

SOIL COLLEMBOLAN (INSECTA: COLLEMBOLA) ASSEMBLAGE STRUCTURE IN RELATION TO UNDERSTOREY PLANT SPECIES AND SOIL MOISTURE ON A EUCALYPT WOODLAND SITE

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Abstract

Rodgers, D., 1997. Soil collembolan (Insecta: Collembola) assemblage structure in relation to understorey plant species on a eucalypt woodland site. *Memoirs of the Museum of Victoria* 56(2): 287–293.

In order to investigate the hypothesis that the structure of soil collembolan assemblages beneath different plant species differs, four understorey plant species were studied in a eucalypt woodland site in southeast Queensland. Collembola were extracted from soil cores taken from ten replicate 1 m² sample plots for each of the four plant species: *Leptospermum attenuatum*, *Hibbertia stricta*, *Themeda triandra*, and *Xanthorrhoea johnsonii*. Relationships between the structure of the collembolan assemblage and the plant species were then examined using multivariate analysis of similarity (ANOSIM). The relationships between collembolan species abundance and plant species, and soil moisture contents were analysed using univariate methods.

Of the 25 species found, only one, *Willowsia* sp, differed significantly in abundance between plant species. *Willowsia* sp was significantly more abundant in association with *T. triandra* than with any other plant species ($\alpha = 0.05$). The abundance of many species was positively correlated with soil moisture. Soil texture did not vary significantly across the site but soil moisture did, such that *X. johnsonii* plots were found to be significantly drier than the other plot types, while *H. stricta* plots were significantly wetter than all others ($\alpha = 0.05$).

Analysis of similarity showed no relationship between the structure of the collembolan assemblages and the different plant species. Exploratory analyses of the relationship between soil moisture and assemblage dissimilarity showed high dissimilarity when two dry plots were compared and low when two wet plots were compared. This led to the hypothesis that dissimilarity would be higher in comparisons between *X. johnsonii* plots than in comparisons between *H. stricta* plots. This hypothesis was tested and accepted ($\alpha = 0.05$). It was concluded that more subtle distinctions in the structure of those collembolan assemblages associated with different plant species, might be found in a more experimentally oriented study in which soil moisture was controlled.

Introduction

The Collembola are known to respond to a number of environmental variables such as soil moisture and the food quality of the available microflora. Many plant species are known to have a distinctive effect upon these same variables. The potential therefore exists for some detectable association between the individual plant and collembolan species within a plant community.

Soil moisture is a critical factor in determining the distribution of Collembola. Low relative humidity generally results in increased migration and mortality and lower reproduction (Butcher et al., 1971). Although the Collembola lack a hard exoskeleton which might reduce rates of water loss (Fjellberg, 1985), a range of morphological adaptations such as waxed cuti-

cular tubercles (Greenslade, 1991), scales and setae may reduce transpiration from the body surface (Fjellberg, 1985). Transpiration rates may vary by an order of magnitude between species and there is evidence of a relationship between transpiration rate and habitat selection (Verhoef and Witteveen, 1980). Soil pH may also have an effect on the distribution and abundance of Collembola. Collembolan oviposition rates are known to be dependent on substrate pH (Butcher et al., 1971). With respect to dietary requirements, the Collembola can be considered to be primarily microphytophages and saprophytophages. Within this general description there is considerable evidence of dietary specialisation in the Collembola (e.g., Chapman et al., 1988; Klironomos et al., 1992; Shaw, 1985; Vegter, 1983; Wiggins and Curl, 1979), such that many species have been shown to feed pref-

erentially on particular groups or species of fungi and algae. There is, therefore, a strong and clear relationship between the Collembola and many soil properties.

