

Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia

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Abstract Chemical knockdown procedures were used to sample canopy arthropods at 3 month intervals over 1 year at two sites, one in eastern Australia and the other in western Australia. Samples were taken from narrow-leaved ironbark, *Eucalyptus crebra*, and grey box, *Eucalyptus moluccana*, in the east and from jarrah, *Eucalyptus marginata*, and marri, *Eucalyptus calophylla*, in the west. Arthropods were more abundant on trees in eastern Australia and exhibited different seasonal patterns from those in the west. Members of different functional groups exhibited different seasonal patterns, with some herbivorous groups responding to times of leaf production, decomposers and fungus feeders responding to high moisture availability, and predators/parasites responding to the abundance of food items. Seasonal variability was slightly higher in the west, possibly reflecting the greater seasonal amplitude in rainfall. In the eastern forest, proportionately more taxa peaked in spring or summer and declined to minimum numbers in winter. In the western forest several taxa attained peak numbers in autumn, winter or spring, while others declined to minimum values in winter or summer. The phenological patterns of canopy arthropods appear to be linked to the condition of the host plant and/or to climatic factors. Comparison of the western Australian data to those from a second year of sampling at a time when rainfall was greater and fell later into the season indicated that variability in arthropod numbers between years can be as great as that between seasons. Implications of the variability in seasonal and annual patterns of canopy invertebrate communities are discussed in relation to the need for long-term sampling and in relation to evaluating the impact of disturbance on forest communities.

Key words: arthropods, canopy, *Eucalyptus*, seasonality.

INTRODUCTION

Despite a surge of interest in canopy faunas, there are only limited data on the temporal and spatial patterns of abundance of canopy invertebrates. Much of the seminal work in this area has been done in the tropics. For example, Erwin and Scott (1980) described the seasonal patterns of beetles in the canopy of one tree species in Panama and Stork and Brendell (1990) investigated seasonal variation in arthropod communities in the forests of Sulawesi, Indonesia. Rainforests have also received attention in Australia, where seasonal patterns of rainforest arthropods have been described by Lowman (1982) and Basset (1991). Although seasonal patterns of invertebrate abundance have been investigated in Australian eucalypt forests and woodlands (Recher *et al.* 1983; Woinarski & Cullen 1984; Bell 1985; Yen 1989; Abbott *et al.* 1992; Heatwole *et al.* in press), the data are limited

and most work has been carried out in southeastern Australia. Only Woinarski and Cullen (1984) attempted to compare temporal patterns of canopy invertebrate abundances between locations over a large geographical area and a variety of forest types. None of the studies considered long-term patterns of community composition and species abundance, with most monitoring invertebrate communities for 1 year or less. The paucity of information on spatial and temporal patterns in eucalypt invertebrate communities has prevented consideration of invertebrates when developing plans of management for the conservation of eucalypt forest faunas (Recher 1996). Eucalypt forests are subject to increasingly intensive use for wood production (Resource Assessment Commission 1992), and particular concern has been expressed by forest biologists for the conservation of remnants of old-growth forests on nutrient-rich soils (Recher 1996). These old-growth forests have rich vertebrate faunas (Braithwaite 1983; Braithwaite *et al.* 1983, 1984; Recher 1985; Recher *et al.* 1991a) and probably sustain equally diverse

invertebrate communities (Majer *et al.* 1992, 1994). Before the effects of logging and other human-induced disturbances can be evaluated fully and management plans, which consider the entire forest biota, can be developed, it will be necessary to have more information on eucalypt forest invertebrate communities and their spatial and temporal patterns of abundance than is presently available.

In 1985, we initiated studies, in eucalypt forests and woodlands, on the relationships between arboreal invertebrate communities, foliage nutrient levels and tree species selection by foraging birds (Majer & Recher 1988; Recher 1989; Majer *et al.* 1990, 1992; Recher *et al.* 1991a, 1993; Recher & Majer 1994). Arboreal invertebrates were sampled seasonally on each of two species of eucalypts in marri-jarrah forest in western Australia and box-ironbark forest in eastern Australia. Samples were initially identified to order or family, but a subset of the samples has now been sorted to morphospecies (Majer *et al.* 1994). In this paper we present ordinal data on the seasonality of the arboreal invertebrate faunas in both forests. Specifically, we ask the questions 'What are the seasonal trends in taxa in each forest' and 'Are these patterns in seasonality the same in both areas?' Subsequent papers will analyse the similarity of species composition between the eastern and western faunas, the extent of tree species specificity within each forest type, the variation in faunal composition within a tree species and the extent to which seasonal changes in community composition contribute to overall patterns of species richness.

METHODS

Site description

Sampling was done at Scheyville, NSW (33°53'S, 150° 51'E), where we sampled narrow-leaved ironbark (*Eucalyptus crebra* F. Muell.) and grey box (*Eucalyptus moluccana* Roxb.), and at Karragullen, WA (32°04'S, 116° 07'E), where we sampled jarrah (*Eucalyptus marginata* Donn. ex. Smith) and marri (*Eucalyptus calophylla* R. Br. ex. Lindley). The forest at Scheyville was dominated by narrow-leaved ironbark (51% of trees, 42% of tree foliage) and grey box (40% of trees, 51% of tree foliage), with smaller numbers of forest red gum (*Eucalyptus tereticornis* Smith; 7% of trees) and thin-leaved stringybark (*Eucalyptus eugenoides* Sieb. ex Spreng.; <1% of trees). Canopy cover was 40–45%, with the canopy averaging 15–18 m in height. Individual trees emerged above the canopy to 25 m. The understorey consisted of eucalypt saplings; grasses and forbs comprised the ground cover. There was a discontinuous shrub layer of blackthorn, *Bursaria spinosa* Cav. At Karragullen, jarrah (92% of trees and foliage) dominated the forest while marri comprised only 8% of all trees. Canopy cover was 60%, and mean canopy height was 15–18 m,

with individual trees to 30 m. Karragullen had a more diverse understorey than the forest at Scheyville, with a dense understorey of eucalypt saplings, sheoak (*Allocasuarina fraseriana* [Miq.] L. Johnson) and bull banksia (*Banksia grandis* Willd.). The site had a rich herb and shrub layer.

Climate at the Karragullen site is Mediterranean, with cool, wet winters and hot, dry summers. The mean annual rainfall at nearby Kalamunda is 992 mm, with most rain falling between May and October. At Scheyville, although late-winter and spring (July–October) tend to be drier than other seasons, and late-summer (January–March) is wetter, rain falls fairly evenly throughout the year. The mean annual rainfall at nearby Richmond Airport is 805 mm, summers are warm and winters are cool with occasional frosts. The monthly rainfall and maximum and minimum temperatures from January 1987 to January 1988 are shown for the NSW and WA sites in Fig. 1. This encompasses the period when arthropods were sampled at both sites (autumn 1987–summer 1988). Total rainfall for Kalamunda and Richmond during this period was 1050 mm and 957 mm, respectively. The climatic pattern at the WA site for this period conforms closely to the long-term trend, whereas the NSW site experienced exceptionally wet periods in

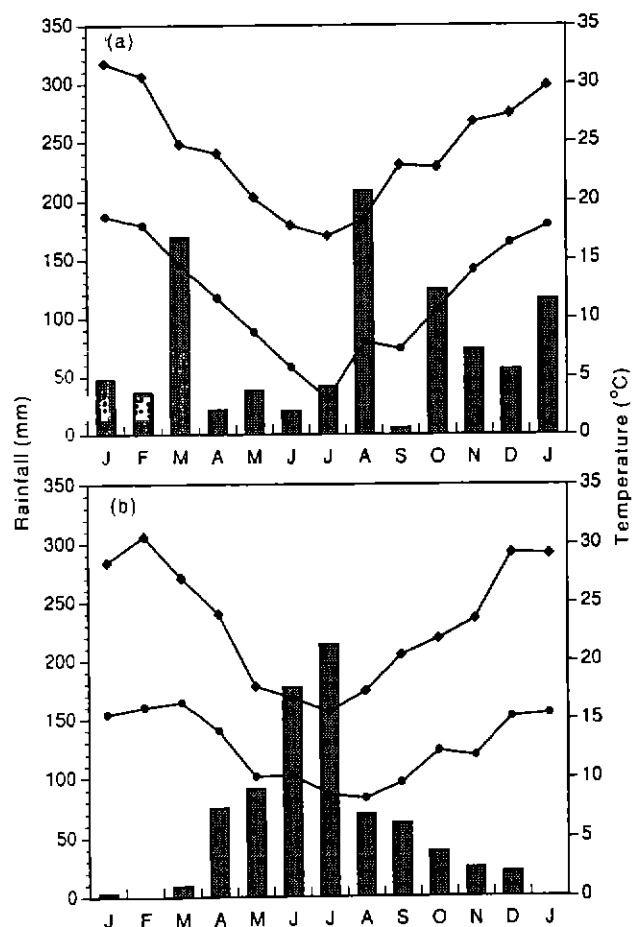


Fig. 1. Total monthly rainfall (histogram) and mean maximum (◆) and minimum (●) temperature for the period when canopy samples were taken at (a) Scheyville, NSW and (b) Karragullen.

March, April, October and January. Rainfall at Kalamunda from autumn 1988 to summer 1989, when samples were collected only from the WA site, was greater (1187 mm) and proportionately more rain fell later in the season than in the preceding year.

