SOIL ORGANISMS 88 (3) · December 2016 pp. 175–192

Differences in composition and vertical distribution of Collembola from canopies of three Australian rainforests

Penelope Greenslade[1, 2,*], Sutrisno[3] and Singarayer K. Florentine[1]

[1] Environmental Management, School of Applied and Biomedical Science, Faculty of Science and Technology, Federation University Australia, Ballarat, Victoria 3353, Australia
[2] Department of Biology, Australian National University, GPO Box, Australian Capital Territory 0200, Australia
[3] Formerly of the Department of Ecosystem Management, University of New England, Armidale, New South Wales, 2350, Australia
* Corresponding author, e-mail: p.greenslade@federation.edu.au

Received 6 September 2016 | Accepted 20 October 2016
Published online at www.soil-organisms.de 1 December 2016 | Printed version 15 December 2016

Abstract

Invertebrates from three rainforest canopies (tropical TRF, subtropical STR and cool temperate CTR) were sampled by insecticidal knockdown in order to compare biodiversity of canopy faunas in Australia; lower and higher TRF and STR were sampled separately. Numerous Collembola were collected, mainly in the family Entomobryidae but relative family abundance of taxa differed between forest types. TRF was characterised by Dicyrtomidae, STR by Entomobryidae and CTR by Isotomidae and Neanuridae. Also morphospecies abundances differed between forest types. The high canopy of TRF was dominated by *Lepidocyrtoides* sp. 3 while the low canopy was dominated by *Lepidocyrtoides* sp. 6. SRF had a high proportion (80 % of individuals) of a single species, the canopy specialist, *Epimetrura rostrata*, in both high and low canopies. In CTR, the dominant species was *Entomobrya* sp. cf. *varia*. Significant differences were found in either or both abundance and species composition of Collembola between trees within each rainforest. A significant difference was found in species abundances between lower and upper canopies in TRF and STR but not in species composition, also between canopies, pitfall samples and soil/leaf litter faunas. High levels of apparent rarity were found in all the three rainforests, being most marked on STR. Only four species occurred in all three types of rainforest indicating that beta diversity (i.e. species turnover between the three sites) was high. Our results are the first to compare faunal composition between three rainforest types and have implications for management of forests under a climate change scenario.

Keywords abundance | Entomobryidae | beta diversity | Paronellidae | specialists | species richness

1. Introduction

Research into forest canopy faunas in order to understand biodiversity and to inform management was emphasised by Stork (2001) and, significantly, Ozanne et al. (2003) noted that a rainforest canopy supports 40 % of all species in it. Insecticidal knockdown using sprayers that are either raised on pulleys or on canopy cranes have proved valuable in providing data on canopy faunas, in particular in tropical rainforests. Estimates of global arthropod biodiversity have, as a result, increased several fold. Relevant studies are those of Stork and his co-workers from Borneo and Sulawesi (Stork 1987a, b; Hammond 1990; Stork & Brendell 1990, 1993) and Erwin and his colleagues in Panamanian and Amazonian rainforest (Erwin & Scott 1980; Erwin 1982, 1983) who all sampled canopy faunas. In Australia, Basset sampled a single tree species in subtropical rainforest (Basset 1990, 1991a, b, Basset & Kitching 1991), Majer and colleagues (Majer 1990, Heterick et al. 2001) reported on canopy arthropods from Northern and Western Australian woodland, and Kitching and his co-workers collected from rainforest canopies in Queensland (Kitching et al. 1993).

ISSN 1864-6417 (print) · ISSN 2509-9523 (digital)

Collembola are cosmopolitan organisms, found abundantly in every terrestrial habitat in the world. They are one of the major groups of soil detritivore micro-arthropods and have been shown to be one of the most abundant taxa in rainforest canopies (Stork 1991, Kitching et al. 1993, Guilbert et al. 1994, 1995, Camann et al. 2000, Tovar-Sánchez et al. 2003). Basset (2001) noted that abundance of Collembola in tropical rainforest canopies is 'almost certainly seriously underestimated'. Even so, the Class has been ignored by some authors in canopy studies (Stork & Brendell 1990, Southwood et al. 2005). In contrast, Collembola are rare in the canopy of drier forest types, as shown by Majer et al. (1994) for eucalypt woodland (0.2 %) and Yen (1989) in mallee woodland (0.13 %), in both studies in southern Australia

Studies on arboreal Collembola in Australia have lagged behind those of soil and leaf litter and little work here or elsewhere have identified Collembola to species. The only published report of arboreal rainforest Collembola at species level in Australia is that of Greenslade in Coy et al. (1993) from Tasmanian and Rodgers & Kitching (1998 2011) from Queensland. Yen & Lilywhite (1990) in Coy et al. (1993) only reported on the fauna in summary form but Rodgers & Kitching (1998, 2011) compared faunas of canopies, suspended soils and ground surface at species level in rainforest in north Queensland.

Vertical stratification is said to be one of the characteristics of a mature rainforest (Terborgh 1992, Park 1992, Lindo & Winchester 2013) and is determined by age and height of trees, presence and size of understorey species and emergent species. These variables create layered strata which may form barriers modifying convection air currents, resistance to lateral air movement, and reducing light penetration (Szujecki 1987). Microhabitats are modified within the strata, each with its own microclimate, offering a range of habitats for climbing and epiphytic vegetation, so influencing the distribution and abundance of rainforest fauna. For instance, Nadkarni & Longino (1990) found stratal differences in ant faunas, Sutton & Hudson (1980) in small flying insects, Ashton et al. (2015) in moths and Rodgers & Kitching (1998, 2011) in collembolan assemblages between suspended soils, canopies and ground faunas.

The aim of the current study was to compare Collembola assemblages from the canopies of three different types of rainforests in Australia, tropical, subtropical and cool temperate, located along the coastal ranges of eastern Australia and to provide data to inform the conservation planning process. We aimed to compare beta diversity, which is likely to be influenced by climate change, and inform conservation planning (Socolar et al. 2016). The collections also allowed comparisons between the upper and lower strata of tropical and subtropical forest types and between ground and canopy faunas in subtropical forest.

2. Materials and methods

2.1. Study sites

Sites were selected on similarity of canopy structure, tree composition and accessibility to equipment. Three sampling methods were employed: an insecticidal knockdown technique to collect Collembola from high (6 m in height and above) and low (2–6 m height) canopies, pitfall traps to collect surface active Collembola and litter extraction to obtain less mobile Collembola. Kitching et al. (1993) described the sites in detail and only a summary is provided here.

The tropical rainforest was located near Cape Tribulation (16°04'S, 145°28'E), North Queensland. Six sites, (each equivalent to a single tree), were fogged during the wet season in January 1991. Two were on the property, 'Pilgrim Sands', within 0.5 km of the coast. The other four sites were located approximately 4 km south-west and about 1 km inland. All were at less than 100 m a.s.l. A distinct wet season occurs in February and March, with monthly rainfall over 600 mm. Mean maximum temperatures range from 27°C in July to 34°C in January and mean minimum temperatures from 21°C in July to 26°C in January.

The vegetation is classified as complex mesophyll vine forest (Webb 1959, Webb et al. 1976, Tracey 1982). Plant species present were nearly all palms and included *Calamus* sp., *Licuala ramseyi*, *Linospadix* sp. and *Normanbya normanbyi* as dominants (Jessup & Guymer 1985). Shrub and tree species per 10 m^2 plot range from 12 to 22, with most species only occurring on one or two plots. There were none in common with subtropical sites and little overlap between sites within the rainforest.

The subtropical rainforest was on Green Mountain, near O'Reilly's Guesthouse, Lamington National Park, southern Queensland (28°13'S, 153°07'E) at an altitude of 900 m a.s.l. Nine trees were sampled in December–January 1990 and two additional trees were sprayed and pitfall traps set in the ground and leaf litter samples taken beneath them in March 1991. This region, in the Macpherson-Macleay overlap (Cranston & Naumann 1991), has a high level of endemism and diversity, possibly because it is where tropical and temperate climates overlap (Burbidge 1960). Cyclones and minor clearing are disturbing features of this site and there is a substantial growth of secondary species in the understorey in some areas. Rainfall is distributed throughout the year, with a summer peak of 500 mm per month in February and March and a winter minimum of 100 mm per month in August. Mean maximum temperatures range from 16°C in July to 25°C in January, and mean minimum temperatures range from 8°C in July to 16°C in January.

The subtropical site is classified as complex notophyll vine forest (Webb 1959, Webb et al. 1976, McDonald & Thomas 1990) although Floyd (1990) describes it as a 'subtropical rainforest', i.e. *Agyrodendron actinophyllum* alliance, sub-alliance 11 (*Caldcluvia-Crytocarya erythroxylon-Orites-Melicope octandra-Acmena ingens*) with a high species diversity and only one or two species dominant. Canopy height ranged from 2–25 m, and the understorey cover was abundant because the upper stratum permitted light penetration. Seventy-four woody species were recorded. Dominants in the upper stratum were *Argyrodendron actinophyllum*, *Ficus watkinsiana, Lophostemon conferta, Pseudowienmannia lachnocarpa, Geissois benthamii* and *Baloghia lucida.* The most common understorey species were *Acrademia eudoiiformis, Synoum glandulosum, Dysoxylon rubrum, Trunia youngiana* and *Wilkea* sp..