While variables such as soil moisture holding capacity, and pH may be considered intrinsic properties of different soils, there is substantial evidence that plants modify these soil characteristics. Because plant species may differ markedly with respect to water uptake and transpiration rates (Weier et al., 1982), and differences in plant architecture may have a distinctive effect on microclimate at the soil surface, different plant species may have differential effects on the soil moisture regime. Soil pH can be similarly affected. The absorption and secretion of different ionic species by plant roots may change the pH of the rhizosphere soil by as much as 2 pH units (Grubb and Suter, 1970; Foster, 1983; Bowen and Rovira, 1991). There is also substantial evidence of differential plant rhizosphere effects on the soil microflora. Curl and Trulove (1986), for example, found the ratios of microbial populations in rhizosphere soil to adjacent non-rhizosphere soil were 24, 6 and 3 for red clover, oats and barley respectively. Different plant species are also known to both inhibit and stimulate the growth of different microbial species via biochemically active root exudates (e.g. Bowen and Rovira, 1991; Curl and Trulove, 1986; Neill and Rice, 1971; Robinson, 1972; Malik and Tesfai, 1988).

It is therefore clear that plants may substantially modify many of the soil properties that determine the distribution and abundance of the Collembola.

These plant-soil-collembolan interactions were hypothesised to play a role in the distribution of collembolan species in a eucalypt woodland site in Toohey Forest in southeast Queensland.

In this paper the relationship being examined is that between plant and collembolan species within a single plant community, rather than between plant communities (e.g., van der Drift, 1963; Hagvar, 1982; Knight and Read, 1969; Hutson and Veitch, 1983, 1987). It was also hypothesised that soil moisture was likely to vary across the site, and was almost certain to be an important factor in determining the nature of any variation in the structure of the collembolan assemblage.

To test these hypotheses a 1 Ha site was selected in Toohey Forest. The plant community on the site has been described by Coutts (1987) as, Planchon's stringybark (*Eucalyptus planchon-*

iana), broadleaved white mahogany (*Eucalyptus umbra* ssp. *carnea*) and smudgee (*Angophora woodsiana*) layered woodland to 20 m, and the soil is described by Stock (1987) as, a red-yellow podzolic of between 60 cm and 1 m depth. The understory plant species *Hibbertia stricta*, *Lepidospermum attenuatum*, *Themeda triandra* and *Xanthorrhoea johnsonii* were selected for study. Beneath each plant species, ten plots of approximately 1 m² were randomly selected across the site, giving a total of 40 plots. Collembola were sampled from six randomly placed soil cores of 5 cm depth and 5 cm diameter from each plot. An additional soil sample of approximately 100g was taken from each plot for soil moisture and texture analyses. Extraction of Collembola from the soil cores was carried out by inverting undisturbed soil cores in a modified Tullgren funnel type system with a controlled temperature gradient of 20° across the sample (35° above, 15° below the sample), for 72 hours.

Standard univariate statistical methods were used in the data analysis. A variety of data transformations were used in an attempt to obtain homoscedasticity or to normalise percentage data, prior to the application of parametric testing procedures. Where transformed data remained heteroscedastic, nonparametric testing procedures were used. Multivariate analysis using analysis of similarity (ANOSIM) in the PRIMER statistical package (Plymouth Marine Laboratory, 1994) was carried out to test the significance of the ratio of within/ between group similarity of collembolan assemblages by plant species. The Bray/ Curtis association measure was calculated using the PATN statistical package (Belbin, 1995) to give an association data matrix for the analysis of similarity. The PATN statistical package was also used for Semi-strong-hybrid multidimensional scaling (MDS) to plot the similarity relationships of the samples in an ordination space. Experience with such analyses has shown that samples in which zero data are recorded for all species should be excluded from analysis since they are identical in terms of similarity, and tend to downweight any similarity between samples with nonzero data. Rare taxa also tend to add "noise" to such analyses and taxa with less than five nonzero data in a matrix were also excluded from multivariate analyses.

Results and discussion

A total of 3272 individuals and 25 species of Collembola were collected from the site, giving

an estimated density of 6943 Collembola/m² for the 0–50 mm soil horizon. The relative abundance of the species are plotted in Figure 1. A ranked species list is given in Table 1, which also shows the number of plots in which each species occurred. Variability in the abundance of all species was high as can be seen from the means and standard deviations in Table 1. Figure 1 reflects the fundamental structure of the collembolan assemblage of the site as a whole, and clearly shows the dominance of *Lepidocyrtus* sp. in terms of abundance, while Table 1 shows that *Lepidosira* sp. was the species found on most plots. The asymptotic form of the species/ area curve plotted in Figure 2 indicates that the majority of the soil collembolan species on the site were collected.