Arthropod sampling

Arthropods were separately sampled from the canopy (7.1–20 m) and eucalypt understorey (1–7 m) of narrow-leaved ironbark, grey box, jarrah and marri during 1987–89 by a chemical knockdown procedure. In view of the fact that we were primarily interested in foliage-associated arthropods we only sampled trees not in flower. Ten upper canopy and 10 understorey trees of each species were sampled on each occasion and sampling continued at 3-monthly intervals from May 1987 to January 1988 in NSW and from April 1987 to January 1989 in WA (Table 1). In this paper we present data for the sampling periods that coincide for the two areas, namely autumn 1987 to summer 1988 (Table 1). We also discuss seasonal trends for the second year of sampling in WA. Cotton, funnel-shaped nets with a sampling area of 0.5 m² were used to collect pyrethrin samples. Each net was fitted with a sleeve that held a 100 mL plastic tube. Nets were held about 60–70 cm below the vegetation. Within a given tree (or cluster of saplings in the case of the smaller understorey trees), 10 nets were suspended at different heights according to the distribution of suitable branches for attachment, so that no nets overlapped. As nearly as possible, net positions were selected to equalize the amount of foliage (determined by visual inspection) in the column directly above the nets. Nets were positioned the afternoon prior to spraying, to allow disturbed invertebrates to return.

In the morning (06:00–10:00 h) of the following day the canopy above each net was sprayed with 0.2% synthetic pyrethrin pesticide, synergized with piperonyl butoxide, using a motorized-knapsack mist-blower.

Spraying was done only when it was dry and calm. In the event of poor weather, nets were left in place and sprayed on the first suitable morning (usually the next day). Two litres of diluted (10:1) pesticide were used per tree and trees were left for at least 30 min to allow silk-attached invertebrates to drop into nets. The canopy was then shaken to dislodge remaining invertebrates and specimens were brushed into the collecting tubes and preserved in 70% ethanol prior to sorting and counting to ordinal level.

Data analysis

Following sorting, the number of animals was summed for the 10 nets placed within each tree or, in the case of the understorey, each cluster of saplings. Although present in some samples, certain taxa were considered to be present in insufficient samples to provide ecologically meaningful data. Accordingly, these taxa (Isopoda, Thysanura, Odonata, Blattodea, Mantodea, Dermaptera, Phasmatodea, Embioptera and Neuroptera) were excluded from further analysis. The means of the remaining taxa were then plotted separately for canopy and understorey against season in order to provide a visual representation of seasonal trends.

We then investigated the effect of tree species and season within each forest on the abundance of each taxon. In view of the fact that data were collected in different ways for the canopy (one tree per sample) and understorey (clusters of trees per sample) we performed the analysis separately for the two strata. The design we used was therefore for a factorial experiment with the factors being 'season' (autumn 1987; winter 1987; spring 1987 and summer 1988) and 'tree species', with 10 tree replications. Prior to performance of ANOVA we checked the data for homogeneity of variance and normality. It was found that $\log_e(1 + \text{number of animals})$ transformations of data were necessary in order to stabilize the variance and justify normality. The model for ANOVA may then be expressed as:

$$z_{ijk} = m + s_i + t_j + (s \times t)_{ij} + e_{ijk}$$

Table 1. Dates when chemical knockdown samples were taken from the NSW and WA trees

Season	Sampling date	
	NSW	WA
Autumn*	05–15 May 1987	06–17 April 1987
Winter*	20–31 July 1987	13–24 July 1987
Spring*	13–29 October 1987	12–23 October 1987
Summer*	12–23 January 1988	12–23 January 1988
Autumn	—	11–22 April 1988
Winter	—	04–15 July 1988
Spring	—	17–29 October 1988
Summer	—	16–27 January 1989
Autumn	—	06–17 November 1989

The samples marked with an asterisk are those that are specifically reported on in the present paper.

where z_{ijk} is the $\log_e(1 + \text{number of animals})$ from the k^{th} tree replication for the i^{th} season and the j^{th} tree species, m is the overall mean, s_i and t_j are the respective main effects of the i^{th} season and the j^{th} tree species $(s \times t)_{ij}$ is the interaction between the i^{th} season and the j^{th} tree species, and e_{ijk} is the random error (or residual effect) associated with the k^{th} replication. Note that $i = 1, \dots, 4$ represents the four seasons (autumn, winter, spring and summer), $j = 1, 2$ represents the two tree species in each forest (grey box and ironbark in NSW, jarrah and marri in WA) and $k = 1, \dots, 10$ represents the 10 tree replications. We used the $P < 0.05$ level as criterion for significance of effect and used multiple pairwise comparison (Fisher's LSD) tests (Ott 1988) to elucidate

which of the seasonal means of a given taxon were significantly different from another.

The first part of the analysis was designed to see how overall seasonal trends in arthropods on each tree species in each forest related to each other. In this way we hoped to be able to answer questions such as whether spring in WA was equivalent to spring in NSW from an arthropod's point of view and also whether arthropods on individual tree species in one forest were following similar phenological patterns. We also employed canonical variate analysis (CVA; Manly 1986; Digby & Kempton 1987) to investigate how the 16 groupings (2 tree species × 2 forests × 4 seasons) of data points related to each other in terms of taxonomic composition. In other words, the difference between the 16 groups of samples were examined using the 16 arthropod taxa as response variables, with the total number of arthropods per tree being the response.

First, within-group covariance matrices were examined. As no differences between the covariances for the different groups were found, it was considered that the covariance structure of the groups was homogeneous. Correlations between the 16 taxa were found to be moderately high. Hence, it was considered most appropriate to make inference from the total canonical structure rather than from the canonical coefficients themselves. The canonical coefficients were, however, used to provide an indication of the taxa that contributed to the separation of samples on the resulting CVA diagrams.

In view of the fact we report only on the 1987-88 sampling 'year', we checked to see if the WA samples exhibited similar seasonal trends in the corresponding samples for autumn, winter and spring of 1988 and the summer of 1989 to those reported on here. As patterns were the same in canopy and understorey samples, only the canopy samples are presented. Using canopy samples only, a full factorial model of season, tree species and year effects was fitted. The model used was:

$$z_{ijk} = m + s_i + t_j + y_k + (s \times t)_{ij} + (s \times y)_{ik} + (t \times y)_{jk} + (s \times t \times y)_{ijk} + e_{ijk}$$

where z_{ijk} is the $\log_e(1 + \text{number of animals})$, s_i , t_j and y_k are the main effects of season, tree species and year and $(s \times t)_{ij}$, $(s \times y)_{ik}$, $(t \times y)_{jk}$ and $(s \times t \times y)_{ijk}$ are the various interactions. Once again we used the $P < 0.05$ level as the criterion for significance of effect and the multiple pairwise comparison test used was the Fisher's LSD test.

A further comparison was made to see whether the 1987-88 and 1988-89 data from WA matched between seasons in terms of their overall taxonomic composition. In this instance we were not specifically concerned with differences between the two tree species so we calculated average total arthropods per tree for jarrah and marri combined. Once again CVA was employed to investigate how the eight groupings (4 seasons × 2 years) of data points related to each other across years.

Table 2. Summary of statistical differences between arthropod numbers on different tree species and between different seasons for both NSW and WA forests

Taxon	NSW				WA			
	Tree species		Season		Tree species		Season	
	Understorey	Canopy	Understorey	Canopy	Understorey	Canopy	Understorey	Canopy
Arachnida-Acarina	I*		*(+)	*	J*		*	*
Arachnida-Araneae	I*		*				*	*
Collembola	I*		*	*(+)			*	*
Insecta-Orthoptera			*	*			*	*
Insecta-Psocoptera			*	*			*	*
Insecta-Hemiptera (psyllids)	I*	I*	*	*	J*	J*	*(+)	*
Insecta-Hemiptera (others)	I*	I*	*(+)	*(+)		J*	*(+)	*
Insecta-Thysanoptera	I*		*	*(+)		M*	*	*(+)
Insecta-Coleoptera (adults)			*	*		M*	*	*
Insecta-Coleoptera (larvae)		I*	*	*			*	*
Insecta-Diptera (adults)	I*	I*	*(+)	*(+)	J*	M*	*	*
Insecta-Diptera (larvae)	I*		*(+)	*	J*	J*	*	*(+)
Insecta-Lepidoptera (adults)		I*	*	*	J*		*	*
Insecta-Lepidoptera (larvae)		I*	*	*			*	*
Insecta-Hymenoptera (ants)			*	*	J*		*	*
Insecta-Hymenoptera (others)	I*	I*	*	*			*	*
Total arthropods		I*	*	*			*	*
Total arthropods (excl. ants)		I*	*	*			*	*
Total significant differences (excluding arthropod totals)	9	7	16	15	6	6	14	14

* $P < 0.05$; I, J and M indicate that animals are most abundant on ironbark, jarrah or marri, respectively. The NSW and WA data sets are treated separately and values marked '+' indicate that there is an interaction between tree species and season.

