Seasonal invertebrate communities in multiple use jarrah forests. Implications for conservation and management

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ABSTRACT

The response of ground-dwelling jarrah forest invertebrates to logging (but not a post-harvest burning) was examined in the Kingston, Warrup and Winnejup forest blocks, approximately 25 km north-east of Manjimup in the south-west of Western Australia. Twenty sites, comprising eight Internal Controls, four External Controls and eight Impact sites, were sampled simultaneously before and after logging. These sites were sampled 18 times (8 pre- and 10 post-logging) over a period of 22 months (May 1994- March 1996). Logging occurred between March and April 1995.

Approximately 500 000 invertebrates were collected from 35 Classes, sub Classes or Orders. The most dominant taxa were Collembola and Formicidae which accounted for 77.6% of the total abundance. Marked seasonal trends were present, with overall invertebrate activity (excluding Collembola) being highest during spring and lowest during winter. The main factors correlated with invertebrate activity were temperature and rainfall. Numerical dominance of taxa changed between seasons and between years. Significant spatial variability was also evident and appeared to be associated with changes in microclimatic conditions and small scale spatial variations in habitat.

Timber harvesting had no significant impacts on total invertebrate abundance and richness. Only 5 of the 35 taxa studied, Blattodea, Coleoptera, Diptera, Hemiptera and Orthoptera, were significantly affected, with Blattodea being the most severely affected. At the level of order, the impacts were only of short duration, with post logging communities resembling those of undisturbed sites after 10 months. Similarly, the impacts of logging on Araneae, Blattodea and Orthoptera assemblages were also only of a short duration. Logged sites followed the same seasonal patterns as control sites in the ordination plots, indicating that seasonal and inter-annual climatic changes appear to be more important determinants of community structure and function of the ground-dwelling invertebrate fauna than a logging event.

Key words: Jarrah forest, invertebrates, disturbance, timber harvesting.

Introduction

Western Australia's jarrah forests are tall open sclerophyll forests that extend throughout the south-west of the state. They are dominated by jarrah *Eucalyptus marginata* Donn ex Smith, and to a lesser degree, marri *Corymbia calophylla*. The understorey comprises small trees (4-7m) such as *Allocasuarina fraseriana*, *Banksia grandis* and *Persoonia longifolia*, while the ground cover is dominated by woody shrubs (Bell and Heddle 1989). Jarrah forests are complex ecosystems, although they are not as species rich as communities such as the Banksia woodlands of the Swan Coastal Plain. Nevertheless, approximately 784 vascular plant species (Bell and Heddle 1989), 29 species of native mammal, and some 150 species of native birds have been recorded in the northern jarrah forest alone (Nichols and Muir 1989).

Similar to other Australian forests, Western Australia's publicly-owned jarrah forests are managed for multiple uses such as recreation, wildlife conservation, water supplies, mining and timber production (CALM 1987a, b, c), with the latter two having the greatest potential to damage these ecosystems. Both mining and timber production are of great economic importance to the state and considerable concessions are made for them. All of the northern jarrah forest, for example, is held under mining leases (CALM 1987a.; Bradshaw *et al.* 1991), while the remaining forest, with the exception of that protected under the reserve system, is available for timber harvesting. To date, approximately 10 000 hectares of high quality jarrah forest have been cleared for mining and another 600-700 hectares are expected to be cleared

Pp 830 - 844 in the *Conservation of Australia's Forest Fauna* (second edition) 2004, edited by Daniel Lunney. Royal Zoological Society of New South Wales, Mosman, NSW, Australia.

annually for this purpose (Bradshaw 1999). An additional 178,570 hectares of jarrah forest were harvested for timber production between 1990–2000 (CALM 2001). As a result of this extensive logging, questions have been raised about the ecological sustainability of multiple use forest management.

The Department of Conservation and Land Management (CALM) is the agency responsible for the management of the state's ecosystems on publicly owned land. CALM maintains that current timber harvesting techniques are sustainable and that no ecological processes have been impaired and no single plant or animal species has become extinct or endangered as a result of past and present logging practices (Abbott and Christensen 1994; CALM 1994). They conclude that current silvicultural practices include measures designed to protect these systems. "Gaps" (or areas to be logged), for example, can only be 10 hectares. In most cases, gaps are smaller for aesthetic reasons (CALM 1994). A minimum of three tree age classes representing each development stage of the forest need to remain in each coupe (*i.e.* forest area that is harvested as a single unit) (CALM 1994). No clearfelling is permitted in jarrah forests instead, a minimum of four habitat trees per hectare are retained in each gap to provide wildlife refuge (CALM 1994; 1995). Less destructive harvesting techniques are also employed. Shelterwood logging, for example, only removes 40-60 percent of the trees. Strips or buffer zones of native vegetation are retained between gaps (CALM 1994; 1995). No harvesting is permitted in river and stream zones (CALM 1994). Clearly, some conservation measures have been incorporated in the harvesting process. However, the effectiveness of these measures in preserving the flora and fauna, including the invertebrate fauna, still needs to be determined.