Willowsia sp. was the only species for which a significant difference was detected between plant species ($p = 0.05$). Post-hoc testing (Mann-Whitney U test) showed that *Willowsia*

sp. was significantly more abundant beneath *T. triandra* than any other plant species ($p = 0.05$). No significant differences were detected between plant species for any other collembolan species. Differences between plant species for the community descriptors, H' (Shannon-Weiner species diversity index), S (species richness) and N (number of Collembola per plot) were also nonsignificant. No Collembola were recorded in the sample from one of the *X. johnsonii* plots and this sample was therefore excluded from multivariate analyses. The seven least common species were found in less than five plots (see Table 1) and so these data were also excluded from the multivariate analyses.

The results of the analyses of similarity using species abundance and presence/ absence data (Table 2), show that there is no evidence of a significant structural distinction between collembolan assemblages associated with the different plant species.

Table 1. Collembolan species collected, ranked by abundance

Species	Total number collected	Mean number per plot	S.D.	Number of plots containing species
<i>Lepidocyrtus</i> sp.	1336	33.4	39.76	33
<i>Isotomiella prussiana</i> (Olivera & Deharveng, 1990)	500	12.5	15.94	31
<i>Lepidosira</i> sp.	452	11.3	16.78	37
<i>Dinaphorura</i> sp.	188	4.7	6.17	25
<i>Folsomides</i> sp.	152	3.8	6.23	24
<i>Mesogastrura</i> sp.	109	2.72	5.2	22
<i>Sinella</i> sp.	105	2.62	3.59	22
<i>Pseudosinella</i> sp.	92	2.3	4.27	20
<i>Megalothorax</i> sp.	92	2.3	4.37	15
<i>Isotoma</i> sp.	53	1.32	4.74	11
<i>Katianna</i> sp.1	44	1.1	2.43	15
<i>Lepidobrya</i> sp.1	33	0.83	1.57	13
<i>Sminthurus</i> sp.	30	0.75	1.15	16
<i>Willowsia</i> sp.	21	0.53	1.54	9
<i>Hemilobella</i> sp.	17	0.42	0.87	10
<i>Cephalochorutes</i> sp.	16	0.4	1.77	4
<i>Lepidocyrtoides</i> sp.	8	0.2	0.46	7
<i>Jeannenotia</i> sp.	8	0.2	0.46	7
<i>Homidia</i> sp.	5	0.13	0.52	3
<i>Katianna</i> sp.4	3	0.08	0.47	1
<i>Pseudoparonella</i> sp.	2	0.05	0.22	2
<i>Lepidobrya</i> sp.2	2	0.05	0.22	2
<i>Katiannini</i> gen. sp.	2	0.05	0.32	1
<i>Katianna</i> sp.3	1	0.03	0.16	1
<i>Katianna</i> sp.2	1	0.03	0.16	1

Table 2. Global and pairwise comparisons of assemblage similarity for collembolan abundance and presence/ absence data by plant species (ANOSIM).

Comparison	Within/between groups similarity	Significance level*	Within/between groups similarity	Significance level*
Global	0.039	13.5%	0.065	4.1%
<i>H. stricta</i> – <i>L. attenuatum</i>	0.02	52.8%	0.068	11.4%
<i>H. stricta</i> – <i>T. triandra</i>	0.005	36.5%	0.056	14.7%
<i>H. stricta</i> – <i>X. johnsonii</i>	0.078	10.4%	0.081	9.0%
<i>L. attenuatum</i> – <i>T. triandra</i>	0.044	19.4%	0.094	6.6%
<i>L. attenuatum</i> – <i>X. johnsonii</i>	0.047	20.0%	0.035	22.9%
<i>T. triandra</i> – <i>X. johnsonii</i>	0.072	11.9%	0.053	15.5%

*significance = % of 20000 random permutations which exceed actual within/ between groups similarity ratio. 5% significance threshold weighted for multiple comparisons = 0.36%.

Table 3. Texture analyses and moisture of soils beneath the four understorey plant species. (ANOVA: NS = non-significant p value; * = $p < 0.05$).