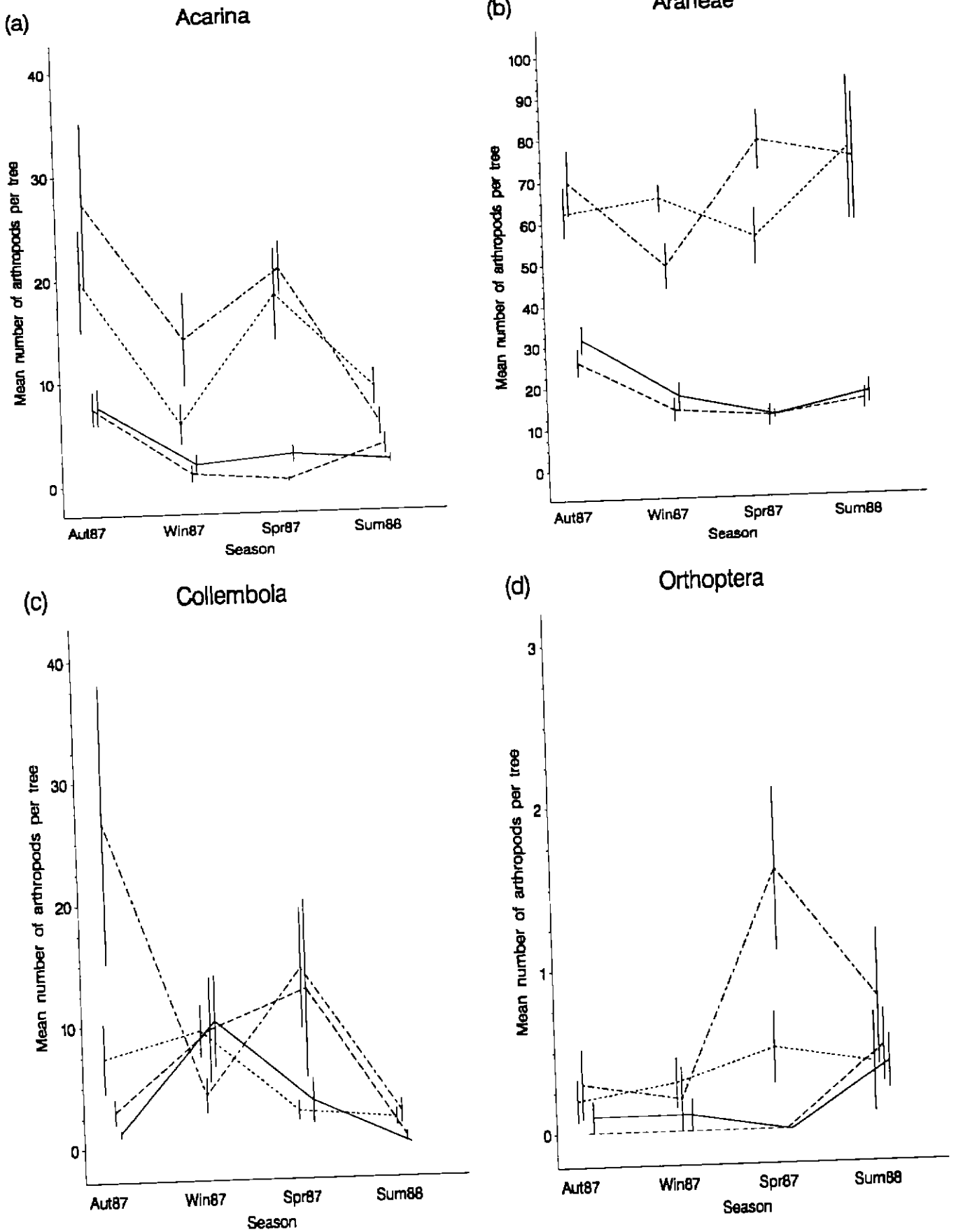


Fig. 2a-r. Mean (\pm standard error) of arthropods from the most abundant taxa that were sampled on narrow-leaved ironbark (*Eucalyptus crebra* - - - -), grey box (*Eucalyptus mollucana* ·····), marri (*Eucalyptus calophylla* —) and jarrah (*Eucalyptus marginata* - · - ·) trees.

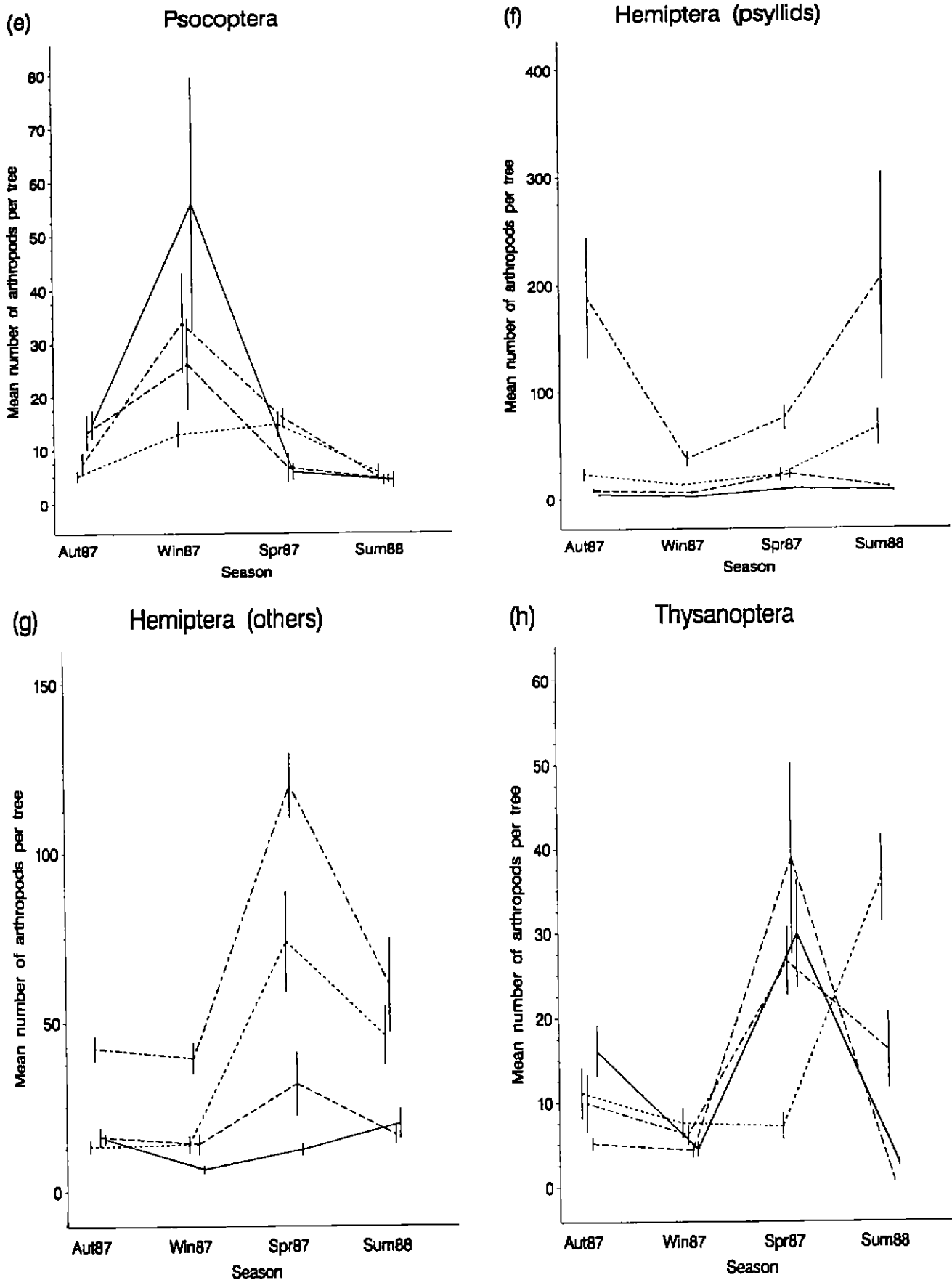


Fig. 2e-h.