Invertebrates play an important role in ecosystem processes such as pedogenesis, decomposition, mycorrhizal activity, herbivory, pollination, seed dispersal and other species interactions (Majer and Heterick 1997). They comprise the bulk of the world's biomass and biodiversity. In the jarrah forest, densities of 39 400 – 133 700 m^2 and 1300-3400 m^2 have been recorded for soil and litter invertebrates respectively (Postle *et al.* 1986). Furthermore, some estimated 15-20,000 invertebrate species (Abbott 1995) are believed to inhabit these forests. Many of these invertebrates are endemic or have families with Gondwanan affinities (eg. Main 1987; Van Heurck *et al.* 2000). As a result, this fauna may be of high conservation value. However invertebrates are usually excluded from most ecological studies and are consequently not considered in the decision-making process.

Jarrah forest invertebrate communities are among the best studied in Australia (Majer and Abbott 1989), yet there are still gaps in the knowledge base. Some taxa such as spiders, ants and termites have been well researched and their distribution, composition and biology are reasonably well understood. For the remaining taxa, the information available is limited (Majer and Heterick 1997; Brennan and Majer 2003). Similarly, more research is needed to determine the impacts of disturbances on the invertebrate fauna of jarrah forests. Considerable research effort has been aimed at investigating the effects of fires and mining on these populations (Majer and Heterick 1997). However, only two studies have examined the impacts of forest harvesting on Western Australia's arthropod communities.

The first study examined the effects of logging and burning on arachnid communities in Karri *Eucalyptus diversicolor* forests (Curry *et al.* 1985). It found that there was no long term reduction in arachnid richness, but that considerable changes to the community structure and composition had occurred as a result of these disturbances.

This is the second study. It was part of a larger interdisciplinary study, the Kingston Project, which was initiated by CALM to determine the long-term effects of current timber harvesting techniques and associated activities on the jarrah forest ecosystem. A team of researchers from CALM, Curtin University of Technology, Murdoch University and the University of Western Australia undertook a series of experimental studies to investigate the impacts of logging on the vegetation, abundance of hollow-bearing trees, small terrestrial vertebrates, medium sized mammals, birds and invertebrates over a five to ten year period (Burrows *et al.* 1993 CALM, 1997) commencing in 1994. This particular study examined the immediate impacts of timber harvesting on ground-dwelling invertebrate communities.

The impacts of logging on ordinal invertebrate communities were reported by Strehlow *et al.* (2002). This paper builds upon it and examines the influence of season on these communities and their response to logging. The effects of logging on three taxa, Blattodea, Orthoptera and Aranea, is examined in more detail.

Methods

Field

The impacts of timber harvesting operations on epigeal invertebrates were examined in a modified Before/After, Control/Impact (BACI) experiment established in the low to medium rainfall Jarrah forest at Kingston, Warrup and Winnejup forest blocks, 25 km north-east of Manjimup (34°15'S, 116°9'E) Western Australia. Two standard harvesting techniques, Gap release (creation of a gap <10ha, leaving a minimum of three habitat trees/ha) and Shelterwood (removal of 40-60% of the basal area) (CALM 1995) were examined.

Twenty sample sites, eight Impact sites (I), eight Internal Controls (IC) and four External Controls (EC), were established prior to harvesting in the proposed coupes and buffer zones. Buffer zones consisted of strips of a minimum 100 m width of native vegetation, surrounding the logged area. All sites were representative of the jarrah forest of this region, both in terms of plant composition and past disturbance history. A detailed description of the vegetation is given in Havel and Mattiske (2000). Each treatment site was located on an individual logging coupe to avoid pseudo-replication (Hulbert 1984) and was paired to an internal control site located in the adjoining buffer zone. External controls were located in the adjacent Warrup and Winnejup forest blocks. Treatments and Internal Controls were both subjected to post-harvest burns to promote the regeneration of jarrah and to reduce the amount of fuel. External control sites were neither logged nor burned.

As the invertebrate study imposed on a larger experimental design (CALM's Kingston Study) and on a commercial timber operation, logistic constraints and unexpected difficulties were unavoidable. Problems encountered were related to the logging operations and lead to the loss of the pairing of impact and internal control sites. Of the original 8 paired control and impact sites, six remained after logging. The severity of the disturbance on the sites also varied leading to a reclassification of the impact sites based on the actual damage (mild versus severe) rather than logging prescription. Finally, the post harvest burns were delayed and could therefore not be included in this study.

Invertebrates were collected by one of the most commonly used methods to sample surface active invertebrates, pitfall traps. This method has been widely used in Western Australian studies (eg. Friend and Williams 1996; Van Heurck and Friend 1996; Van Heurck *et al.* 1998, 2000), and its use here made comparisons between studies possible. Moreover, the low cost and relative ease of operation of these traps made them ideal for long term monitoring studies such as this. However, pitfall traps cannot provide absolute density estimates or complete species lists (see Adis 1979; Topping and Sunderland 1992). Instead, they reflect the activity levels, mobility, size, sex and behaviour of the animals caught (Greenslade 1964; Uetz and Utzicker 1976; Adis 1979; Topping and Sunderland 1992). The limitations of this method however, can be addressed in the experimental design and in the interpretation of the results.

