorded in the present experiments, and Noordijk & Berg (2002) only collected it off four plane trees (out of 450). The present species list differs more from that given by Shaw et al. (2007), who fogged conifer canopies in Yorkshire (Northern England) and recovered a fauna dominated by *E. nivalis*, *L. lanuginosus*, *V. arboreus* and *Anurophorus laricis* Nicolet, 1842. Only *L. lanuginosus* was common to both species lists – this may reflect differences in the tree type or climate.

Although PCA is a descriptive technique, not an inferential analysis, it allows an over-view of the structure of a data set. In this case PCA showed that the largest single source of variance was the difference between the ground-level community and the bark community (shown by their separation on the first principal axis). The second largest trend in the data was the difference between summer and winter communities, with higher densities and species richness in winter. The summer collections were sparse and dominated by scaly species (*Willowsia* and *Lepidocyrtus*), presumably due to drought conditions, to which scaled species are apparently adapted.

The vertical migration data suggest that *W. platani* mainly climbed upwards, but we are unable to reject the null hypothesis of random non-directional movement. The small sample size and potential unreliability of the excluder baffles leaves this conclusion lacking statistical strength.

5. Acknowledgements

6. References

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