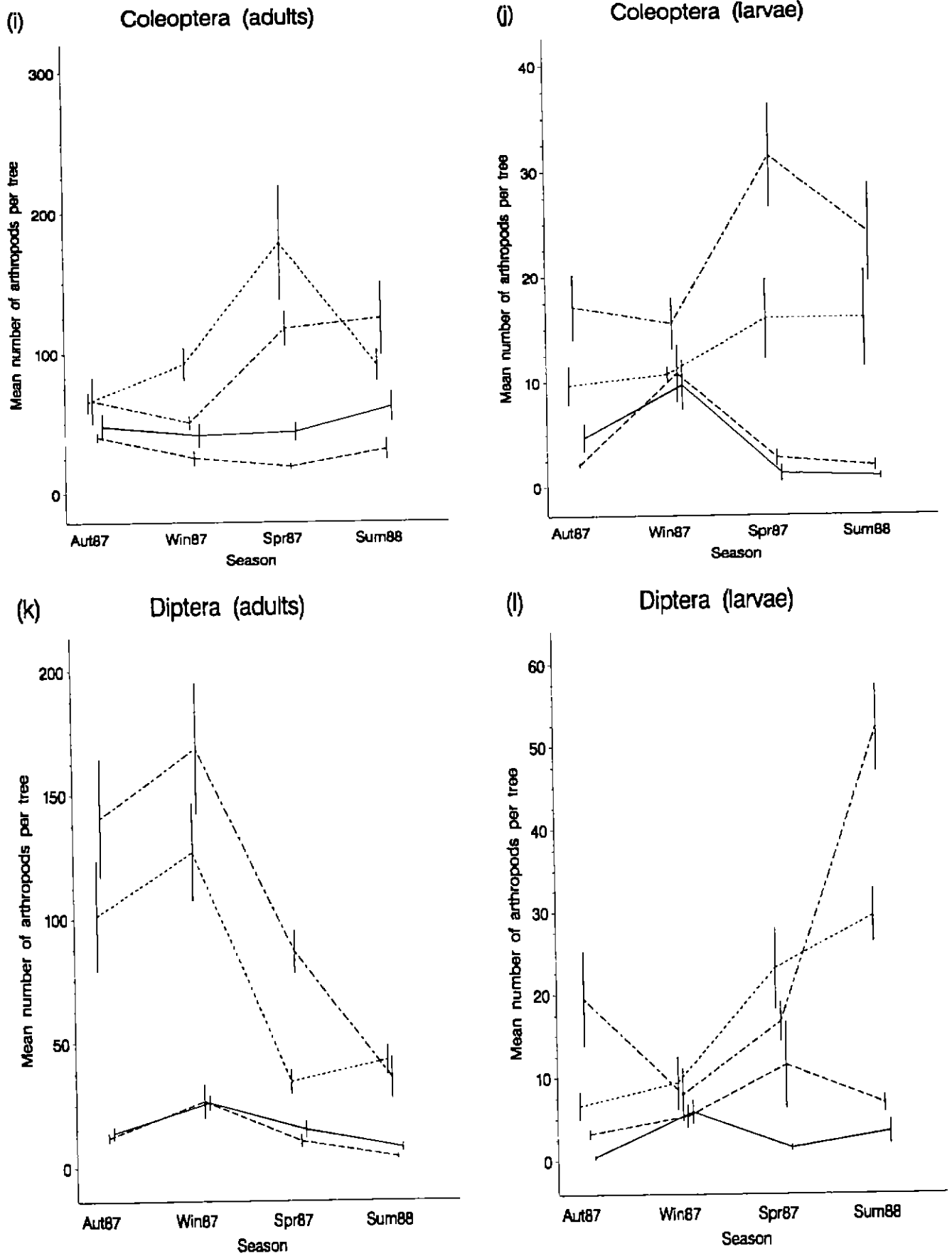
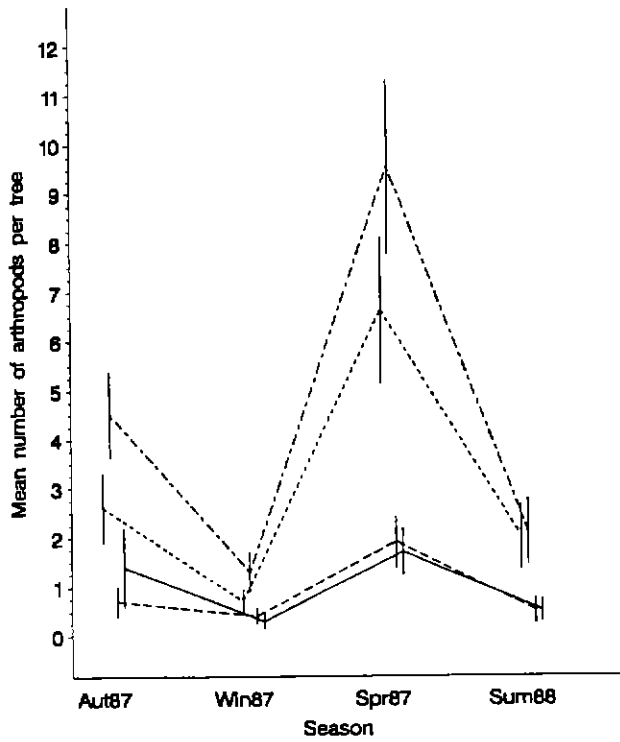
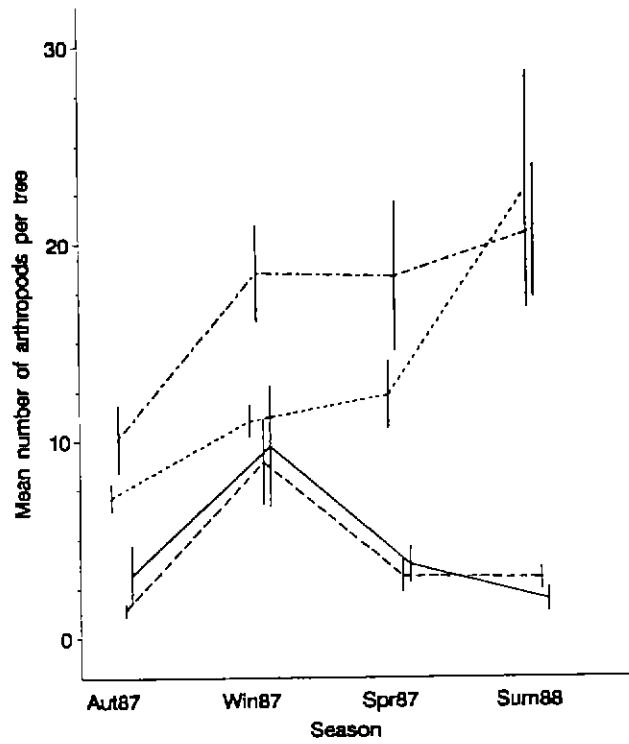


Fig. 2i-l.

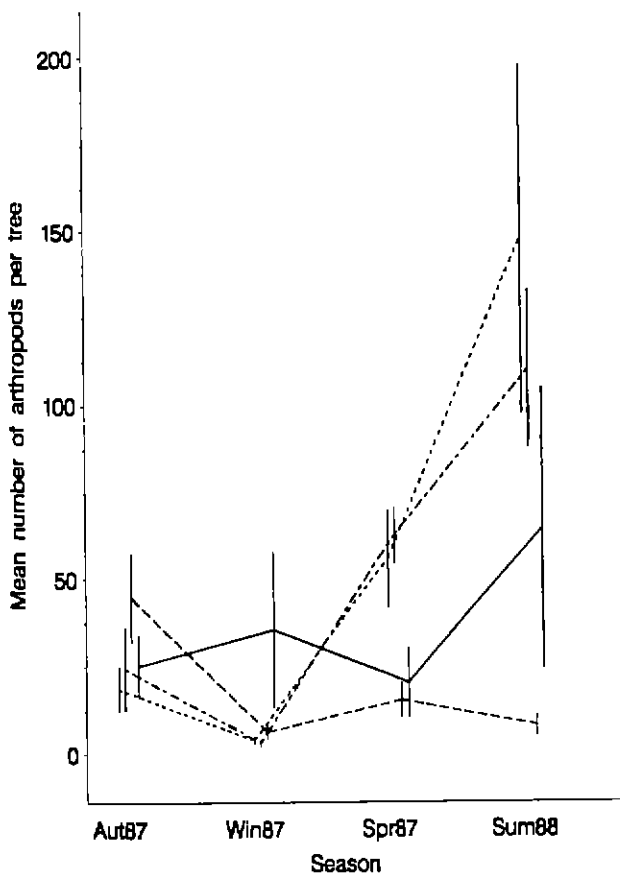
(m) Lepidoptera (adults)



(n) Lepidoptera (larvae)



(o) Hymenoptera (ants)



(p) Hymenoptera (others)

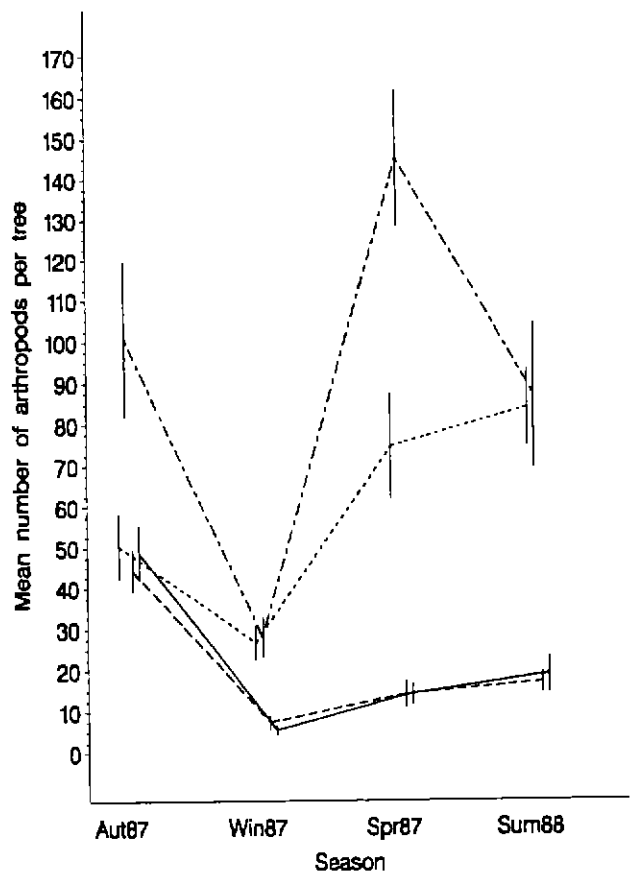


Fig. 2m-p.