Invertebrate sampling grids consisted of a 15x15 m plot oriented in a N-S direction. Sixteen pitfall traps were placed 5 m apart forming a 4 x 4 grid. Each pitfall trap consisted of an outer PVC sleeve (120 mm deep and 90 mm diameter) which had its top slightly flanged. The sleeves were buried vertically with their top flush to the ground. Plastic cups (Solo P12, 90 mm diameter, and 110 mm deep) were placed in the outer sleeve.

On each sampling occasion pitfall traps, filled with Galt's solution as a preservative, were left open for a period of 10 days after which the contents were sieved in the field and placed in a container with 70% ethanol. The four pitfall traps nearest to each corner were bulked to form four replicate samples for each grid, thereby permitting the analysis of between and within-site variation.

Invertebrate sampling occurred on 18 occasions (8 pre and 10 post logging samples), over a period of 22 months (May 1994 – March 1996). Logging occurred during March and April 1995.

All invertebrates were sorted and counted to class and/ or order. Animals belonging to the orders Orthoptera, Blattodea and Araneae were then identified to family and to morphospecies using keys by Davies (1986) and CSIRO (1991). Classifications were verified by taxonomic experts (see Acknowledgements). A voucher collection was deposited with CALM.

A number of habitat variables were also recorded at each of the 20 sites. Habitat measurements were taken in 20x20m plots centred on the invertebrate plots and included records of the vegetation structure and composition, soil temperature, soil moisture (%), litter moisture (%), litter cover (%), litter type litter depth (cm) presence/absence of logs, woody litter and soil profiles.

Statistical analysis

A combination of univariate ANOVAs, Multivariate Analysis of Variance (MANOVA) and multivariate techniques such as non-metric Multi Dimensional Scaling (MDS) and Cluster Analysis was used to determine the seasonal and spatial variability of the invertebrate communities and to examine the effects of logging on these populations. Analysis of temporal and spatial variation in the invertebrate communities was carried out on samples collected only from the 12 control sites. Prior to analysis, the data was examined for homogeneity and for the assumption of compound symmetry of the variance-covariance matrix using Cochran's C test, Bartlett-Box F test and Mauchly's criterion respectively. The data were found to be heteroscedastic and were transformed when necessary. Following this, an ANOVA (SAS 1986) was used to determine whether seasonal changes in the abundance of invertebrate taxa were significant. Seasonal changes in the composition of invertebrate, spider, cockroach and grasshopper/cricket communities were examined by non-parametric multivariate analyses using the PRIMER (Plymouth Routines in Multivariate Ecological Research) package described by Clarke and Warwick (1994).

The data were classified using Hierarchical Agglomerative Clustering and ordinated by non-metric Multi-Dimensional Scaling (Kruskal and Wish 1978). An association matrix using Bray-Curtis similarity was calculated for the classification and ordination. Following this, the species responsible for the observed groupings were identified using SIMPER (Similarity Percentages) in the PRIMER package. The percent similarities within groups and dissimilarities between groups were also determined. A detailed description of the procedure is given in Clarke (1993) and Clarke and Warwick (1994). A Spearman's Rank correlation was used in PRIMER's BIOENV procedure to determine the environmental variables best predicting the observed community patterns (Clarke 1993). Correlations were not only calculated for single parameters but for all possible combinations using all or only a subset of the variables. Finally, environmental variables were superimposed onto the ordinations to examine the relationship between the biotic clusters and the environmental parameters.

The same procedures were repeated to determine the impacts of logging on the invertebrate populations identified to the level of Order. In this instance the complete data set, *ie*. 20 sites and 18 sampling occasions, was used. A detailed description of these analyses and of the power analysis used is given in Strehlow *et al.* (2002).

The impacts of logging on Blattodea, Orthoptera and Arachnida morphospecies were examined using almost exclusively non-parametric multivariate techniques (Hierarchical Agglomerative Clustering and non-metric Multi-dimensional Scaling, MDS), as these approaches are robust at the low mean sample abundances observed at the species level. Repeated measures analysis of variance was therefore only carried out for Blattodea, Orthoptera and Araneae richness, but not abundance.

RESULTS

Community composition of jarrah forest invertebrates

A total of 528 716 invertebrates, comprising 35 Classes, Sub Classes or Orders was collected during this study. The most abundant group identified was the Collembola (springtails), followed by Hymenoptera: Formicidae (ants), Diptera (flies), Coleoptera (beetles), Apocrita (wasps), Araneae (spiders), Acarina (mites), Hemiptera (true bugs), Blattodea (cockroaches) and Orthoptera (crickets and grasshoppers). These 10 main groups accounted for more than 98% of all the individuals and were found at all sites.

Of the three groups that were examined more closely at the morphospecies level, spiders were the most abundant (12 152 individuals) and species-rich group, with 31 families and 108 morphospecies identified. Six families with Gondwanan affinities (Actinopidae, Idiopidae, Micropholcommatidae, Nemesiidae, Orsolobidae and Toxopidae) were also recorded. The four most abundant families were Corinnidae, Salticidae, Lycosidae and Gnaphosidae. These accounted for 52.2% of the total abundance. The most abundant species was *Supunna albopunctata* (1439 individuals), followed by Lycosidae genus 1 sp.1 (864) and *Lycidas michaelseni* (654). Juveniles accounted for 26.5% of the total abundance.