Understorey species	Soil texture		% Soil moisture content Mean \pm sd*
	% Sand ^{NS} Mean \pm sd	% Clay ^{NS} Mean \pm sd	
<i>X. johnsonii</i>	81.8% \pm 3.7	10.9% \pm 2.1	5.1% \pm 1.5
<i>L. attenuatum</i>	81.8% \pm 2.0	10.6% \pm 2.0	8.4% \pm 1.8
<i>T. triandra</i>	81.4% \pm 4.3	12.0% \pm 2.3	9.3% \pm 2.6
<i>H. stricta</i>	79.5% \pm 3.7	12.4% \pm 2.1	11.1% \pm 1.7

Table 4. Spearman Rank correlation for collembolan species abundance and community descriptors versus soil moisture. (* indicates significance at $\alpha = 0.05$).

Species	Rho
<i>Lepidocyrtus</i> sp.	0.592*
<i>I. prussianae</i>	0.346*
<i>Lepidosira</i> sp.	0.073 n.s.
<i>Dinaphorura</i> sp.	0.511*
<i>Folsomides</i> sp.	0.399*
<i>Mesogastrurasp.</i>	0.347*
<i>Sinella</i> sp.	0.458*
<i>Pseudosinella</i> sp.	-0.13 n.s.
<i>Megalothorax</i> sp.	0.366*
<i>Isotoma</i> sp.	0.089 n.s.
<i>Katianna</i> sp.1	0.484*
<i>Lepidobrya</i> sp.1	0.012 n.s.
<i>Smynthurus</i> sp.	0.241 n.s.
<i>Willowsia</i> sp.	0.019 n.s.
<i>Heinilobella</i> sp.	0.348*
Species richness — S	0.551*
Species diversity — H	0.451*
Total Collembola — N	0.500*

The primary hypothesis of this study must be rejected at this point. There is insufficient evidence to conclude that distinct collembolan assemblages are associated with the selected understorey plant species in this site. The apparent preference of *Willowsia* sp. for soils beneath *Theneda triandra* is worthy of further investigation. However *Willowsia* sp. made only a minor contribution to the structural character of the assemblage.

Table 3 shows that while there was no significant difference between plot types in soil texture, soil moisture was significantly different ($\alpha = 0.05$), with *H. stricta* plots being significantly wetter than other plot types and *X. johnsonii* plots being significantly drier than other plot types ($\alpha = 0.05$) (Fisher PLSD). As shown in Table 4, abundances of many of the collembolan species of the site were significantly and positively correlated with soil moisture content, as were the community descriptors S, H and N. Some variation in the structure of the collembolan assemblage on the site might therefore be expected to be associated with variation in soil moisture.

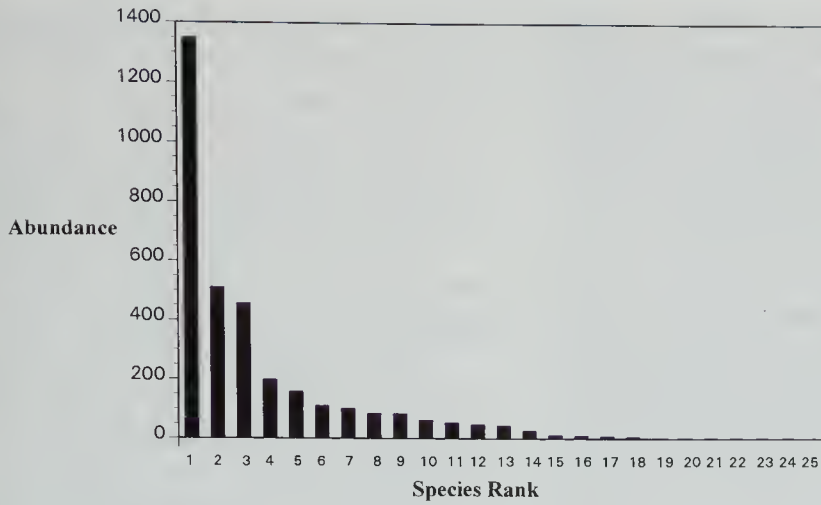


Figure 1. Ranked abundance of collembolan species collected.