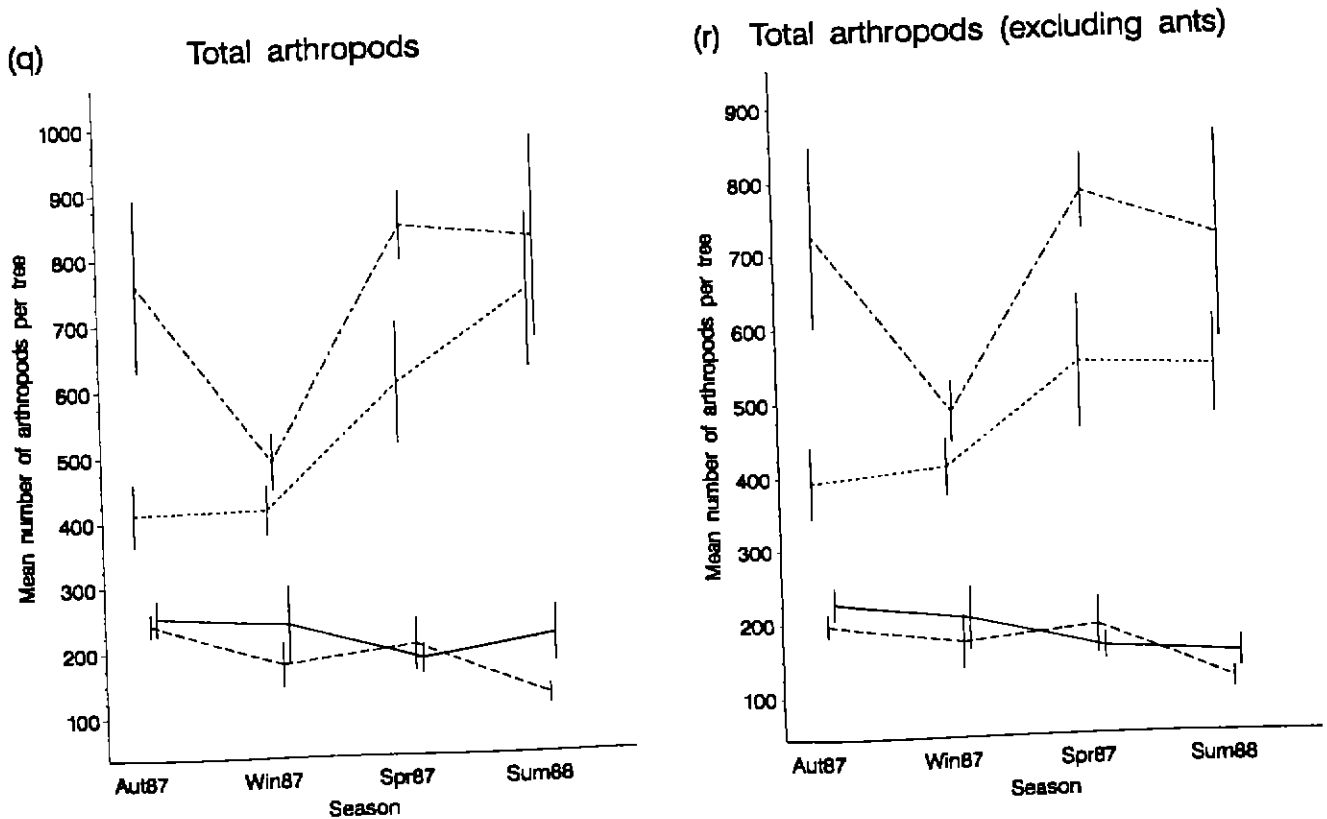


Fig. 2q-r.

RESULTS

General trends

The mean number of animals per tree per season are shown for each tree species in Fig. 2a-2r. The numbers of arthropods are, with the exception of the Collembola (Fig. 2c), Psocoptera (Fig. 2e) and Thysanoptera (Fig. 2h), considerably higher on the NSW than the WA trees.

Differences between tree species

Table 2 summarizes the ANOVA which, within each forest, revealed statistically significant differences between tree species and/or between seasons. The ANOVA for both canopy and understorey are included in Table 2. The number of statistically significant interactions was relatively low, indicating that differences between tree species were consistent throughout the seasons. In those cases where interactions occurred, the *F*-values for the interaction were low in relation to those associated with the main effects of tree species and season, indicating that overall trends in arthropod numbers between tree species and between season could be considered to be meaningful. When considering both strata together, 12 taxa exhibited differences in numbers between tree species in the NSW forest and nine exhibited differences between tree species in the WA forest. In the NSW forest all 12 taxa were most abundant on narrow-leaved ironbark trees. The situation was less clear-cut in WA,

where five taxa that exhibited significant differences in the understorey were more abundant on jarrah, while on the upper canopy three taxa were more abundant on jarrah and three more abundant on marri.

Variability between seasons

Almost all taxa exhibited significant differences between season on trees from both strata and from both forests (Table 2). Table 3 shows the seasonal rankings of each taxon for the upper canopy samples. The mean ranks across seasons were tested for significance by Kendall's coefficient of concordance. In NSW there was a tendency for taxa to be most abundant in spring, followed by summer, autumn and then winter (Kendall's coefficient of concordance = 0.204, $P < 0.05$). This was not the case in the WA forest, where taxa tended to be more abundant in autumn, followed by spring, winter and, finally, summer. The overall trend in taxa ranks was not statistically significant in WA, suggesting that the abundances of the individual taxa were less in phase with each other than in NSW.

The amplitude of seasonal variation in each taxon was compared between NSW and WA by calculating the mean and standard error of the four seasonal means of each taxon on each tree species. The resulting values were used to calculate the coefficient of variation, the average of which was taken for values on the two tree species in each forest. The coefficients for the 16 indi-

vidual taxa were then compared between forests using a paired *t*-test. The mean coefficient in WA (79%) was higher than that in NSW (61%), but the difference was not significant ($t = -1.8$, d.f. = 30, $P = 0.08$).

Relative influence, tree species, season and forest

The CVA analysis enables trends in the arboreal arthropod community as a whole to be compared between tree species, seasons and forests. Table 4 summarizes the results of the first CVA analysis, which investigated the separation between the 16 groupings (tree species \times season) using the number of animals of the 16 taxa as

responses. This table indicates that at least four canonical variates (CV1-4) are required to explain about 80% of all the variation among the respective groups. The first CV accounts for about 34% of the separation among the groups, while CV2 accounts for about 20%. Inspection of the correlation coefficients between the taxa responses and the first canonical variate (Table 4) indicates that Hymenoptera (others), closely followed by Hemiptera (others) are the most important taxa in explaining the variation among the 16 tree species \times season groups. Taxa such as Araneae, Coleoptera (larvae), Diptera (larvae) and Lepidoptera (adults) also seem to influence this separation of the groups. A further 20% of the

Table 3. Upper canopy arthropods ranked by seasonal abundance (1, most abundant to 4, least abundant) in the NSW and WA forests

	Season			
	Autumn 1987	Winter 1987	Spring 1987	Summer 1988
New South Wales forests				
Arachnida-Acarina	1 ^a	3 ^b	2 ^a	4 ^b
Collembola	1 ^a	2 ^{ab}	3 ^{bc}	4 ^c
Insecta-Diptera (adults)	2 ^a	1 ^a	3 ^b	4 ^c
Insecta-Psocoptera	3 ^b	1 ^a	2 ^a	4 ^b
Insecta-Coleoptera (adults)	4 ^c	3 ^{bc}	1 ^a	2 ^{ab}
Insecta-Coleoptera (larvae)	4 ^b	3 ^b	1 ^a	2 ^{ab}
Insecta-Lepidoptera (adults)	2 ^b	4 ^c	1 ^a	3 ^c
Insecta-Orthoptera	3 ^b	4 ^b	1 ^a	2 ^{ab}
Insecta-Hymenoptera (others)	3 ^c	4 ^c	1 ^a	2 ^b
Insecta-Hymenoptera (ants)	3 ^b	4 ^c	1 ^a	2 ^{ab}
Arachnida-Araneae	3 ^a	4 ^a	2 ^a	1 ^a
Insecta-Thysanoptera	3 ^{bc}	4 ^d	2 ^b	1 ^a
Insecta-Diptera (larvae)	3 ^d	4 ^c	2 ^b	1 ^a
Insecta-Hymenoptera (ants)	3 ^b	4 ^c	2 ^a	1 ^a
Insecta-Lepidoptera (larvae)	4 ^b	2 ^a	3 ^a	1 ^a
Insecta-Hymenoptera (psyllids)	2 ^{ab}	4 ^c	3 ^{bc}	1 ^a
Mean rank	2.8	3.2	1.9	2.2
Best rank	3	4	1	2
Western Australian forests				
Arachnida-Acarina	1 ^a	4 ^c	3 ^c	2 ^b
Arachnida-Araneae	1 ^a	3 ^b	4 ^b	2 ^b
Insecta-Coleoptera (adults)	1 ^a	4 ^a	3 ^a	2 ^a
Insecta-Hymenoptera (ants)	1 ^a	4 ^a	2 ^a	3 ^a
Insecta-Hymenoptera (others)	1 ^a	4 ^c	3 ^b	2 ^b
Insecta-Psocoptera	2 ^a	1 ^a	3 ^b	4 ^b
Insecta-Coleoptera (larvae)	2 ^b	1 ^a	3 ^c	4 ^c
Insecta-Diptera (adults)	2 ^b	1 ^a	3 ^b	4 ^c
Collembola	3 ^b	1 ^a	2 ^{ab}	4 ^c
Insecta-Diptera (larvae)	4 ^b	1 ^a	3 ^a	2 ^a
Insecta-Lepidoptera (larvae)	4 ^b	1 ^a	2 ^b	3 ^b
Insecta-Thysanoptera	2 ^b	3 ^c	1 ^a	4 ^d
Insecta-Lepidoptera (adults)	2 ^b	4 ^b	1 ^a	3 ^b
Insecta-Hymenoptera (psyllids)	3 ^{bc}	4 ^c	1 ^a	2 ^b
Insecta-Hymenoptera (others)	3 ^a	4 ^b	1 ^a	2 ^a
Insecta-Orthoptera	3 ^b	2 ^b	4 ^b	1 ^a
Mean rank	2.2	2.6	2.4	2.8
Best rank	1	3	2	4

Ranks that share the same letter of the alphabet indicate that seasonal means do not differ statistically. The taxa are grouped so that ones that are most abundant in a particular season are listed together.

separation between the groups along CV2 seems to be controlled mainly by Diptera (adults). Araneae and Diptera (larvae) also seem to control CV3, while CV4 is determined by no particular taxa.