Cockroaches were the second most abundant, but least species-rich group of the three analysed. Only 2321 individuals, belonging to 4 families and 32 morphospecies were caught. Most species belonged to the Blattidae, followed by Blaberidae, Blattelidae and Polyphagidae. The most abundant species, Blattidae sp.6, Blattidae sp.5, Blattidae sp.3 and Blaberidae sp.1 accounted for 68% of the total Blattodea abundance. (Note that as the majority of these species are yet to be named, they were assigned species codes eg. sp. 1).

Finally, the 2094 orthopterans collected were identified into three subfamilies and 67 morphospecies. The most abundant was the Gryllidae (crickets), which accounted for 88.7% of the total Orthoptera abundance. Grasshoppers and locusts belonging to the Acrididae accounted for 10.4%, while members of the Pyrgomorphidae accounted for less than one percent of the total. Overall, abundances of most individual species were low, with six species (Gryllidae sp.8, Gryllidae sp.8b, Gryllidae sp.16, *Namungia balyarta*, Gryllidae sp.25 and Gryllidae sp.18) accounting for 66.6% of the total abundance.

Most individual species in all three groups were rare, occurring only patchily in both space and time. Some species were only found once, or were only found at some sites. Other species had a short phase of activity and were only captured for limited periods.

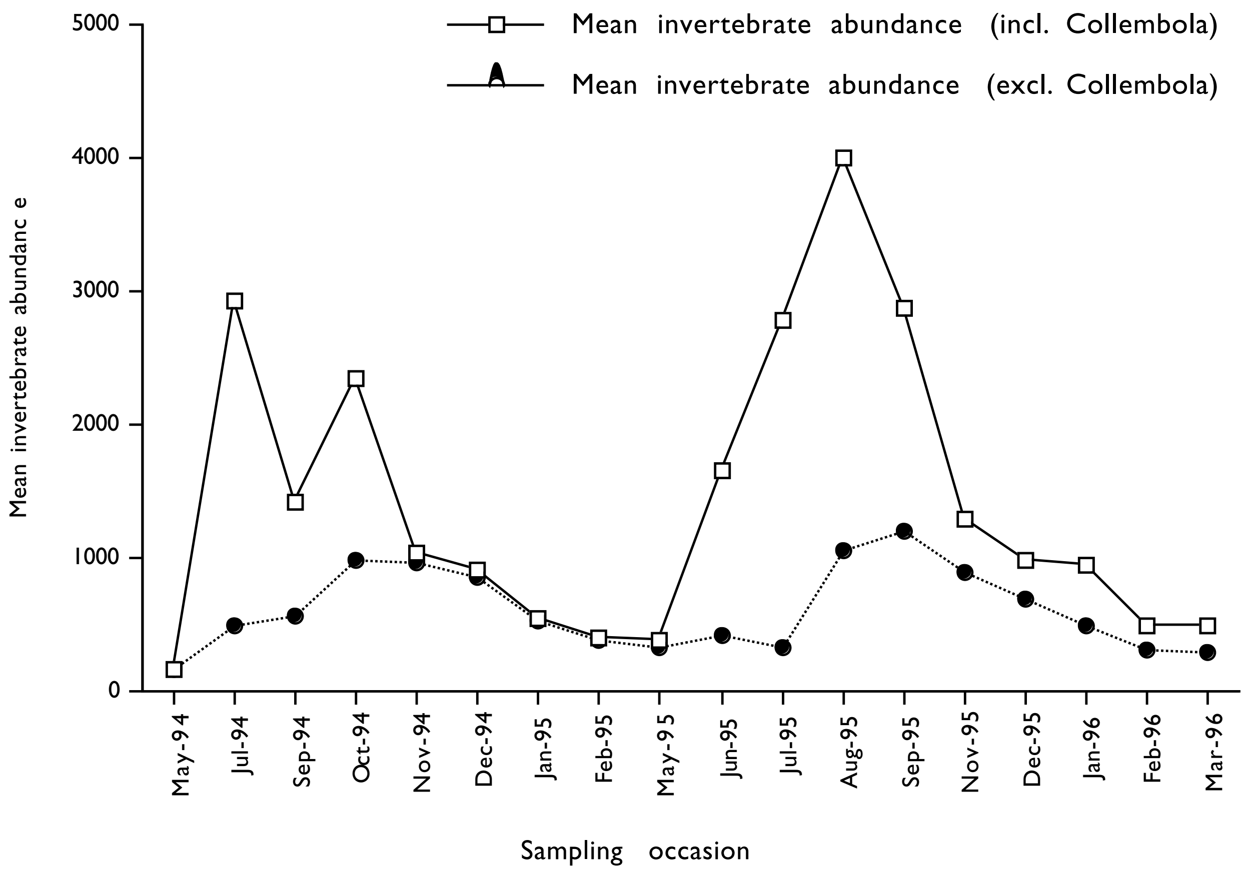

Figure 1: Seasonal changes in mean invertebrate abundance, including and excluding Collembola at the Kingston study sites (control sites only), south-west Western Australia. Standard errors were too small to be included in this Figure.