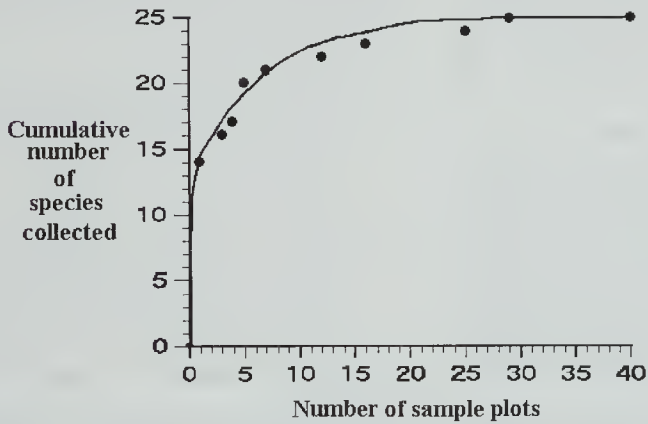


Figure 2. Species area curve for soil Collembola collected over 40 sample plots.

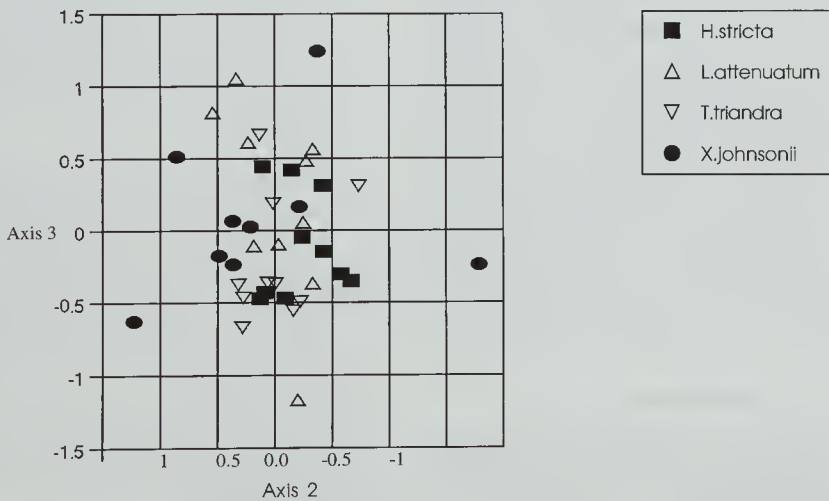


Figure 3. Ordination of collembolan assemblage dissimilarity, axes 2 and 3 (Semi-strong hybrid MDS, stress = 0.143, axes are unitless).

Since the dissimilarity coefficient quantifies the relationship between two sets of species data, quantification of the relationship between soil moisture contents of two plots was a necessary preliminary step to an analysis of the relationship between soil moisture and assemblage similarity. An exploratory 3-dimensional plot of assemblage dissimilarity against the soil moisture content of the two relevant plots, indicated that dissimilarity was low when two wet plots were compared, and high when wet and dry, or two dry plots were compared. Given the results of the soil moisture analyses in Table 3, it might be expected that dissimilarity in comparisons between *X. johnsonii* plots would be significantly higher than in comparisons between *H. stricta* plots. Tests of this hypothesis (Mann-Whitney U test) showed that dissimilarity was significantly higher in comparisons between *X. johnsonii* plots (the driest on the site) than in comparisons between *H. stricta* plots (the wettest on the site), for both species abundance and presence/absence data ($\alpha = 0.01$) ($Z = -3.06$ and -4.466 respectively).

The MDS plot (Figure 3), represents dissimilarity as distance between the points in the ordination space. The greater spread of *X. johnsonii* points in the figure is consistent with the higher level of dissimilarity between these plots than that between *H. stricta* plots. The distribution of the points in Figure 3 is also consistent with the conclusion that there is no significant structural difference between the assemblages associated with these two plant species.

The results of the above analyses provide justification further testing of the primary hypothesis. For example if soil moisture were controlled (i.e. by irrigation), then the points plotted in Figure 3 may condense to form tighter clusters. Whether or not the points for *X. johnsonii* and *H. stricta* would condense around the same centroid seems open to question. If some dissimilarity attributed to variation in soil moisture was controlled for in a more experimentally oriented study, then more subtle differences in collembolan assemblage structure associated with different plant species, such as the distribution of *Willowsia* sp., might increase in significance.

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