To enhance the nature of the separation of the groups by the various CV, the means of the canonical scores of the sample observations in each group were plotted against their corresponding CV. As the CV are not correlated with each other, only two plots were obtained to show the separation along the directions of each CV. As there are 16 groups and each has 10 observations, a plot of canonical scores of these sample observations would be very clumsy. Furthermore, the variation of these scores within each group was fairly small and homogeneous among the groups. Hence, the group means were used for plotting, instead of the actual scores. These CVA diagrams are shown in Fig. 3. In order to provide further insight into the reasons for the separations of

groups on the CVA diagrams, the correlation coefficients between the CV and the 16 taxa responses (i.e. the 'total canonical structure') were calculated. These correlations are also shown in Table 4.

A seasonal trend in the samples was evident on the CV1 vs CV2 diagram (Fig. 3a). The winter samples from both forests were grouped on the upper left of the diagram and a less compact grouping of autumn samples from both forests occurred in the centre. The spring and summer samples from the WA forest formed a compact grouping on the negative axes of CV1 and CV2, while a more dispersed group of spring/summer samples from the NSW forest was placed on the positive part of CV1. The third CV separated six of the eight samples from NSW from those of the WA forest; the spring samples from NSW were grouped with the WA samples. No interpretable separation of samples was evident on CV4 (Fig. 3b).

Table 4. Proportion of separation represented by the first four canonical variates derived from the canonical variate analysis of the NSW and WA tree species \times four season data

Taxon	CV1	CV2	CV3	CV4
Arachnida-Acarina	0.42 0.0001	0.48 0.0001	-0.09 0.2607	-0.18 0.0211
Arachnida-Araneae	0.61 0.0001	0.29 0.0002	-0.509 0.0001	-0.02 0.8392
Collembola	0.15 0.0597	0.31 0.0001	0.09 0.2562	0.02 0.8174
Insecta-Orthoptera	-0.44 0.0001	0.08 0.3448	0.05 0.5413	0.14 0.0896
Insecta-Psocoptera	-0.21 0.0094	0.19 0.0152	0.07 0.3943	0.27 0.0006
Insecta-Hemiptera (psyllids)	0.46 0.0001	0.02 0.7862	-0.27 0.0005	0.15 0.0637
Insecta-Hemiptera (others)	0.76 0.0001	0.13 0.1099	0.16 0.0381	0.32 0.0001
Insecta-Thysanoptera	0.30 0.0001	-0.20 0.0128	0.19 0.0175	0.02 0.7673
Insecta-Coleoptera (adults)	0.45 0.0001	-0.05 0.5007	-0.27 0.0007	0.09 0.2548
Insecta-Coleoptera (larvae)	0.62 0.0001	0.27 0.0006	-0.19 0.0175	0.36 0.0001
Insecta-Diptera (adults)	0.12 0.1174	0.81 0.0001	-0.41 0.0001	0.16 0.0471
Insecta-Diptera (larvae)	0.62 0.0001	-0.31 0.0001	-0.48 0.0001	0.37 0.0001
Insecta-Lepidoptera (adults)	0.63 0.0001	0.25 0.0015	0.27 0.0007	0.04 0.6200
Insecta-Lepidoptera (larvae)	0.44 0.0001	0.12 0.1178	-0.39 0.0001	0.42 0.0001
Insecta-Hymenoptera (ants)	0.30 0.00001	-0.28 0.0004	-0.19 0.0155	-0.04 0.5909
Insecta-Hymenoptera (others)	0.85 0.0001	0.19 0.0175	-0.06 0.4227	-0.11 0.1612
% Separation explained	34.09	19.66	14.93	10.60
Cumulative %	34.09	53.75	68.68	79.28

The correlations between the taxa variables and the canonical variates are also shown (with *P*-values).

Variability between years

The results of the ANOVA that investigated the effects of different years, as well as tree species and season, in the WA forest are shown in Table 5. Once again, the trends between tree species are not consistent, with two taxa being more abundant on marri and a further two more abundant on jarrah. As in the previous sampling year, all taxa except Orthoptera exhibited significant differences between seasons. Generally speaking, arthropods were more abundant in the first sampling year, with six taxa being significantly more so; only Hemiptera (psyllids) were significantly more abundant in the second sampling year. All but two taxa (Orthoptera and Lepidoptera [adults]) exhibited a significant year \times season interaction (i.e. they did not display the same seasonal trends in the two sampling years). Table 6 shows the seasonal rankings of each stratum for the second sampling year. In comparison with the first sampling year (Table 3), fewer taxa

reached a peak in autumn and considerably more reached a peak in summer. The overall trend in ranks was: taxa most abundant in summer, followed by spring, winter and then autumn. This ranking was statistically significant (Kendall's coefficient of concordance = 0.290, $P < 0.01$) and differed from that of the first sampling year in that the ranks for summer and autumn were transposed (cf. Tables 3 and 6).

Table 7 summarizes the results of the second CVA, which compared the WA samples collected during the two successive 12 month periods. The first four CV explained 90% of the variation in the data, although the majority of this variation (67%) was explained by the first two. The correlation coefficients between the taxa responses and each canonical variate (Table 7) indicate that the Araneae, Coleoptera (adult) and Diptera (adult) were important contributors to CV1, the Hemiptera (psyllids) and Coleoptera (larvae) to CV2, the Coleoptera (adult) to CV3, while the Acarina and Diptera (larvae) seemed to control CV4.

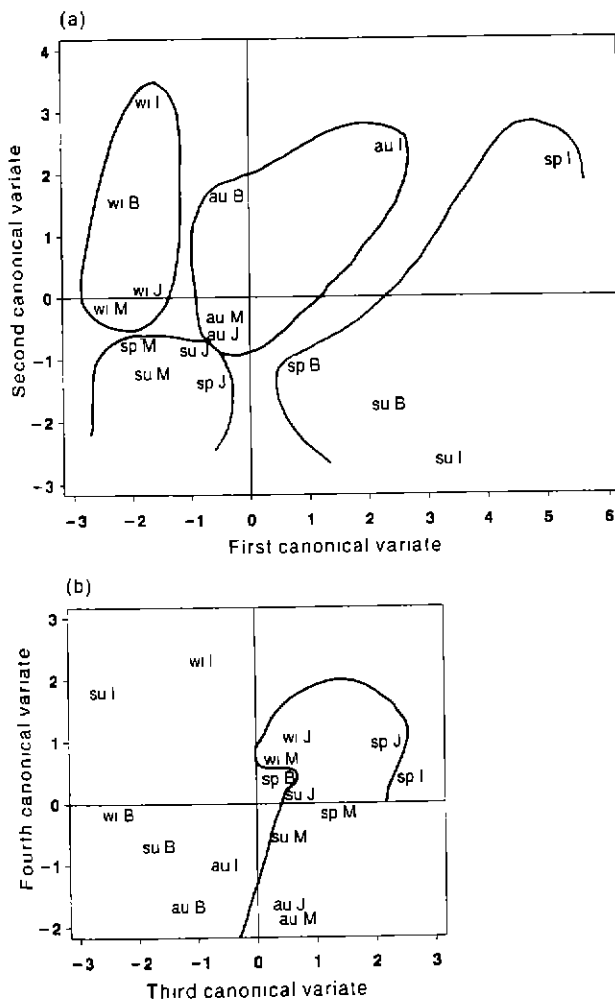


Fig. 3. Spring (sp), summer (su), autumn (au) and winter (wi) samples from each of the four tree species plotted against (a) first and second and (b) third and fourth axes of the canonical variance analysis, derived using total number of animals per tree for the 16 taxa as response data. The solid lines delineate samples that appear to be grouped by season and/or forest. (B) *Eucalyptus moluccana*; (I) *Eucalyptus crebra*; (M) *Eucalyptus calophylla*; (J) *Eucalyptus marginata*.