Table 1: ANOVA of seasonal invertebrate abundance.

Variable	Transformation	F	Sig. of F
Total abundance	*no transformation*	35.95	0.0001
Arachnida	*log transformation*	44.81	0.0001
Coleoptera	*log transformation*	26.26	0.0001
Diptera	*log transformation*	55.55	0.0001
Hymenoptera	*log transformation*	27.89	0.0001
Apocrita	*log transformation*	25.07	0.0001
Acarina	*log transformation*	33.52	0.0001
Blattodea	*log transformation*	4.33	0.0055
Orthoptera	*log transformation*	16.16	0.0001
Collembola	*sqrt transformation*	139	0.0001
Hemiptera	*log transformation*	52.48	0.0001
Isopoda	*log transformation*	32.36	0.0001
Dermaptera	*log transformation*	16.65	0.0001

Seasonal and spatial variation in jarrah forest invertebrate communities.

Jarrah forest invertebrates were highly seasonal. Generally, invertebrate activity (excluding Collembola) tended to peak during spring and decrease during summer, reaching the lowest abundances during winter. However, winter abundance peaks were observed when Collembola were included (Fig. 1). Most individual taxa also displayed marked seasonal trends. Araneae, Coleoptera, Hemiptera, Hymenoptera: Formicidae, and Orthoptera showed distinctive spring/summer peaks, with winter/autumn minima. The reverse seasonal cycles were observed for the Collembola and Diptera. The remaining taxa displayed less distinctive seasonal patterns. All seasonal changes were significant (Table 1).

Seasonal and yearly oscillations were also noted in invertebrate community structure. During the first year of the study (May 1994-February 1995), late spring, summer and autumn communities were primarily dominated by ants, with secondary domination by beetles, spiders, mites and wasps (Fig. 2). Wasps increased during late summer. In contrast, early winter to late spring communities were primarily dominated by the litter decomposing collembolans, with secondary domination by ants, flies and beetles (Fig. 2). A shift in the community structure was observed during the second year. This shift was expressed in a change in the rank position of the 10 more common taxa, particularly during late spring and summer.

Seasonal influences on the invertebrate communities were also evident in the classification and ordination (Fig. 3). The three main groupings obtained in the classification were largely based on season (Fig. 3a). Similarly, the MDS ordination showed clear seasonal and inter-annual patterns of change in the invertebrate community (Fig. 3b). A larger seasonal variability was observed during the first year than in the second year of this study, with summer samples of the second year being closer to spring and winter samples.

Despite the obvious seasonal trends, single environmental parameters showed only modest correlations (rainfall: $r=0.558$; maximum temperature: $r=0.476$; minimum temperature: $r=0.363$; soil moisture: $r=0.272$; soil temperature: $r=0.128$; litter moisture: $r=0.065$; and litter depth: $r=-0.049$). Higher correlations were obtained from the examination of combined variables. The most important factors influencing these communities with a Spearman's rank correlation of ($r=0.603$) were rainfall and maximum temperature combined.

In addition to seasonal and inter-annual changes, ground-dwelling invertebrate communities displayed spatial differences, despite the fact that some sites were only a few hundred metres apart. While total invertebrate abundance did not vary significantly between the 12 control sites, the abundance of Diptera ($p=0.0057$), Apocrita ($p=0.0004$), Hymenoptera ($p=0.0003$), Orthoptera ($p=0.0008$), Dermaptera ($p=0.0001$) and Hemiptera ($p=0.048$) communities were significantly different.

Impacts of logging on invertebrate communities

The immediate and most visible impact of logging was a reduction in vegetative cover and abundance (Fig. 4). The percentage cover of jarrah trees was reduced by as little as 10% to up to 90% in some sites depending on logging intensity (mild vs. severe). A large proportion of mid- and understorey plant species was also removed. These changes in vegetation cover resulted in changes in the microclimate. Significant decreases in litter depth and cover and a significant increase in soil temperature were observed in the impact sites following logging (all $p < 0.05$). Soil and litter moisture remained unaffected by the disturbance. A more detailed account of these results is given in Strehlow *et al.* (2002).

Contrary to the obvious impacts on the vegetation, the invertebrate community experienced less pronounced effects. The impacts of logging on ordinal invertebrate