Five trees in cool temperate rainforest were sampled in January 1991 in the Styx River State Forest (30°31'S, 152°17'E) which is located about 53 km east of Armidale in northern New South Wales, 1125 m a.s.l. Rainfall is distributed throughout the year with no marked peak. Average monthly totals vary from 34.8 mm in August to 342.2 mm in April. Mean maximum temperatures range from 9.1°C in July to 22.8°C in December, and mean minimum temperatures range from -1.2°C in July to 11.4°C in January. The cool temperate rainforest was classified as microphyll fern forest dominated by *Nothofagus moorei* as a *Nothofagus-Ceratopetalum* suballiance with *Quintinia sieberi* (Webb et al. 1976, Floyd 1990).

2.2. Canopy sampling

A lead-weighted fishing line attached to a rope and pulley was catapulted over a high central branch of the tree to be fogged. A cats-cradle of lighter ropes was erected at head height beneath the canopy and ten circular, cotton collecting trays, each of 0.5 m^2, were hung from it. In the centre of each tray, a collecting vial containing 70% alcohol was inserted. Collembola were sampled by misting the canopy with a pyrethroid insecticide, 'Pyrethrin 2ELTM', delivered using Stihl SG-17TM backpack. The insecticide comprised natural pyrethrum at 20 gl^{-1} with piperonyl butoxide at 80 gl^{-1} and was mixed with water at the rate 1.25 l to 9 l of water.

On the tropical and subtropical rainforest sites separate samples were taken from high and low canopies. The first spraying was delivered from the ground and focussed on the understorey from 2–6 m in height (LC) and the second, delivered after the sprayer had been hauled into the canopy, was focussed on the high canopy (HC). The height of high canopy sprays varied according to the height of the tree being sprayed and the area sprayed was 6–8 m in diameter. Low and high sprays were separated by at least 24 hours. Spraying was carried out mainly in the early morning in windless conditions and lasted for about five minutes. After spraying, trays were left for at least three hours, to ensure that all fauna had fallen. Finally, the inside of each tray was brushed to ensure all animals fell into the vials. Specimens were stored in 70% alcohol. The sampling technique used in cool temperate rainforest was similar to that used on the tropical and subtropical sites except that spraying was carried out from a cherry-picker and a single species of tree (*Nothofagus moorei*) was sampled. In this forest, the whole tree was sprayed without any separation of low and high canopies.

2.3. Pitfall traps and leaf litter samples

In order to confirm that a suspected canopy specialist, only found in STR, was restricted in habitat and to compare species composition between canopy and leaf litter, twenty pitfall traps, 3 cm in diameter and 10 cm deep, half filled with 70% alcohol were set on two sites in subtropical rainforest under each tree that was to be fogged. They were inserted into a hole made with a soil corer until the rim was level with the soil surface and were left in place for 48 hours. The subtropical site was selected for this experiment, to test the degree to which the canopy specialist, *Epimetrura mirabilis* Greenslade & Sutrisno, 1994 was restricted to an arboreal habitat.

Five samples of soil and leaf litter from an area 25 cm^2 to a depth of 1 cm were taken from each site (tree) in the subtropical forest and fauna extracted into 70% alcohol using Tullgren funnels. They were heated with a 25 watt light bulb and extraction continued for 24 hours.

All taxa were sorted to order and Collembola were sorted to family and the most abundant families, the Entomobryidae and Paronellidae, were identified to species or morphospecies. A reference collection is deposited in the South Australian Museum.

2.4. Analysis

Abundance was measured as the number of individuals per tray (0.5 m^2) for insecticidal knockdown samples, number of individuals per 25 cm^2 for litter extraction and individuals per trap for pitfall trap samples. The following indices were calculated from the Entomobryidae and Paronellidae species data: species richness (*S*), Shannon-Wiener index (*H*) and Evenness (*E*).

Differences in species composition between the three forest types, were analysed using multidimensional scaling (nMDS) based on Bray-Curtis similarity matrix with a fourth root transformation. This was followed by ANOSIM and SIMPER to examine whether there were significant differences between forests. MDS plots were used to assist with the interpretation as they provide a diagrammatic illustration of differences. Primer 6© (Primer-E, Ltd, Luton, UK) was used for multivariate analyses.

To overcome unbalanced sites in the Tropical Rainforest and Sub tropical Rainforest, we fitted a logistic regression model using the GLM function in R (R Core Team 2015) specifying a Poisson distribution (Faraway 2006) . Because of the different sampling methods, this quantitative comparison of species abundance between rainforest strata was only carried out for the tropical and subtropical rainforest sites.

3. Results

3.1. Completeness of collections

A species discovery curve (cumulative species curve) was drawn (Fig. 1). There is no indication that an asymptote is being approached in tropical rainforest. For subtropical forest, the curve is curvilinear and there is an indication that an asymptote is being approached at 33 identified taxa. The plots for the cool temperate forest are more or less curvilinear with no obvious asymptote reached.

3.2 Percentage abundance of Collembola compared to all arthropods in three rainforests and three sampling methods

The dominant higher taxa and relative abundances collected from the canopy of tropical, subtropical and cool temperate sites are given in Table 1 and Kitching et al. (1993: Figs 2, 3). Out of a total of 38.280 arthropods collected, more than 7.900 (21%) were Collembola. They were most abundant in cool temperate (at 44.9%), less in subtropical forest (at 28.7%), and least in tropical forests (at 5.4%) of all invertebrates caught. Samples from different collecting methods contained different dominant arthropod groups. Litter collections were dominated by Acarina (33.0%), Collembola (20.3%) and Thysanoptera (21.0%) of a total 4052 individuals. Here density was 1,600 ± 16.88 individuals per 25cm^2. In the pitfall traps Acarina was the most abundant group (31.1%) followed by Collembola (27.0%) out of 480 invertebrate individuals (Sutrisno unpublished thesis 1994). The lowest percentage abundance of Collembola was found in high canopy samples (8.2% of 1523 individuals) of tropical and subtropical forests followed by the low canopy samples (16.1% of 1571 individuals) of tropical and subtropical forests.

3.3. Family composition of collections from different methods in subtropical forest

Combining all methods, eleven collembolan families were found out of a total of 19 in Australia (Greenslade 2007) in this rainforest. The family composition of collections from the different field methods differ markedly. The Entomobryidae were the most numerically abundant in all methods but the relative abundance of other families differed between sampling methods. Fig. 2 compares the mean relative abundance in each family collected from upper canopy (A), lower canopy (B), pitfall traps (C) and soil and leaf litter samples (D). Family composition differed with method with pitfall traps and soil/leaf litter samples collecting a greater range of families than the canopy samples. Canopy samples were dominated by entomobryids (high canopy 80.7%, low canopy 90.0%, pitfall traps 50.2%) and the soil and leaf litter samples by isotomids (44.2%). The Symphypleona were relatively abundant in canopies (high canopy 14.1%, low canopy 6.4%). The pitfall traps collected Paronellidae most abundantly after the Entomobryidae. The ground level samples contained a high proportion of unidentifiable immature Collembola (pitfall traps 18.8%, litter 14.0%).

3.4. Composition of tropical rainforest canopies

Eighteen morphospecies were identified in the two target families and more than half the individuals were Entomobryidae followed by the Dicyrtomidae, particularly in the low canopy. The Neanuridae, Paronellidae and unidentified immature forms occurred in similar numbers (approximately 7% for each). The Symphypleona, Isotomidae, Brachystomellidae and Odontellidae together comprised 7% of the total Collembola from these sites and each of these families was represented by only a few individuals.

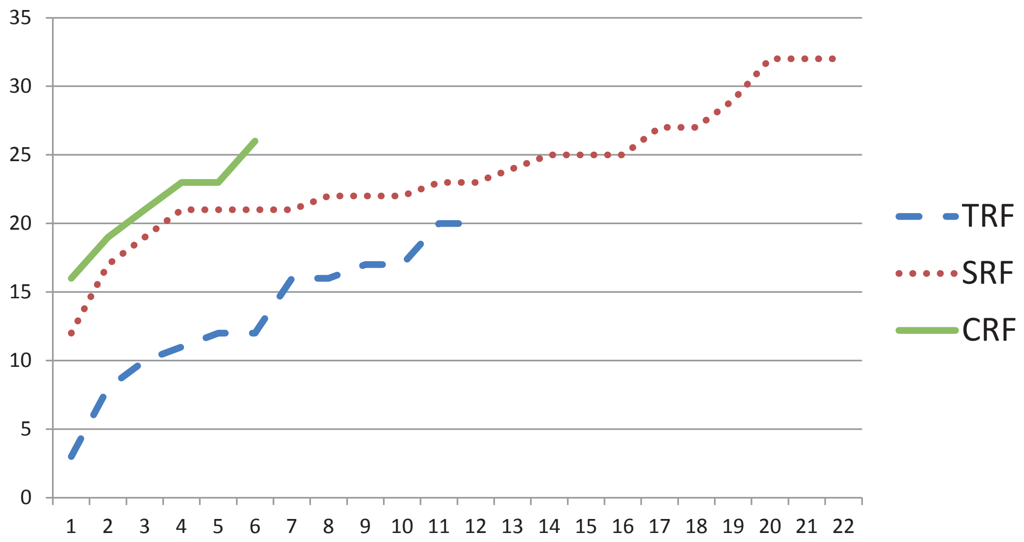

Figure 1. Cumulative species curve for Entomobryidae, Paronellidae and other families recognised from tropical (TRF) (6 trees), subtropical (SRF) (11 trees) and temperate canopies (CRF) (5 trees), low and high canopies combined.