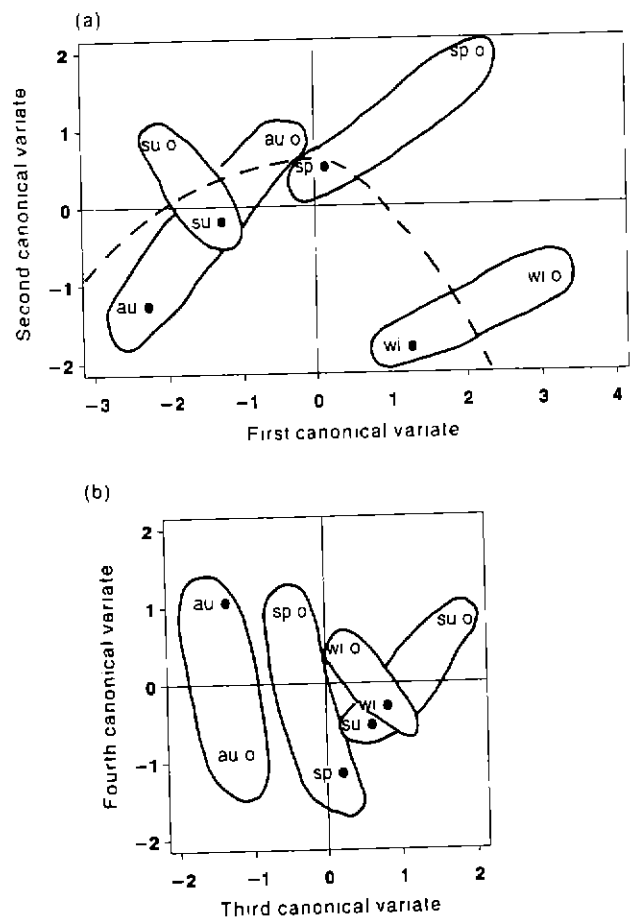


Fig. 4. Spring (sp), summer (su), autumn (au) and winter (wi) samples from the 1987/88 (●) and 1988/89 (○) sampling periods in the Western Australian forest plotted against (a) first and second, and (b) third and fourth axes of the canonical variance analysis, derived using total number of animals per tree (average of jarrah and marri) for the 16 taxa as response data. The solid lines delineate samples by season and the dotted line separates samples from the two 12 month sampling periods.

The means of the canonical scores of the sample observations in each group were plotted against their corresponding CV (Fig. 4). A degree of grouping of samples by season was evident on both the CV1 vs CV2

and the CV3 vs CV4 diagrams, although there was no clear separation of the autumn and summer samples from the two 12 month sampling periods on the CV1 vs CV2 diagram or the winter and summer samples on the

Table 5. Summary of statistical differences between arthropod numbers on different species, between different seasons and between the 1987-88 and 1988-89 sampling years

Taxon	Main Effects			Interactions			
	Tree Species	Season	Year	Year/tree species	Year/season	Tree species/season	Year/tree/season
Arachnida-Acarina		*		*	*	*	
Arachnida-Araneae		*	1987/8*		*		
Collembola		*			*	*	
Insecta-Orthoptera							*
Insecta-Psocoptera	M*	*	1987/8*		*		
Insecta-Hemiptera (psyllids)		*	1988/9*	*	*	*	*
Insecta-Hemiptera (others)		*			*		*
Insecta-Thysanoptera		*			*		*
Insecta-Coleoptera (adults)	M*	*	1987/8*		*		
Insecta-Coleoptera (larvae)		*	1987/8*		*		
Insecta-Diptera (adults)		*		*	*		
Insecta-Diptera (larvae)	J*	*	1987/8*		*	*	
Insecta-Lepidoptera (adults)		*			*		
Insecta-Lepidoptera (larvae)		*			*		
Insecta-Hymenoptera (ants)		*	1987/8*		*		
Insecta-Hymenoptera (others)	J*	*		*	*		
Total arthropods		*			*		
Total arthropods (excl. ants)		*			*		
Total significant differences (excluding arthropod totals)	4	15	7	4	14	4	4

* $P < 0.05$; M and J indicate that the animals are most abundant on marri or jarrah, respectively; 1987/8 or 1988/9 indicate the sampling 'year' when animals were most abundant. The data are for WA samples only, taken from the upper canopy.

Table 6. Upper canopy arthropods ranked by seasonal abundance from the second sampling year in the WA forest

	Season			
	Autumn 1988	Winter 1988	Spring 1988	Summer 1989
Insecta-Coleoptera (larvae)	4 ^c	1 ^a	3 ^b	2 ^b
Collembola	4 ^b	1 ^a	2 ^a	3 ^b
Insecta-Diptera (adults)	4 ^c	1 ^a	2 ^a	3 ^b
Insecta-Lepidoptera (adults)	2 ^a	4 ^b	1 ^a	3 ^{ab}
Insecta-Hymenoptera (ants)	2 ^b	4 ^c	1 ^a	3 ^b
Insecta-Psocoptera	4 ^b	2 ^{ab}	1 ^a	3 ^{ab}
Insecta-Hemiptera (psyllids)	4 ^c	3 ^b	1 ^a	2 ^b
Arachnida-Araneae	2 ^b	4 ^b	3 ^b	1 ^a
Insecta-Thysanoptera	2 ^b	4 ^b	3 ^b	1 ^a
Insecta-Hymenoptera (others)	2 ^a	4 ^b	3 ^a	1 ^a
Arachnida-Acarina	4 ^c	3 ^c	2 ^b	1 ^a
Insecta-Orthoptera	4 ^a	3 ^a	2 ^a	1 ^a
Insecta-Coleoptera (adults)	4 ^c	3 ^b	2 ^b	1 ^a
Insecta-Hemiptera (others)	3 ^b	4 ^b	2 ^a	1 ^a
Insecta-Diptera (larvae)	4 ^b	2 ^b	3 ^b	1 ^a
Insecta-Lepidoptera (larvae)	4 ^c	2 ^{ab}	3 ^b	1 ^a
Mean rank	3.3	2.8	2.1	1.8
Best rank	4	3	2	1

Ranks which share the same letter of the alphabet indicate that seasonal means do not statistically differ. The taxa are grouped so that ones which are abundant in a particular season are listed together.

CV3 vs CV4 diagram. On both diagrams the separation between the two samples from a given season tended to be as great as between samples from different seasons. The consistent separation of seasonal samples from the two 12 month sampling periods on the CV1 vs CV2 diagram suggests that the degree of difference in faunal composition between these two periods was just as great as between individual seasons.

DISCUSSION

Consideration of trends

The results presented here confirm our earlier observation that canopy arthropod levels are higher on trees in the NSW than the WA forest (Majer *et al.* 1990, 1994; Recher *et al.* 1991a; Fig. 2a-r). Whether this is a peculiarity of the two forests that we studied or applies to

the two regions of Australia in general is currently unknown. However, a current study of canopy arthropods on wandoo (*Eucalyptus wandoo* Blakely) in the WA wheatbelt and on yellow box (*Eucalyptus melliodora* A. Cunn. ex Schau.) on the New England Tablelands of NSW (J. D. Majer & H. F. Recher unpubl. data) is producing similar differences in arthropod levels between the two states, so this could represent a general trend.

In an earlier paper (Majer *et al.* 1990) we suggested that invertebrate abundances were greater on marri than jarrah and greater on ironbark than box. These conclusions were based on the first season that was sampled. The more extensive analyses presented in this paper confirm the greater abundance of invertebrates on ironbark than box, although total numbers converge in winter (Fig. 2q-r). Differences in abundance between marri and jarrah were not as pronounced as previously suggested (Fig. 2q-r) and were not statistically significant in either stratum during the 1987-88 or 1988-89 sampling

Table 7. Proportion of separation represented by the first four canonical variates derived from the canonical variate analysis of the WA data collected in the 1987-88 and 1988-89 periods

Taxon	CV1	CV2	CV3	CV4
Arachnida-Acarina	-0.35 0.0001	0.24 0.0020	0.38 0.0001	0.62 0.0001
Arachnida-Araneae	-0.64 0.0001	-0.35 0.0001	0.13 0.1086	0.37 0.0001
Collembola	0.35 0.0001	-0.15 0.0677	0.07 0.3885	-0.05 0.5409
Insecta-Orthoptera	-0.05 0.5172	0.01 0.8598	0.22 0.0049	0.10 0.1958
Insecta-Psocoptera	0.10 0.1981	-0.40 0.0001	0.06 0.4779	-0.02 0.7691
Insecta-Hemiptera (psyllids)	0.23 0.0036	0.55 0.0001	0.01 0.9956	0.38 0.0001
Insecta-Hemiptera (others)	-0.23 0.0036	-0.34 0.0001	0.38 0.0001	0.24 0.0022
Insecta-Thysanoptera	-0.17 0.0337	0.14 0.0727	0.33 0.0001	0.16 0.0445
Insecta-Coleoptera (adults)	-0.47 0.0001	-0.02 0.7978	0.46 0.0001	0.27 0.0005
Insecta-Coleoptera (larvae)	0.35 0.0001	-0.67 0.0001	0.30 0.0001	0.14 0.0692
Insecta-Diptera (adults)	0.65 0.0001	-0.11 0.1714	0.16 0.0477	0.55 0.0001
Insecta-Diptera (larvae)	-0.11 0.1827	-0.05 0.5236	0.37 0.0001	-0.23 0.0040
Insecta-Lepidoptera (adults)	-0.08 0.2950	0.23 0.0031	-0.26 0.0009	-0.19 0.0154
Insecta-Lepidoptera (larvae)	0.05 0.5307	-0.18 0.0233	0.43 0.0001	0.11 0.1685
Insecta-Hymenoptera (ants)	-0.17 0.0332	-0.09 0.2405	-0.11 0.1546	-0.03 0.6940
Insecta-Hymenoptera (others)	-0.37 0.0001	0.25 0.0015	-0.15 0.0606	0.39 0.0001
% Separation explained	48.02	18.82	13.96	9.28
Cumulative %	48.00	67.00	81.00	90.00

The data for trees are the average of values on marri and jarrah. The correlations between the taxa variables and the canonical variates are also shown (with *P*-values).

years (Tables 2, 5). Although mean numbers of arthropods were slightly higher on marri in three of the seasons, the trend was reversed in spring (Fig. 2q-r).