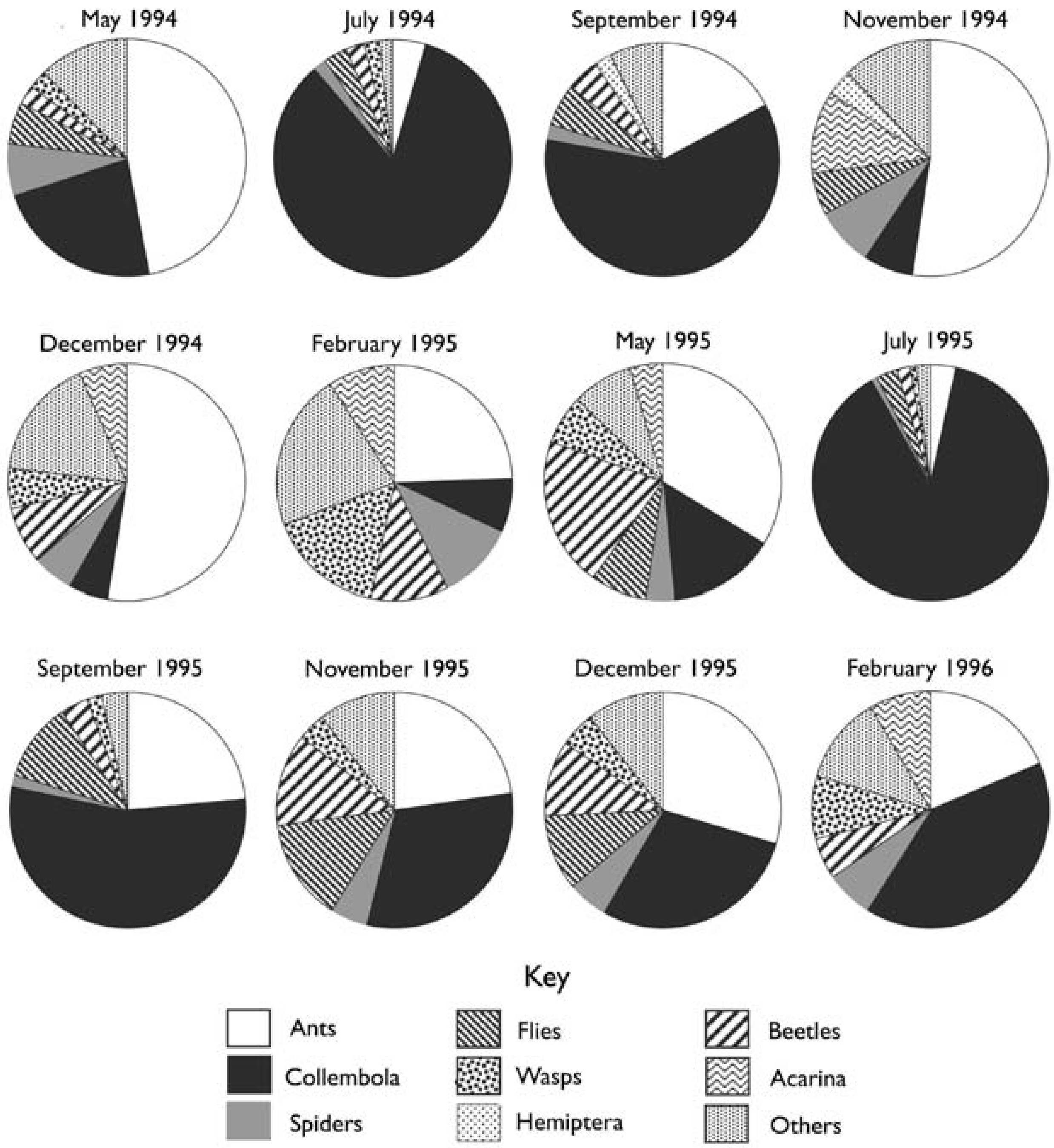

Figure 2: Seasonal changes in the invertebrate community composition at the twelve control sites of the Kingston study, south-west Western Australia.

communities were examined in detail in Strehlow *et al.* (2002) and a summary is presented here as a background to the impacts of logging on individual species.

Logging had no significant impact on ordinal richness, total invertebrate abundance or the abundance of most individual taxa. Only 5 of the 35 taxa studied showed changes in their abundance, with Blattodea being the most severely affected group. Blattodean abundance in impact sites were severely reduced after logging resulting in an increase in the percent difference between internal control and impact sites (Fig. 5). Similarly, reductions in abundance accounted for the percent changes observed for the Diptera and Coleoptera, while Collembola and Orthoptera experienced increases in their abundance following logging (Fig. 5). Of these changes, only those of the Blattodea, Coleoptera, Diptera, Hemiptera and Orthoptera were significant (see Strehlow *et al.* 2002).

Classification and MDS ordination of invertebrate orders revealed that seasonal impacts were much greater than the impacts of logging, with control and impact sites clustering together before and after logging. In fact, changes and controls were more similar at the end of the study than at the beginning (Fig. 6a). As the results of the classification and the ordination are nearly identical, only those of the ordination are shown here.