Lepidocyrtoides sp. 6 was the dominant species (especially in the low canopy), comprising about 70% of total Entomobryidae collected. *Lepidocyrtoides* sp. 10, found more abundantly in the high canopy, was the second most abundant species comprising about 25% of total Entomobryidae. *Plumachaetas queenslandica* (Schött), *Acanthocyrtus* sp. and *Entomobrya* sp. cf. *varia* Schött, were also present in relatively small numbers (approximately 15%, 5% and 4% respectively). The remainder of species (5) were represented by only a few individuals.

In tropical rainforest, the diversity of entomobryids (*H*) was relatively low (0.4 1 and 0.3510 for high and low canopies respectively). However, the evenness (*E*) indices for this area were high i. e. 0.76 and 0.69 for high and low canopies respectively. This indicates low species dominance.

3.5. Composition of subtropical rainforest canopies

On subtropical site canopies, thirty one taxa were collected (18 morphospecies in the two families identified) and the dominance of the Entomobryidae over other families was more marked than in the tropical rainforest. More than 80% Collembola were Entomobryidae followed by Isotomidae, and Paronellidae. The other families (Brachystomellidae, Dicyrtomidae, Neanuridae, Odontellidae and Symphypleona) were represented by relatively few individuals together at 10% of total Collembola (Fig. 2).

In terms of numbers of species, the subtropical sites were the richest, with fifteen species in the high canopy and seventeen species found in the low canopy. The canopy specialist *E. rostrata*, dominated and comprised

Table 1. Mean number of Collembola, and other arthropods per 0.5 m² collecting tray from A – tropical (6 trees), subtropical (9 trees) and B – cool temperate (5 trees) rainforests.

Taxon	Canopy height	Tropical rainforest		Subtropical rainforest		Cool temperate rainforest	
		Mean number	%	Mean number	%	Mean number	%
Collembola	High	3.12 ±0.53	3.70	15.51 ±2.72	17.09	34.73 ±14.39	44.92
	Low	4.14 ±1.10	8.31	46.41 ±6.46	41.88		
Insecta	High	81.02 ±10.83		75.24 ±14.24		42.58 ±6.98	
	Low	45.71 ±3.51		64.41 ±11.75			
Other Arthropoda	High	19.20 ±10.82		16.26 ±2.42		77.31 ±17.06	
	Low	8.84 ±0.86		23.07 ±3.64			
Total Arthropoda	High	103.34 ±10.03		107.00 ±17.28		20.15 ±4.23	
	Low	58.68 ±3.71		133.89 ±18.85			
Grand total		**162.02 ±11.36**		**240.89 ±24.14**		**97.45 ±18.47**	

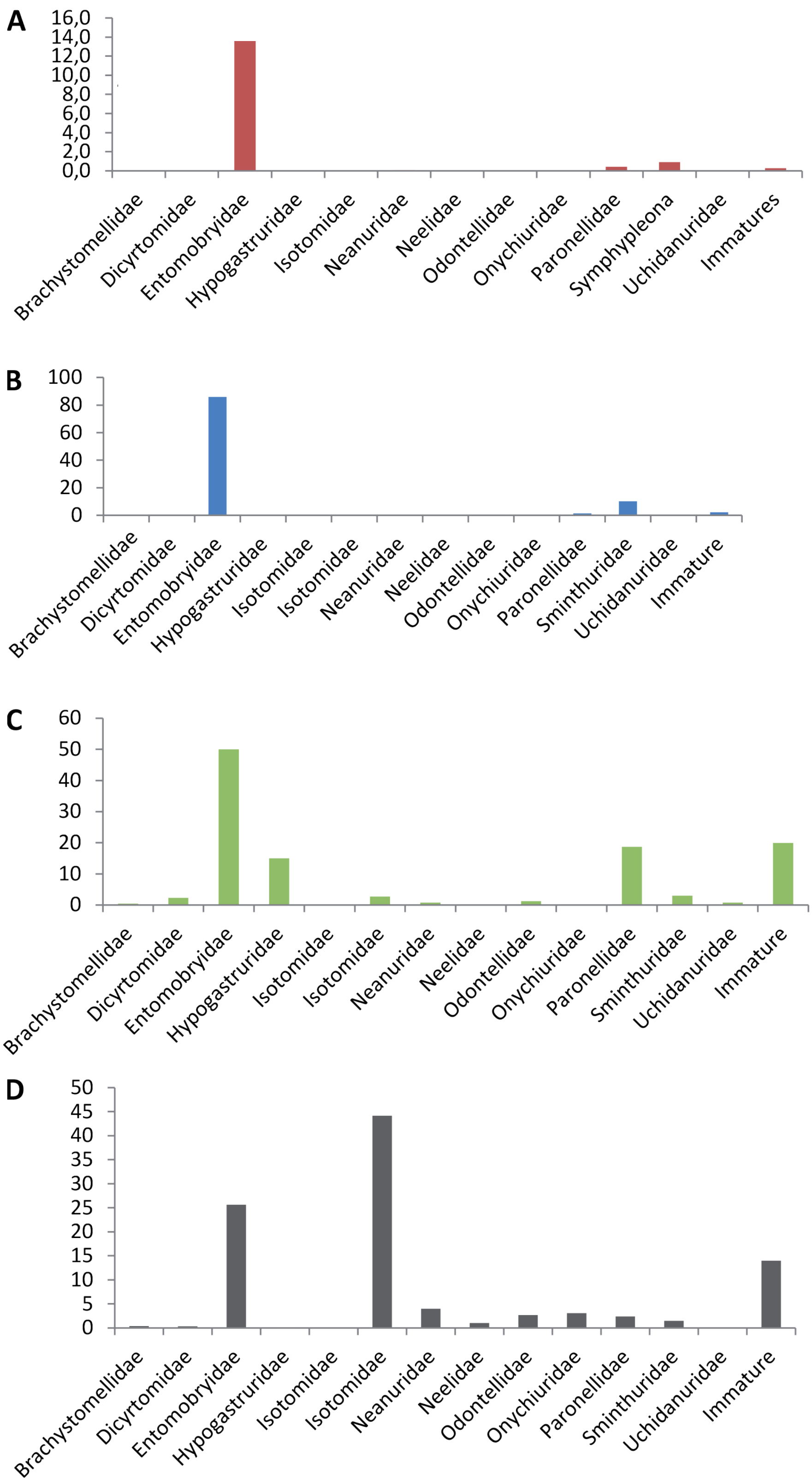

Figure 2. Relative abundance of collembolan families in subtropical rainforest collected by different methods in different strata. (**A**) upper canopy, (**B**) lower canopy, (**C**) pitfall catches, (**D**) soil and leaf litter extraction. Number of trees as in Figure 1. Fogging date is expressed as individuals per tray, pitfall data as individuals per pitfall trap and soil/leaf litter data as individuals per 25 cm^2. Vertical axis denotes individuals.