The invertebrate data presented here were gathered from two forests that experience different climatic patterns. In the WA forest, rain falls predominantly during winter, while in the NSW forest rainfall is less seasonal and appreciable quantities fall during summer (Fig. 1). Both forests exhibited similar monthly maximum temperatures during the study period, although winter minima were generally lower in the NSW than the WA forest (Fig. 1). It is likely that invertebrate phenology is determined through direct influences of climate and also through the condition on the host plant, which itself is tied to climatic and other seasonal factors.

In terms of rainfall, the WA forest experienced a more strongly pronounced seasonal pattern. This was reflected in the higher seasonal variability in numbers of animals across the various taxa in the WA than in the NSW forest. The Mediterranean climate in the WA forest could limit arthropods during winter due to conditions being cold and wet, and also during summer when conditions are hot and dry. This certainly appears to be the case because seven and five taxa, respectively, exhibited minimum numbers during winter and summer, while only four taxa reached minimum numbers in autumn or spring (Table 3). This contrasts sharply with the NSW forest where nine of the 16 taxa reached minimum values in winter (Table 3), a phenomenon also noted on trees on the Tablelands of NSW (Recher *et al.* 1983; Bell 1985) and at mesic sites in Victoria (Woinarski & Cullen 1984). It may well be that the greatest limiting climatic factor in NSW is low temperatures. Certainly frosts during winter can be a cause of high mortality in NSW; on one morning during the July 1987 sampling programme at Scheyville, following a heavy frost and temperatures below 0°C, large quantities of dead arthropods were found in nets that had been left overnight prior to spraying the trees.

Our sampling times did not coincide with flowering on trees so the influence of this factor, which undoubtedly has a major influence on arthropod abundance (Woinarski & Cullen 1984), need not be considered. Our personal observations, and information presented in Abbott and Loneragan (1986) and in Heatwole *et al.* (in press), indicate that the WA trees exhibited pronounced foliage flushes during spring and early summer (late September onwards), while the NSW trees were less seasonal and produced new growth in spring and summer during warm moist periods.

The manner in which animals might respond to the condition of the host plant will depend on the functional group to which they belong. Consideration of the arthropod fauna as a whole did not reveal consistent trends in the WA forest (see also Abbott *et al.* 1992), as different taxa exhibit different phenologies. Treatment of the invertebrate data at the ordinal level will tend to

mask such responses, because a given order may contain representatives from more than one functional group. We have subsequently sorted the material from our samples to species level (Majer *et al.* 1994) and are able to make some generalizations about the feeding habits of the ordinal categories used in this paper. Groups, which in our samples were predominantly represented by herbivores, include Orthoptera, Hemiptera (psyllids and others), Coleoptera (larvae), Diptera (larvae) and Lepidoptera (larvae). Predators and/or parasites are represented by Araneae and Hymenoptera (ants and others), while Coleoptera (adults) and Acarina represent a mixture of herbivores and predators. The Collembola are decomposition-associated animals, while the Psocoptera and Thysanoptera are represented by fungus-feeding species. The remaining two groups, the adult Diptera and Lepidoptera, tend to contain large numbers of tourists, whose presence in the samples may merely have represented their occurrence in the forest at that particular time of the year.

As Lowman (1982) found for phytophagous insects in Australian rainforests, herbivores are most likely to exhibit phenological patterns linked to leaf flush. In WA this is clearly the case with the Homoptera (psyllids and others), which peaked in spring (Table 3); a phenomenon also observed by Casotti and Bradley (1991) and by Abbott *et al.* (1992). In the same forest the Orthoptera peaked later during summer and the other herbivorous groups, the larval Diptera and Lepidoptera, peaked during winter. All herbivorous groups in NSW peaked during either spring or summer when leaf flushing was greatest (Table 3).

The Collembola and Psocoptera might be expected to respond to periods of abundant moisture, when microbial and fungal growth is at a maximum. This was evident in both forests, where peaks occurred in winter, or, in the case of Collembola in NSW, in autumn (Table 3).

The predators/parasites would be expected to reflect availability of major prey items. In terms of biomass, the predominant arthropods were herbivores (see also Abbott *et al.* 1992), so it is not surprising that peaks in predators/parasites in NSW coincided with the spring and summer peaks in herbivores (Table 3). Reasons for the tendency for representatives of this functional group to peak during autumn in WA are unclear (Table 3), although this could result from a combination of adequate food availability and avoidance of harsh desiccating conditions during summer. This is supported by the fact that during the second 12 month sampling period, when rainfall was higher and continued later into spring, most herbivorous groups and all predator/parasite groups peaked in spring or summer (Table 6).

Although some general trends in arthropod phenology have been isolated, these vary from year to year. Comparison of the data from the two 12 month sampling periods suggests that variations in rainfall affect the seasonal pattern of arthropod abundance (cf. Tables 3 &

6; Fig. 4). A delay, or increase, in rainfall can render an otherwise hostile season favourable to arthropod activity and can result in that season supporting high numbers of canopy arthropods. This important source of variability in arthropod abundance has also been noted by Carne *et al.* (1981) and by Bell (1985), who found that the summer peak in canopy arthropods which occurred at his NSW site did not occur during drought years. Differences between years in the composition and abundances of invertebrate communities is not restricted to temperate, or even seasonal forests. Wolda and Broadhead (1985) found only weak correlations in the pattern of abundances of Psocoptera species in a non-seasonal tropical forest in Panama between years. Wolda (1978) had earlier noted that chance events in the pattern of rainfall (e.g. early, heavy rain in the dry season) can have a strong positive effect on foliage production and, through that, on insect populations.

Implications for research and management

In a study of sublittoral kelp in NSW, Kennelly and Underwood (1992) found that the assemblages of species associated with kelp forests were variable within and between locations. Variability extended to temporal changes in abundances. Kennelly and Underwood (1992) concluded that the structure and dynamics of these kelp communities could not be predicted by simple models. The eucalypt canopy invertebrate communities sampled in the study reported here also showed spatial (between location and tree species) and temporal (between seasons and years) variability in ordinal composition and abundances. While some of the variability is attributable to differences between tree species, as well as to temporal variation in weather between seasons and years, some may be in response to historical events (e.g. time since fire, logging history). As in the case of sublittoral kelp forests, because of the spatial and temporal variability in community composition and species abundances, descriptions of eucalypt canopy communities and the assessment of the effects of disturbance on these communities require long-term sampling.

Data on insect abundances from only one year of sampling can be misleading (Wolda 1978). Had we sampled different sites over a wider area of forest in either NSW or WA, our impression is that we would have encountered high levels of variability in invertebrate community composition and species abundances between locations. We are also of the view that we sampled too infrequently to detect the entire range of changes in community composition and species abundances that occurs in eucalypt communities. For example, by restricting sampling to only 1 week at 3 month intervals we almost certainly missed the peak abundances of invertebrates during spring in WA. The peak probably occurs later in the season than we sampled and may only last for a few weeks, certainly for a briefer time than the 3

months between our samples. Stork and Brendell (1990), in discussing temporal fluctuations in insect abundances in Sulawesi, also suggested that the timing of samples may have affected their results by falling between peaks of abundance.

Forest bird communities also fluctuate in composition and species abundances between seasons and years (Recher *et al.* 1980, 1983, 1991a). Seasonal patterns of avian abundance occur in response to changing weather conditions and abundance of food (Recher & Majer 1994; Recher *et al.* 1983, 1991b), but variation in patterns of abundance between years is almost certainly due to a more complex set of interactions including events remote from the location where the pattern was observed. Drought, unusual rainfall, clearing of vegetation and fire are all factors that may affect avian abundances over large geographical regions of Australia including sites seemingly unaffected by the driving event itself. These complex patterns of spatial and temporal variation in the composition and abundances of eucalypt forest faunas lead us to raise the same concerns about evaluating the impact of disturbance (from human or other sources) on forest communities as presented by Kennelly and Underwood (1992) for sublittoral kelp communities. Before we fully understand the nature of disturbance and can develop predictive models for long-term effects on forest ecosystems it will be necessary to sample vertebrate and invertebrate communities over broad geographical regions and to measure changes in abundance (in response to disturbance and climatic differences) over a number of years. For forest invertebrate communities it will be necessary to increase the frequency of sampling in order to assign the proportion of temporal variability attributable to variation in weather patterns and plant phenology and that attributable to the disturbance being studied.

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