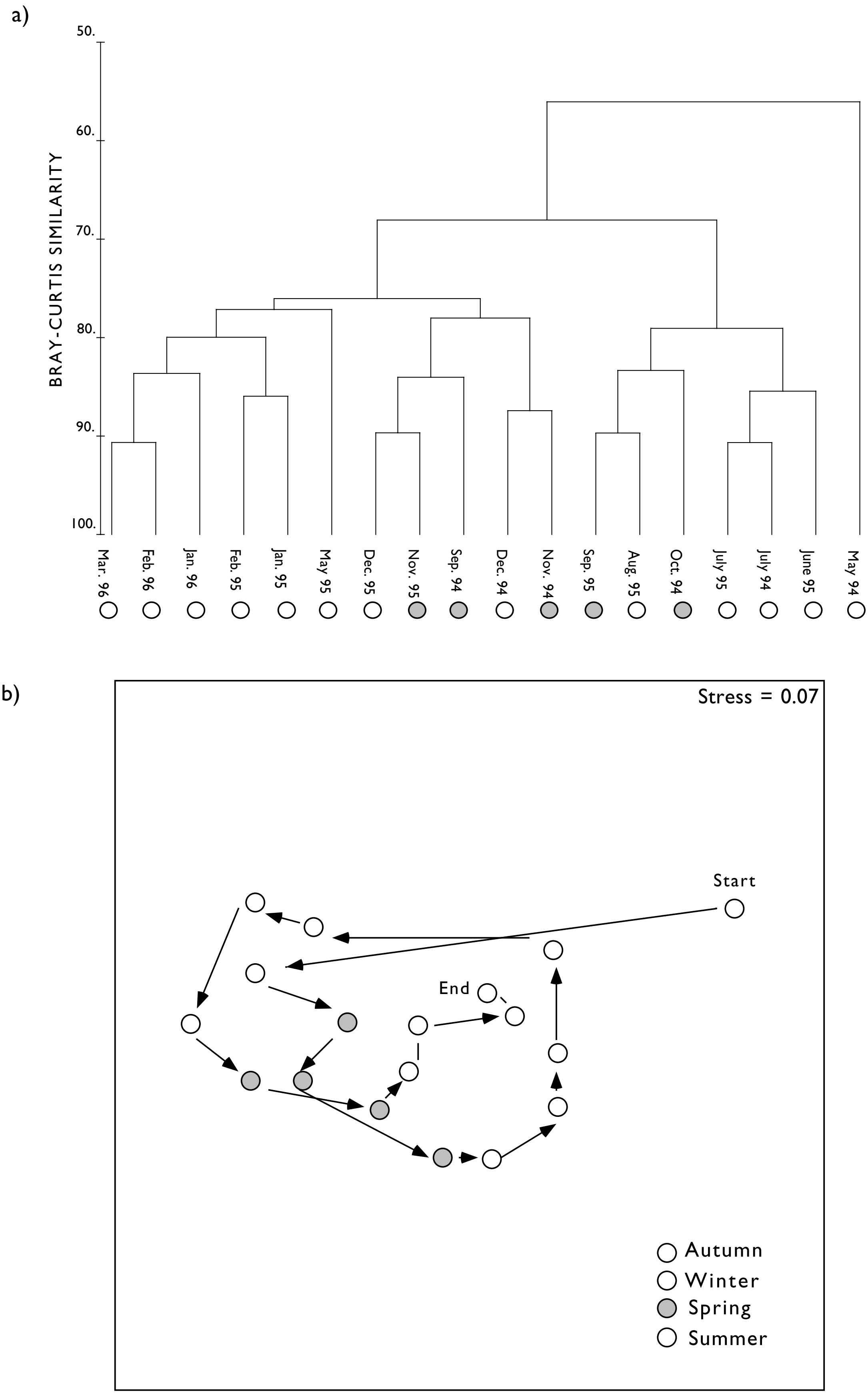

Figure 3: a) Classification and b) non-metric MDS showing the seasonal changes of the invertebrate community in the 12 costal sites identified to the level of Order. The similarity measure used was the Bray-Curtis similarity Index. Seasons are represented through the shaded circles.

Figure 4. Photographs of invertebrate study sites affected by logging. Photographs were taken in April 1994 at the beginning of the study and in March 1996, nine months after logging.

Identification to species did not always reveal further impacts of logging. The Blattodea, for example, were the most severely affected by the logging at the ordinal level, yet at the species level, these impacts were no longer as evident. While richness at impact sites was significantly lower (p=0.001) after the disturbance, no single species could be identified which had been significantly affected. Most species were so rare in space and time that their disappearance could not be attributed to the logging.

Classification and MDS ordination of cockroach morphospecies showed seasonal rather than logging effects on these communities. Control and impact sites showed varying degrees of dissimilarity before and after logging in the ordination (Fig. 6b). Spring samples tended to show the highest dissimilarities to each other in both years. Control and impact sites in summer 1994/95 and winter 1994 were more similar to each other than the summer 1995/96 and winter 1995 samples. However, none of these dissimilarities was large enough to be attributable with certainty to the effects of logging. The exceptions may be control and impact sites during November 1995 and March 1996.

Grasshoppers and crickets showed only a marginal response to logging at the level of order (see Strehlow *et al.* 2002). At the level of morphospecies, no significant impacts of logging were observed on abundance or richness. No species appeared to have disappeared as a result of logging. Note that many species were only found once or twice during this study, consequently their absence from logged sites could not be attributed to the disturbance.

No impacts of logging were also observed in the classification and ordination of orthopteran species, with both analyses again revealing separations based on season only. A distinct pattern of seasonal change was observed in the ordination of Internal Control and impact sites. Control and impact sites tended to cluster together both before and after logging. A marked separation of control and impact sites was observed during August 1995 (Fig. 6c).

Logging had no impact on ordinal spider abundance or richness. At the species level, only *Supunna albopunctata* showed a marked, but non-significant decrease in its abundance eight months after logging. The abundance of this species remained low for the following three months, but was similar to that of control sites twelve months after logging.