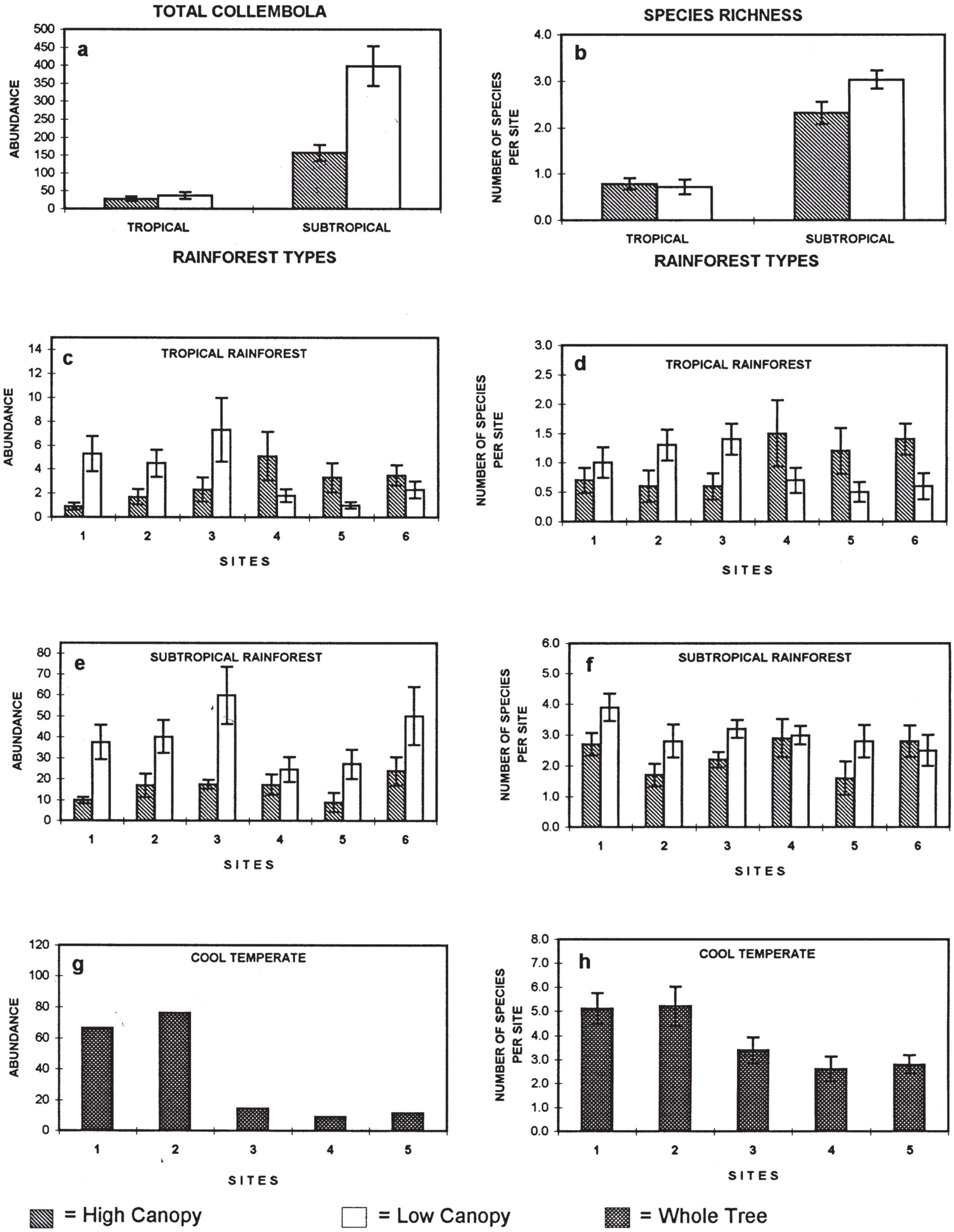

Figure 3. Abundance (mean ± 1SD, *n* = 10 trays) and species richness (mean ± 1SD, *n* = 10 trays) of Collembola in each stratum within two rainforest types and for each site (trees) in all three rainforests. Cool temperate rainforest strata were not sampled separately. Number of trees as in Figure 1.

more than 60 % of total Collembola. Other species present were *E. varia* and *Lepidocyrtus* sp. 5. About half of the total species collected were represented by a single individual**.**

Although in subtropical rainforest the species richness value (*S*) was highest (Annex 1), the diversity and evenness indices were relatively low, the diversity being 0.67 and 0.264 for high and low canopies respectively and the evenness 1.1461 and 1.1139 for high and low canopies respectively (Annex 1). This was presumably due to the considerable skew because of the high abundance of *E. rostrata*.

3.6. Composition of cool temperate forest canopies

Eighteen morphospecies were collected comprising 1900 individuals, where more than 50 % were Entomobryidae. The next most abundant families were Neanuridae (13.9 %) and Paronellidae (12 %). The family Dicyrtomidae, which was present in the other two types of rainforests, was absent from the cool temperate rainforest samples. Hypogastruridae were only found in samples from cool temperate rainforest, although this family was represented by only 1 % of total Collembola.

The most numerically abundant species in this rainforest was *E.* sp. cf. *varia* (63 %), however the degree of dominance did not match that of *E. rostrata* in subtropical sites. Other species occurring in relatively large numbers in cool temperate rainforest were *Paronellides* sp. cf. *dandenongensis* Womersley (15 %), *Willowsia* sp. (9 %), *Entomobrya* sp. 2. (8 %), *Entomobrya* sp. 6 (6 %) and *Lepidocyrtoides* sp. 5 (4 %). Once again, in these samples, about half the species were represented by only a few individuals.

The cool temperate rainforest sites had the highest diversity value (0.62). The evenness index for this area was also relatively high at 0.64 (Sutrisno unpublished thesis, 1994).

3.7. Vertical stratification

Collembola were more abundant in the low canopy than in the high canopy in both tropical and subtropical forests (Fig. 3A, B). On tropical sites, Collembola comprised 3.7 % and 8.31 % of all individuals trapped were in the high and low canopies respectively (Table 1, Fig. 3C) and in the subtropical rainforest, 17.09 % of total individuals trapped were in the high canopy and 41.88 % in the low canopy (Table 1, Fig. 3E).

The MDS plot (Fig. 4) which compares species abundances between upper and lower canopies of subtropical and tropical rainforest suggests there is no difference in vertical difference. Subtropical trees are more similar in this respect than tropical trees based on a tighter clustering of sites and stratification.

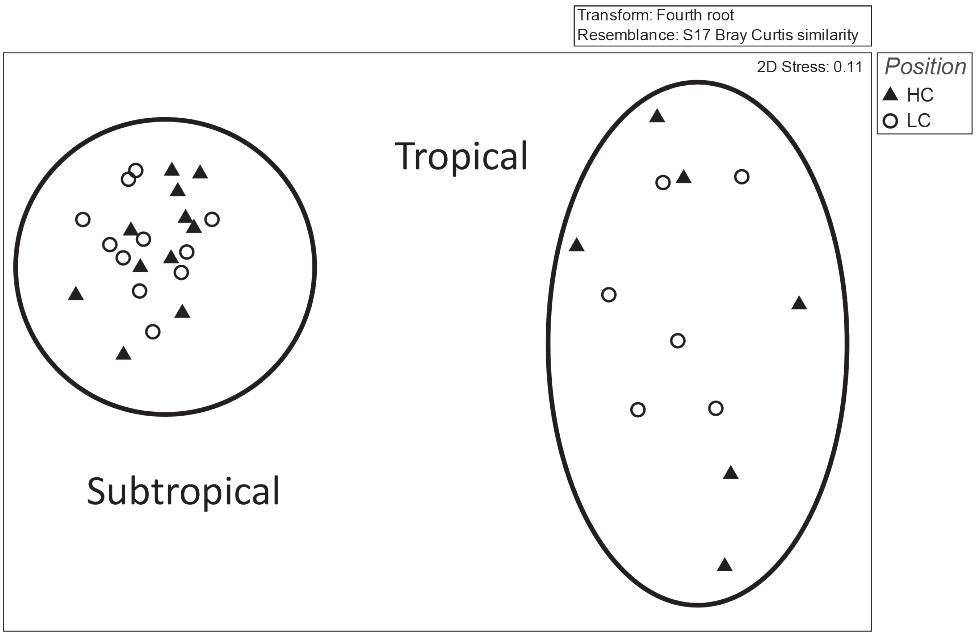

Figure 4. Multi Dimensional Scaling plot of vertical distribution based on species composition for subtropical and tropical rainforests, High canopy (▲) and Low Canopy (○) with stress value of 0.11. Number of trees as in Figure 1.

3.8. Comparison between rainforests

The ordination of species composition (presence and absence) between the tropical and subtropical forests with upper and lower canopies combined, and cool temperate rainforest indicated a clear separation (Stress-0.09) between rainforests (Fig. 5). This is based on the tight clustering of each site (trees) within each of the three rainforest types without any overlap, particularly marked in the subtropical rainforest cluster.

Table 2 provides a breakdown of the results from the logistic regression. It is evident that the forest as well as the canopy strata strongly affect species abundances at a significant level. The interaction of forest type and canopy stratum shows, also, that changes in species abundance between strata differ within the two (subtropical and tropical) forest types. An estimate of the usefulness of the model ($R^2 \sim 0.258$) shows, however, that much of the total variance i.e. nearly 75 %, remains unexplained.

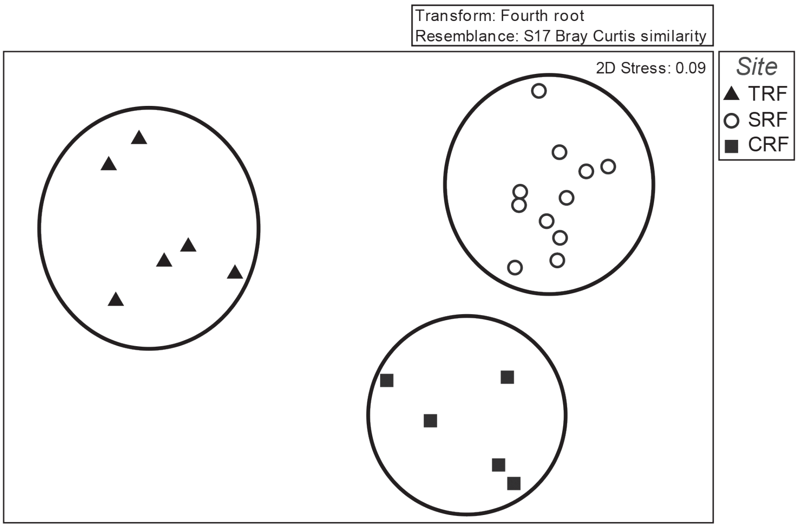

Figure 5. Multi Dimensional Scaling plot of species composition of Tropical rainforest (TRF) (▲), subtropical rainforest (SRF) (○) and cool temperate rainforest CRF (■) with stress value of 0.09. Both upper and lower strata were pooled. Each point represents data from a single tree (10 trays). Number of trees as in Figure 1.

Table 2. General linear model (GLM) with Poisson distribution for tropical and subtropical Collembola, high and low canopies. The estimate of model coefficient is shown to be significant for forest and strata.

Source	Estimate	SE	Z value	P value
Intercept	6.55	0.01	541.24	<0.01
Forest	-2.85	0.07	-47.78	<0.01
Stratum	-1.54	0.03	-54.78	<0.01
Forest *x* Stratum	1.26	0.11	11.84	<0.01

Table 3. Summary of a table of means showing significant differences in collembolan variables (P < 0.05) between sites (trees) within each rainforest type after a Tukey test was performed. For high canopy in tropical rainforest, neither collembolan abundance nor species richness and in subtropical rainforest species richness were not significantly different and so are not included.

	Sites (trees)	1	2	3	4	5	6
Tropical rainforest, low canopy	Abundance	5.3^{ab}	4.5^{ab}	7.3^{b}	1.8^{ab}	1.0^{a}	2.3^{ab}
	Species richness	1.3^{a}	1.0^{ab}	1.4^{a}	0.7^{b}	0.5^{b}	0.6^{b}
Subtropical rainforest, high canopy	Abundance	9.8^{ab}	16.9^{ab}	17.4^{b}	17.3^{ab}	8.8^{a}	23.7^{b}
Subtropical rainforest, low canopy	Abundance	37.5^{ab}	40.1^{ab}	59.8^{b}	24.4^{ab}	27.0^{a}	50.0^{b}
Cool temperate rainforest	Abundance	66.5^{a}	76.0^{a}	14.5^{b}	9.1^{b}	11.4^{b}	
	Species richness	5.1^{ab}	5.2^{ab}	3.4^{bc}	2.6^{c}	2.8^{bc}	

3.9. Comparison between trees (sites)

Table 3 and Figure 3 shows the differences in abundance and species richness of each site (tree) in the three rainforests. There was a significant difference between some trees in both the low canopy and upper canopy in subtropical forest but not in the high canopy. In cool temperate rainforest, the abundance and number of species of Collembola were also significantly different between some trees. In tropical rainforest, higher abundance in lower canopy compared to upper was only exhibited by half the tress.

3.10. Pitfall and leaf and soil samples in subtropical rainforest

The family composition of collections from the different field methods are shown to differ markedly. Sutrisno (unpublished thesis 1994) lists 24 taxa from pitfall traps and 26 from litter samples for subtropical forest. There was little overlap between species found in the surface strata compared to above the ground. Species that were found in all four habitats included *Acanthocyrtus* sp., *E. rostrata* (only low numbers), *Pseudoparonella queenslandica*, *Pseudoparonella* sp. 4 and *Pseudoparonella* sp. 5.

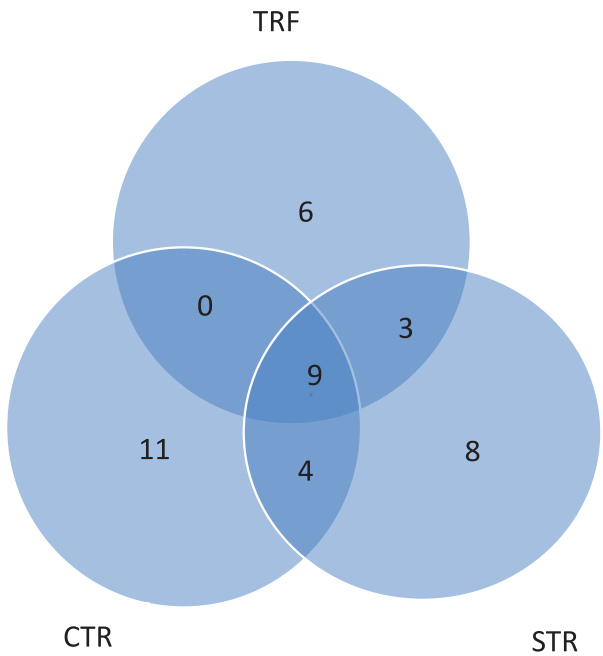

Figure 6. Venn diagram showing distributions of all taxa recognised between three rainforests. Tropical rainforest (TRF), Subtropical rainforest (STR), and Cool Temperate rainforest (CTR). Number of trees as in Figure 1.

The pitfall trap samples were dominated by *Lepidosira* sp. 2 and *Pseudoparonella* sp. 4 at 18% of total Collembola. The other abundant species in this sample were *Pseudoparonella* sp. 2 while *E. rostrata, Lepidocyrtoides* sp. 1 and *Lepidocyrtoides* sp. 6 occurred in a relatively similar abundance (0.5 ind. /trap). The most numerically abundant species in the litter samples were *Lepidosira* sp. 2 (12%) followed by *Lepidocyrtus* sp. 32 (1.2%) after the family Isotomidae.

The soil and leaf litter samples generated the highest level of species diversity (0.4888) as indicated by the Shannon-Wiener Index (*H*) (Annex 1). The lowest diversity was found in the low canopy stratum (0.26). The diversity index of high canopy stratum and pitfall traps were 0.4430 and 0.4098 respectively. A relatively low evenness index for each stratum indicates the uneven distribution of abundance of entomobryid species. Among these the low canopy stratum was the most uneven having an index of only 0.1909 (Annex 1).

3.11. Morphospecies differences between rainforests

Annex 2 lists all the taxa recognised in the canopies of the three rainforest types. Twenty-eight species of Entomobryidae and seven species of Paronellidae were found. Six of the 18 species found in the tropical samples were not collected in the other rainforests. Similarly eight of 24 species in subtropical samples and eleven out of the 24 species in cool temperate samples were restricted. Only nine species occurred in all three rainforests (Fig. 6). As noted above the dominant species varied between rainforest types also.

4. Discussion

Our data demonstrate that the canopies of three different types of rainforests in Australia are significantly different in collembolan composition at both family and species level, indicating a high beta diversity, and that abundance and species richness is high in some families. As no other comparisons have been made of canopy collembolan from different rainforests over a latitudinal range of 15°, our data is new. These results should be qualified for the following reasons. Twenty trees in all were sampled and there were some significant differences in composition and abundance between trees within each forest which suggests that the sampling size was small rather than a bias in sampling. A species discovery curve indicated that the eleven subtropical trees provided an adequately representative sample, although this was not so for tropical and cool temperate rainforests. Although few of our species had been described, which potentially provides problems when comparing sites, all identifications were made by the same person, so potential errors would be minimised.

The lower numbers of Collembola in the tropical rainforest collections may reflect an adverse marine influence, such as periodic cyclonic disturbances, high air salinity and/or the dominance of palms, as this vegetation is not a favoured habitat for Collembola. Lower numbers were also found on ten Tasmanian rainforest trees (Yen and Lilywhite in Coy et al. 1993) (3.7 % of total catch) than for a *Nothofagus* canopy in northern New South Wales (35 %) and differences in methods may, at least partly, account for this. Collembola abundance from 147 Tasmanian rainforest tree trunks (equivalent to low canopy) collected using a pyrethrum knock down technique, comprised from 10 to 60 % of specimens of total catch. Numbers varied directly with the rainfall over the previous three days (Coy et al. 1993). Yen and Lilywhite's sampling in summer (February 1990) may have been conducted under unfavourable weather conditions for Collembola while ours were all conducted during autumn. Significantly, Basset (2001) notes that variance in faunas is better explained by type of forest than by biogeography.

The numerical dominance of species of Entomobryidae, and to a lesser extent, Paronellidae, is the most striking feature of the family profiles of Collembola from each rainforest. This degree of dominance is greater than might be expected as for the whole of Australia Entomobryidae comprise 28 % (Greenslade 2007). Our results are in agreement with the results of Rodgers (1999 unpublished) for subtropical forest canopies although both absolute abundance and relative abundance of Collembola of total arthropods, were found to be higher in the present study.

In Tasmanian rainforests, Paronellidae was the dominant family with 6 species, 4 species of Entomobryidae and 14 species in 6 other families (P. Greenslade in press). Samples from tropical forest in Sulawesi contained 9 species of Entomobryidae, 5 of Paronellidae and 17 species from 5 other families (P. Greenslade unpublished data). This is a reflection of the epigaeic nature of this family, members of which are adapted to living above the ground as they possess long appendages (Ponge 1993).

Each rainforest was distinctive in that the most numerically abundant species differed and each of these was found in lower numbers in the other types of rainforests or was absent. Subdominant families also differed between forests which may be a reflection of different climatic optima for each of them. The percentage of rare species, here considered to be any species represented by no more than a single individual per site, was highest in the tropical rainforest (44 %) compared with subtropical and cool temperate rainforests (13 % and 23 % respectively). McArdle (1990) pointed out that the more samples which are taken from a habitat, the lower the rate at which rare species appear. This may be relevant to results obtained in the present study, given the unequal sampling intensity. Indeed, Basset & Kitching (1991), in their study on arboreal arthropods associated with *Agyrodendron actinophyllum*, suggest that individual species rarity may be a sampling or sorting bias.

Few canopy specialised species have been described worldwide and only one was detected here, *E. rostrata* in the subtropical rainforest. Bretfeld (2002) and Bretfeld & Trinklein (2000) described nearly 20 species, all Symphypleona, from Brazilian and Ecuadorean rainforest canopies but these species are in an Order not identified to species in our samples. There are indications that a number of bark and epiphyte specialists in Isotomidae and maybe other families, occur in Tasmania (Coy et al. 1993). In Europe, *Vertagopus* species (Isotomidae) and a few *Entomobrya* species (Entomobryidae) may be exclusively bark living species and *Willowsia* species (Entomobryidae) are almost invariably associated with trees.

Some studies have shown a close association between arboreal and ground living Collembola, and documented movements of individuals between the ground and above ground habitats, depending on environmental conditions. For instance, Bowden et al. (1976) and Farrow & Greenslade (1992) showed vertical migration of Collembola from the ground up tree trunks into the canopy. Of relevance is that Stork (1991) showed in Borneo that Collembola were one of the groups that reappeared most rapidly in the canopy following insecticidal spraying, indicating the high mobility of this group.

Delamare-Deboutteville (1951) was the first to record an abundant collembolan fauna living on trees in tropical rainforest. He coined the term '*sols suspendues*' to describe this habitat, pointing out that dense lianes, vines, orchids and other plants trap dead plant material matter within plant crevices, which decomposes producing soil which then is colonised by soil fauna. A number of studies, both in Australia and elsewhere, have confirmed and quantified the presence of a well developed arboreal and epiphyte collembolan fauna, including soil species, in rainforests (Paoletti et al. 1991, Stork 1991, Guilbert et al. 1995, Palacios-Vargas & Castaño-Meneses 2003, Palacios-Vargas et al. 1998, Keller et al. 2003, Rodgers & Kitching 1998, 2011, Wardhaugh et al. 2014). Yanoviak et al. (2003) notes that the epiphyte fauna is not efficiently sampled with canopy fogging.

Table 4. A comparison of Collembola species richness and relative abundance in canopies of Australian and other rainforests. Abundance is based on the numbers of individuals per m². Percentage was based on the proportion of Collembola to total arthropods.
* – Number of species is only for Entomobryidae and Paronellidae, w – winter sample, s – summer sample, + – Beating understorey only.

Locality (sites=trees)	Latitude	Abundance (ind./m²)	% of total abundance	No. of species	Sources
Finland	65°N	NA	20	34	Laine et al. 1990
Norway (2 sites)	60°N	NA	NA	23	Thunes et al. 2004
Northern England (2 sites)	54°–55°N	NA	NA	11	Shaw et al. 2007
Ontario, Canada (4 sites)	47°39’	NA	10.7	10	Martin 1966
Japan (6 sites)	40°39’N	NA	NA	18	Uchida 1969
Japan (1 site)	35°	NA	NA	6(?+)	Yoshida & Hijii 2005b
Hawaii (8 sites)	20°N	NA	NA	14	Gagné,1979
Mexico Valley (18 sites)	19°	NA	30	11	Tovar-Sanchez 2009
Chamela, Mexico (7 sites)	19°30’N	15	70	19	Palacios-Vargas et al. 1998
Chajul, Mexico (NA)	17°N	30	9	26	Palacios-Vargas et al. 1998
Panama	9°16’N	NA	NA	33LC 16UC	Basset et al. 2015
Sulawesi, Indonesia (4 sites)	2°N	NA	NA	30	P. Greenslade, unpubl.
Borneo (NA)	4°N	3.7	3.1	22	Stork 1991, 1987 a,b
Seram, Indonesia (‘several trees’)	6°S	18	4.1	21	Stork & Brendell 1993, P. Greenslade, unpubl.
Daintree, North Queensland					
High canopy	16°S	6.2	3	12*	Present study
Low canopy		8	8	4*	
New Caledonia (2 sites)	20°S	NA	18.6	32	Guilbert et al. 1995
Brazil (4 sites)	29°25’S	NA	NA	12	Ribeiro-Troian 2009
Lamington, New South Wales					
High canopy	28°S	NA	NA	16s, 10w+	Rodgers 1999
Low canopy				26s, 13w+	
Lamington, New South Wales					
High canopy	28°S	31	17	15*	Present study
Low canopy		93	42	17*	
Styx River State Forest, NSW, Australia	30°S	70	45	16*	Present study
Tasmania (10sites)	45–45°S	40	3.7	24	Coy et al. 1993

In our study the epiphytic flora differed between each rainforest. Cool temperate rainforest was typified by the prominence of micro-epiphytes such as small ferns, lichens, mosses and algae, while the subtropical and tropical rainforests have a greater variety of larger epiphytes such as orchids. These differences would influence both species composition and abundance of Collembola. For instance, the occurrence of more numerous Neanuridae and Isotomidae species in samples from *Nothofagus* may indicate the influence of moss, as it is known to harbour a diverse fauna of Collembola of which some species may be specialised for living on trees (Cutz-Pool et al. 2010). Paoletti et al. (1991), sampling epiphytic bromeliads and associated root masses in Venezuelan rainforest, reported 'soil' Collembola as the most abundant group of 'soil' micro-invertebrates, after Acarina, inhabiting the canopy in their studies in a cloud forest.

In order to test for any latitudinal trends, we list in Table 4 numbers of Collembola species and percentage abundance of the group from 20 published papers. Data ranged from forests at 60ºN to 40ºS. There appears to be no latitudinal trend in species numbers or relative abundance except possibly lower abundance in the tropics where ants, a predator of Collembola are numerically predominant. However, different methods and expertise in collection and different tree species most likely also influenced results.

The most comprehensive study of vertical stratification in Australian subtropical rainforests was published by Rodgers (Rodgers 1999, Rodgers & Kitching 1998) who compared collembolan faunas of soil, forest floor leaf litter, epiphyte leaf litter, canopy foliage and bark surfaces. They found each habitat had a significantly different fauna and that the major influence on upper and lower canopies was season. We found significant differences in species abundance between low canopy and high canopy as they did in the subtropical and tropical rainforests but not in species composition. Rodgers (1999) identified all families to species so his data was more complete than ours. Also we found significant differences in abundance between trees which is likely to have influenced our results. The greater abundance of Collembola in the low canopy, as opposed to the high canopy, may reflect a difference in habitat type and the harshness of environmental conditions. It is well known that temperature and humidity have been shown to be of major importance within the life cycle of Collembola. Lindo & Winchester (2013) documented strong gradients of moisture, temperature and climatic stability associated with canopy height and distance from trunk in rainforest and showed that epiphytes also influence canopy microclimates. The same effects would be present in Australian rainforest ecosystems.

Rodger's study (1999) examined connections between the ground, *sols suspendues* and canopy stratification in subtropical rainforest but not migration events which have been documented by Bowden et al. (1976) in England, by Yoshida & Hijii (2005a, b) in Japan and Farrow & Greenslade (1992) in Australia. These authors suggested reasons for migration could be dispersal, to avoid flooding on the ground after rain, and/or to forage for food. If vertical dispersal is occurring in Australian rainforests then strata differences are likely to be reduced.

A major question not addressed in this study concerns the functional importance of Collembola in the Australian rainforest canopy. As Stork (1991) wrote 'The immense species richness of the canopy fauna raises immediate questions as to what all these species are doing there and how they interact'. Several authors have emphasised that '*sols suspendues*' provide a major nutrient pool associated with epiphytes in the rainforest canopy and so are likely to contribute to maintaining integrity of the forest ecosystem (Nadkarni 1984, Nadkarni & Longino 1990, Rodgers & Kitching 1998, 2011). Another issue is the conservation significance of our results in the context of climate change. Because each rainforest carried a unique fauna, beta diversity is high. Forests provide a myriad of ecosystem services (Nahuelhual et al. 2007) and any diminution in our forest resource would not only mean the loss of these services but also the loss of a number of species of apparently restricted distributions.

5. Acknowledgements

This study was funded by Australian Research Council and Earthwatch (Australia). Participation of Mr. Sutrisno was made possible through a studentship provided by International Development Program (IDP) of Australian Universities and Colleges. Research assistance for the project was been provided by many volunteers. Mr Sutrisno also thanks supervisors R. Kitching and B. Jenkins of the University of New England, Armidale. Permission to work on the three sites was granted by the O'Reilly family at Green Mountain, and the Truelove family and Mr. P Shears at Cape Tribulation. Lastly we thank the Forestry Commission of New South Wales for permission to work in the Styx River State Forest and Patrick Gratz for statistical advice.

6. References

Ashton, L. A., A. Nakamura & Y. Basset et al. (2015): Vertical stratification of moths across elevation and latitude. − Journal of Biogeography **43**(1): 49–69 [DOI: 10.1111/bi.1261].

Basset, Y. (1990): The arboreal fauna of the rainforest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging: Composition of the fauna. − Entomologist **109**: 173–183.

Basset, Y. (1991a): The taxonomic composition of the arthropod fauna associated with an Australian rainforest tree. − Australian Journal of Zoology **39:** 171–90.

Basset, Y. (1991b): The seasonality of the arboreal arthropods foraging within an Australian rainforest tree. – Ecological Entomology **16**: 265–278.

Basset, Y. (2001): Invertebrates in the canopy of tropical rainforests. How much do we really know? – Plant Ecology **153**: 87–107.

Basset, Y. & R. L. Kitching (1991): Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. − Ecological Entomology **16**: 391–402.

Basset, Y., L. Cizek & P. Cuénoud et al. (2015): Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. – PLOS 1 **10**(12): e 0114410 [DOI: 10.1371/journal. Pone].

Bowden, J., i. H. Haines & D. Mercer (1976): Climbing Collembola. − Pedobiologia **16:** 298–312.

Bretfeld, G. (2002): Known and new genera and species of Symphypleona (Insecta, Collembola) obtained by canopy fogging in Central Amazonia, Brazil. – Amazonia **17**: 109–137.

Bretfeld, G. & N. Trinklein (2000): New Collembola Symphypleona from the tropical cloud forest of Ecuador (Insecta). − Abhandlungen und Berichte des Naturkundemus Görlitz **72**: 177–194.

Burbidge, N. T. (1960): The phytogeography of the Australian region. − Australian Journal of Botany **8**: 75–212.

Camann, M. A., K. L. Lamoncha & B. J. Clinton (2000): Old-growth Redwood forest canopy arthropod prey base for arboreal wandering salamanders: A report to Save-the-Redwoods League. − Humboldt State University, Arcata, USA: 1–104.

Coy, R., P. Greenslade & D. Rounsevel (1993): A Survey of invertebrates in Tasmanian rainforest. A report for the National Rainforest Conservation Programme. – Department of Parks, Wildlife and Heritage, Tasmanian Government. Forestry Commission, Tasmania: 1–104.

Cranston, P. S. & I. D. Naumann (1991): Biogeography. – In: Naumann, I. & E. Nielsen (eds): The Insects of Australia. Vol. 1. Second Edition. – Melbourne University Press, Melbourne, Australia: 181–197.

Cutz-Pool, L. Q., J. G. Palacios-VargasG., Cano-Santana, Z. & Castaño-Meneses, G. (2010): Diversity Patterns of Collembola along an elevational gradient on the northwest slope of Iztaccihuatl volcano, State of Mexico. − Entomological News **121**: 249–261.

Delamare–Deboutteville, C. (1951): Les dépendances du Sol et les Sols suspendus. Considérations sur les facteurs historiques en biocénotique. − College nationale de la récherche scientifique I'Ècologie. Annales Biologia **27**: 267–280.

Erwin, T. L. (1982): Tropical forests: their richness in Coleoptera and other arthopod species. − Coleopterists' Bulletin **36**: 74–75.

Erwin, T. L. (1983): Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In: Sutton, S. L, T. C. Whitmore & A. C. Chadwick, (eds) Tropical rain forest: ecology and management. – Blackwell Science. Publications, Oxford: 59–75.

Erwin, T. L. & J. C. Scott (1980): Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystem: The fauna of the tree *Leuhea seemanii* Triana and Planch in the canal zone of Panama. − Coleopterists' Bulletin, **34**: 305–322.

Faraway, J. J. (2006):Extending the linear model with R: (1st ed.). Boca Raton, Florida: Taylor & Francis Group, LLC.

Farrow, R. A. & P. Greenslade (1992): A vertical migration of Collembola. − The Entomologist **111**: 38–45.

Floyd, A. G. (1990):Australian rainforests in New South Wales, Volume 2. Surrey Beatty, Chipping Norton, NSW: 1–136.

Gagné, W. C. (1979): Canopy-associated arthropods in *Acacia koa* and *Metrosideros* tree communities along an altitudinal transect on Hawaii Island. − Pacific Insects **21:** 56–82.

Greenslade, P. (2007): Check list for Australian Collembola. Australian Faunal Directory [http://www.environment.gov.au/biodiversity/abrs/online-resources/fauna/afd/COLLEMBOLA/tree.html].

Greenslade, P. (In press): Arboreal springtails in Tasmanian rainforests. - Tasmanian Naturalist

Greenslade, P. & Sutrisno (1994): A new species of *Epimetrura* (Collembola: Insecta): from Australian subtropical rainforest canopy. − Annales. Zoological Fennica **195:** 52–57

Guilbert, E., J. Chazeau & L. Bonnet de Larbogne (1994): Canopy arthropod diversity of New Caledonian forests sampled by fogging: preliminary results. Memoirs of the Queensland Museum **36**: 77–35.

Guilbert, E., M. Baylac & J. Najt (1995): Canopy arthropod diversity in a New Caledonian primary forest sampled by fogging. − Pan-Pacific Entomologist **71**: 3–12.

Hammond, P. M. (1990): Insect abundance and diversity in Dumoga Bone National Park, North Sulawesi, with special reference to the beetle fauna of lowland rainforest in the Toraut region. In: Knight, W. J. & J. D. Holloway, (eds), Insects and the rain forests of South East Asia (Wallacea). – Royal Entomological Society of London, London: 197–260.

Heterick, B. E., J. D. Majer, H. F. Recher & A. C. Postle (2001): A checklist of canopy, bark, soil and litter fauna of the Darling Plateau and adjacent woodland near Perth, Western Australia, with reference to the conservation of forest and woodland fauna. − Bulletin **21**. School of Environmental Biology. – Curtin University of Technology, Perth: 1–33.

Jessup, I. W. & G. P. Guymer (1985): Vascular plants recorded from the Cape Tribulation area. − Queensland Naturalist **26**: 2–19.

Keller, H. W., P. G. Davison, C. H. Haufler & D. B. Lesmeister (2003): *Polypodium appalachianum*: an unusual tree canopy epiphyte in the Great Smoky Mountains National Park. − American Fern Journal **93**: 36–41.

Kitching, R. L., J. M. Bergelson, M. D. Lowman, S. McIntyre & G. Carruthers (1993): The biodiversity of arthropods from Australian rainforest canopies: General introduction, methods, sites and ordinal results. − Australian Journal of Ecology **18**: 181–192.

Laine, A., M. Orell & J. Itämies (1990): Invertebrate fauna on Norwegian Spruce (*Picea abies*) branches in northern Finland. − Entomologica Fennica **1**: 193–199.

Lindo, Z. & N. Winchester (2013): Out on a limb: microarthropod and microclimate variation in coastal temperate rainforest canopies. − Insect Conservation and Diversity **6**: 513–521.

Majer, J. D. (1990): The abundance and diversity of arboreal ants in Northern Australia. − Biotropica **22**: 191–199.

Majer J. D., H. F. Recher & A. C. Postle (1994): Comparison of arthropod species richness in eastern and Western Australian canopies: a contribution to the species number debate. − Memoirs of the Queensland Museum **36**: 77–85.

Linton Martin, J. (1966): The insect ecology of red Pine plantations in Central Ontario IV. The crown fauna. − The Canadian Entomologist **98**: 10–27.

McArdle, B. H. (1990): When are rare species not there? − Oikos **57**: 276–277.

McDonald, W. J. F. & M. B. Thomas (1990): Flora of Lamington National Park, 2nd edition. Queensland Department of Primary Industries, Brisbane: 1–25

Nadkarni, N M. (1984): Epiphyte biomass and nutrient capital of a Neotropical elfin forest. − Biotropica **16**: 249–256.

Nadkarni, N. M. & Longino, J. T. (1990): Invertebrates in canopy and ground organic matter in a Neotropical montane forest, Costa Rica. − Biotropica **22**: 286–289.

Nahuelhual, L., P. Donoso, A. Lara, D. Núñez, C. Oyarzún & N. Neira (2007): Valuing ecosystem services of Chilean temperate rainforests. − Environment, Development and Sustainability **9:** 481–499.

Ozanne, C. M. P., D. Anhuf & S. L. Boulter (2003): Biodiversity meets the atmosphere: a global view of forest canopies. – Science **301**: 183–186.

Palacios-Vargas, J. G. & G. Castaño-Meneses (2003): Seasonality and community compositions of springtails in Mexican forests. Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy. – In: Basset, Y., V. Novotny, S. E. Miller & R. L. Kitching (eds): Cambridge University Press: 159–169.

Palacios-Vargas, J. G., G. Castaño–Meneses & H. A. Gŏmez-Abayam (1998): Collembola from the canopy of a Mexican tropical deciduous forest. − Pan-Pacific Entomologist **74**: 47–54.

Paoletti, M. G., R. A. J. Taylor, B. R. Stinner, D. H. Stinner & D. H. Benzing (1991): Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. − Journal of Tropical Ecology **7**: 373–383.

Park, C. C. (1992): Tropical rainforests. – Routledge, London: 188 pp.

Ponge, J. F. (1993): Biocenoses of Collembola in Atlantic temperate grass-woodland ecosystem. – Pedobiologia **37**: 223–244.

R Core Team (2015): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria http: //www.R-project.org/

Ribeiro-Troian, V. R., R. Baldissera & S. M. Hartz (2009): Effects of understorey structure on the abundance, richness and diversity of Collembola (Arthropoda) in Southern Brazil. − Neotropical Entomology **38**(3): 340–245.

Rodgers, D. J. (1999): Structural dynamics of rainforest collembolan assemblages in leaf litter suspended in epiphytes and on the forest floor. – Thesis in fulfilment of a Doctor of Philosophy at the Australian School of Environmental Studies, Faculty of Environmental Sciences, Griffith University, Queensland, Australia: 210.

Rodgers, D. J. & R. L. Kitching (1998): Vertical stratification of rainforest collembolan (Collembola: Insecta): assemblages: description of ecological patterns and hypotheses concerning their genera. – Ecography **21**: 392–400.

Rodgers, D. J. & R. L. Kitching (2011): Rainforest Collembola (Hexapoda: Collembola): and the insularity of epiphyte microhabitats. − Insect Conservation and Diversity **4**: 99–106.

Shaw, P., C. Ozanne, M. Speight & I. Palmer (2007): Edge effects and arboreal Collembola in coniferous plantations. Pedobiologia **51**: 287–293.

Socolar, J. B., J. J. Gilroy, W. E. Kinin & D. P. Edwards (2016): How should beta-diversity inform biodiversity conservation? − Trends in Ecology and Evolution **31(**1): 67–80.

Southwood, T. R. E., G. R. W. Wint, C. E. J. Kennedy & S. R. Greenwood (2005): The composition of the arthropod fauna of the canopies of some species of oak (*Quercus*). − European Journal of Entomology **102:** 65–72.

Stork, N. E. (1987a): Arthropod faunal similarity of Bornean rain forest trees. − Ecological Entomology **12**: 219–226.

Stork, N. E. (1987b): Guild structure of Arthropoda from Bornean rain forest trees. − Entomology **12**: 69–80.

Stork, N. E. (1991): The composition of the arthropod fauna of Bornean lowland rain forest trees. − Journal of Tropical Ecology **7**: 161–180.

Stork, N. E. (2001): The management implications of canopy research. − Plant Ecology **153**: 313–317.

Stork, N. E. & M. J. D. Brendell (1990): Variation in the insect fauna of Sulawesi trees with season, altitude and forest type. Insects and the rain forests of South East Asia (Wallacea). – In: W. J. Knight & J. D. Holloway (eds). – Royal Entomological Society of London, London: 173–190.

Stork, N. E. & M. J. D. Brendell (1993): Arthropod abundance in lowland rain forest of Seram.: The Natural History of Seram. In: Edwards, I. D., A. A. Macdonald & J. Proctor, (eds), Intercept Ltd, Andover, UK: 173–190.

Sutrisno (1994): Collembolan assemblages in Australian rainforest canopies. Unpublished thesis for fulfilment of the degree of Master of Resource Science. – Department of Ecosystem Management, University of New England, Armidale, New South Wales, Australia: 1–117.

Sutton, S. L. & P. J. Hudson (1980): The vertical distribution of small flying insects in the lowland rain forest of Zaire. − Zoological Journal of the Linnaean Society **66**: 111–123.

Szujecki, A. (1987): Ecology of forest insects. – W. Junk, Dordrecht: 1–530.

Terborgh, J. (1992): The maintenance of diversity in tropical forests. – Biotropica **24**: 283–292.

Thunes, K. H., J. Skartveit & I. Gjerde (2004): The arthropod community of Scots pine (*Pinus sylvestris* L.) canopies in Norway. – Entomologica Fennica, **15**: 65–90.

Tovar-Sánchez, E. (2009): Canopy arthropod communities within and among oak species in central Mexico. – Current Zoology 55(2): **115:** 79–87.

Tovar-Sanchez, E. M., Z. Cano-Santana & K. Oyama (2003): Canopy arthropod communities on Mexican oaks at sites with different disturbance regimes. – Biological Conservation **115**: 79–87.

Tracey, J. G. (1982): The vegetation of the humid tropical region of north Queensland. – CSIRO, Melbourne, Australia: 1–124.

Uchida, H. (1969): Studies on the arboreal Collembola. I Results of faunal survey of Mt Hakkoda area, IBP Main Area. – Scientific Reports of Hirosaki University **16**: 12–29.

Wardhaugh, C. W., N. E. Stork & E. W. Edwards (2014): Canopy invertebrate community composition on rainforest trees: Different microhabitats support very different invertebrate communities. − Austral Ecology **39**: 367–377.

Webb, L. J. (1959): A physiognomy classification of Australian rainforest. − Journal of Ecology **47**: 551–570.

Webb, L. J., J. G. Tracey & W. T. Williams (1976): The value of structural features in tropical forest typology. − Australian Journal of Ecology **1**: 3–28.

Wilkinson, L., M. Hill, J. P. Welna & G. K. Birkenbeuel (1992): SYSTAT Statistics. – SYSTAT Inc. Illinois.

Yanoviak, S. P., N. M. Nadkarni & C. Jon (2003): Arthropods in epiphytes: a diversity component that is not effectively sampled by canopy fogging. − Biodiversity and Conservation **12**: 731–741.

Yen, A. L. (1989): Overstorey invertebrates in the Big Desert, Victoria. Mediterranean landscapes in Australia. Mallee Ecosystems and their Management. – In: Noble, J. C. & R. A. Bradstock (eds): CSIRO Australia: 285–299.

Yen, A. L. & P. K. Lilywhite (1990): A preliminary report into the invertebrates collected from the canopy of Tasmanian rainforest trees, with special reference to the Myrtle beech. – A report to the Tasmanian Department of Parks, Wildlife and Heritage. Hobart, Tasmania: 1–5.

Yoshida, T. & N. Hijii (2005a): Seasonal distribution of *Xenylla brevispina* (Collembola) in the canopy and soil habitat of a *Cryptomeria japonica* plantation. – Pedobiologia **50**(3): 235–242.

Yoshida, T. & N. Hijii (2005b): Vertical distribution and seasonal dynamics of arboreal collembolan communities in a Japanese cedar (*Cryptomeria japonica* D. Don) plantation. – Pedobiologia **49**: 425–434.

Annex 1. Abundance and diversity of entomobryid species in each stratum only in subtropical rainforest.

Note: The abundance was based on individuals/tray for fogging canopy, individuals/trap for pit-fall traps and individuals/25 cm² for soil/litter extraction; SE: standard error.

	HIGH CANOPY		LOW CANOPY		PIT-FALL TRAPS		SOIL/LITTER	
Species	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE
Acanthocyrtus sp.	0.09	0.095	0.05	0.05	0.07	0.5	0.3	0.122
Acrocyrtus sp.	0.09	0.091	0.09	0.091	0	0	0.3	0.3
Entomobrya sp. 1	0.95	0.447	0.41	0.202	0	0	0	0
Entomobrya sp. 2	0.05	0.05	0	0	0	0	0	0
Entomobrya sp. 3	0.27	0.157	0.05	0.05	0	0	0	0
Entomobrya sp. 4	0.27	0.157	0	0	0.1	0.08	0	0
Entomobrya sp. 5	0.09	0.095	0	0	0	0	0	0
Entomobrya sp. 6	0.23	0.152	0	0	0	0	0	0
E. termitophila Schött	0.05	0.05	0	0	0	0	0	0
E. varia Schött	1.55	0.374	0.55	0.267	0	0	0	0
Epimetrura rostrata Sutrisno & Greenslade	5.23	1.111	19.14	3.859	0.55	0.232	0.2	0.2
Lepidocyrtoides sp. 1	0	0	0	0	0.58	0.228	1.6	0.77
Lepidocyrtoides sp. 2	0	0	0.05	0.045	0	0	0	0
Lepidocyrtoides sp. 3	0	0	0.05	0.045	0	0	0	0
Lepidocyrtoides sp. 4	0	0	0.64	0.399	0	0	0	0
Lepidocyrtoides sp. 5	0	0	0.09	0.091	0.13	0.071	1.2	0.647
Lepidocyrtoides sp. 6	0	0	0	0	0.58	0.188	2.8	1.282
Lepidocyrtoides sp. 8	0.23	0.197	0.14	0.07	0	0	0	0
Lepidocyrtoides sp. 9	0.23	0.137	0.5	0.216	0	0	0	0
Lepidocyrtoides sp.14	0	0	0	0	0.3	0.177	6.4	1.761
Lepidocyrtoides sp.18	0	0	0	0	0.05	0.05	0	0
Lepidocyrtoides sp.19	0	0	0	0	0	0	0.1	0.1
Lepidosira sp. 2	0	0	0	0	1.03	0.206	12.7	6.09
Sinella sp.	0	0	0	0	0.05	0.05	0.3	0.3
TOTAL ABUNDANCE	**9.32**		**21.73**		**3.35**		**25.9**	
NUMBERS OF SPECIES (S)	**13**		**12**		**10**		**10**	
SHANNON-WIENER INDEX (H)	**0.67**		**0.264**		**0.803**		**0.636**	
Hmax $Log_{10}(S + 1)$	**1.1461**		**1.1139**		**1.0414**		**1**	
EVENNESS (E=H/Hmax)	**0.62**		**0.245**		**0.771**		**0.636**	

Annex 2. Presence and absence of Entomobryidae and Paronellidae species and other families, high and low canopies combined. **TRF** – tropical rainforest, **SRF** – subtropical rainforest, **CTR** – cool temperate rainforest.

	TRF	SRF	CTR
Acanthocyrtus sp.1	x	x	x
Acrocyrtus sp.	0	x	0
Brachystomellidae	x	x	x
Dicyrtomidae	x	x	0
Entomobrya sp.1	x	x	0
Entomobrya sp.2	0	x	x
Entomobrya sp.3	0	x	0
Entomobrya sp.4	0	x	x
Entomobrya sp.5	x	x	0
Entomobrya sp.6	0	x	0
Entomobrya sp.7	0	x	0
Entomobrya sp.8	0	0	x
Entomobrya termitophila	0	x	x
Entomobrya varia	x	x	x
Epimetrura	0	x	0
Hypogastruridae	0	0	x
Isotomidae	x	x	x
Lepidocyrtoides sp.10	x	0	0
Lepidocyrtoides sp.11	x	0	0
Lepidocyrtoides sp.12	x	0	0
Lepidocyrtoides sp.13	0	0	0
Lepidocyrtoides sp.15	0	0	x
Lepidocyrtoides sp.2	0	0	0
Lepidocyrtoides sp.3	0	0	0
Lepidocyrtoides sp.4	0	0	0
Lepidocyrtoides sp.5	0	x	0
Lepidocyrtoides sp.6	x	0	0
Lepidocyrtoides sp.8	0	x	0
Lepidocyrtoides sp.9	0	x	x
Lepidocyrtus sp.1	0	0	x
Lepidosira sp.1	0	0	x
Lepidosira sp.2	0	0	x
Lepidosira sp.2a	0	0	x
Lepidosira sp.2b	0	0	x
Neanuridae	x	x	x
Odontellidae	x	x	x
Paronellides mjobergi	0	0	0
Peudoparonella sp.5	0	0	x
Plumachaetas queenslandica	x	x	x
*Paronellidae*sp.1	0	0	x
*Paronellidae*sp.4	0	x	0
*Paronellidae*sp.6	x	x	x
*Paronellidae*sp.7	x	0	0
Sinella sp.2	x	0	0
Sminthuridae	x	x	x
Willowsia sp.	0	0	x