Classification of the spider data, identified to family level and to morphospecies, failed to reveal any impacts of logging, instead seasonal impacts dominated the communities. However, in the ordinations, an increased dissimilarity in spider families between control and impact sites was observed in the first four months after logging (May – August 1995) (Fig. 6d). Disturbed sites were similar to undisturbed sites five months after logging. These impacts, however, were not evident at the morphospecies level.

The degree of the disturbance (*i.e.* mild versus severe) had differing impacts on cockroaches, grasshopper/crickets and spiders. Cockroach species, in particular, showed larger responses in severely logged sites than

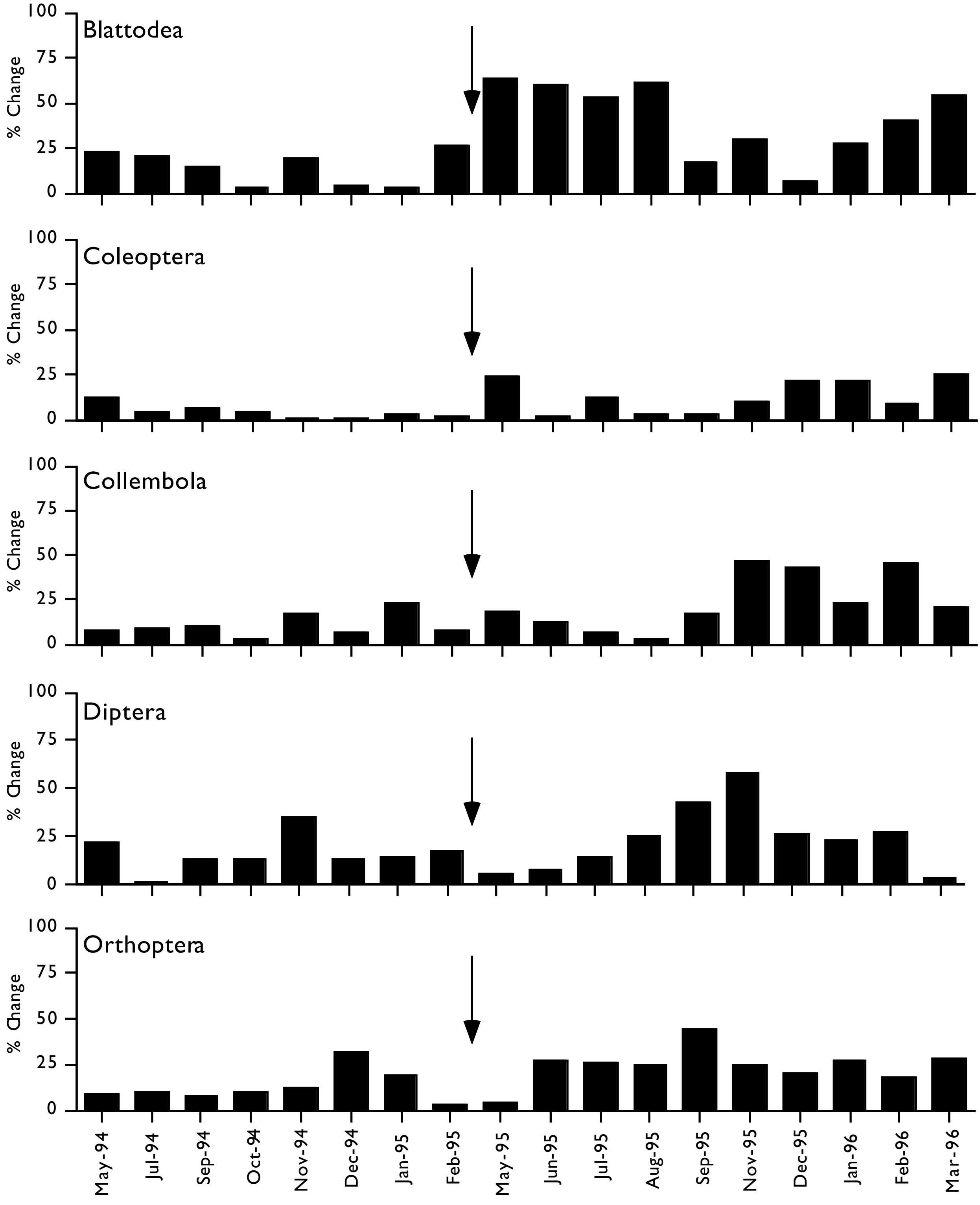

Figure 5. Percentage change between control and impact sites in five taxa (n°/m²) before and after logging.

in mildly logged sites. These severely logged sites also experienced the largest reduction in the depth of the litter layer. The same was not true for the other two taxa, whose response to logging was not influenced by the severity of the disturbance.

Power analysis using simulated impacts revealed that sufficient power to detect change (*i.e.* a power of 0.8 or higher) was only observed after simulated impacts produced a >30% reduction in overall invertebrate abundance. Similar results were obtained for most individual taxa. A 10% reduction in abundance could only be detected in Araneae, Coleoptera and Blattodea. For the remaining taxa, only changes of >50% could be detected with reasonable power.

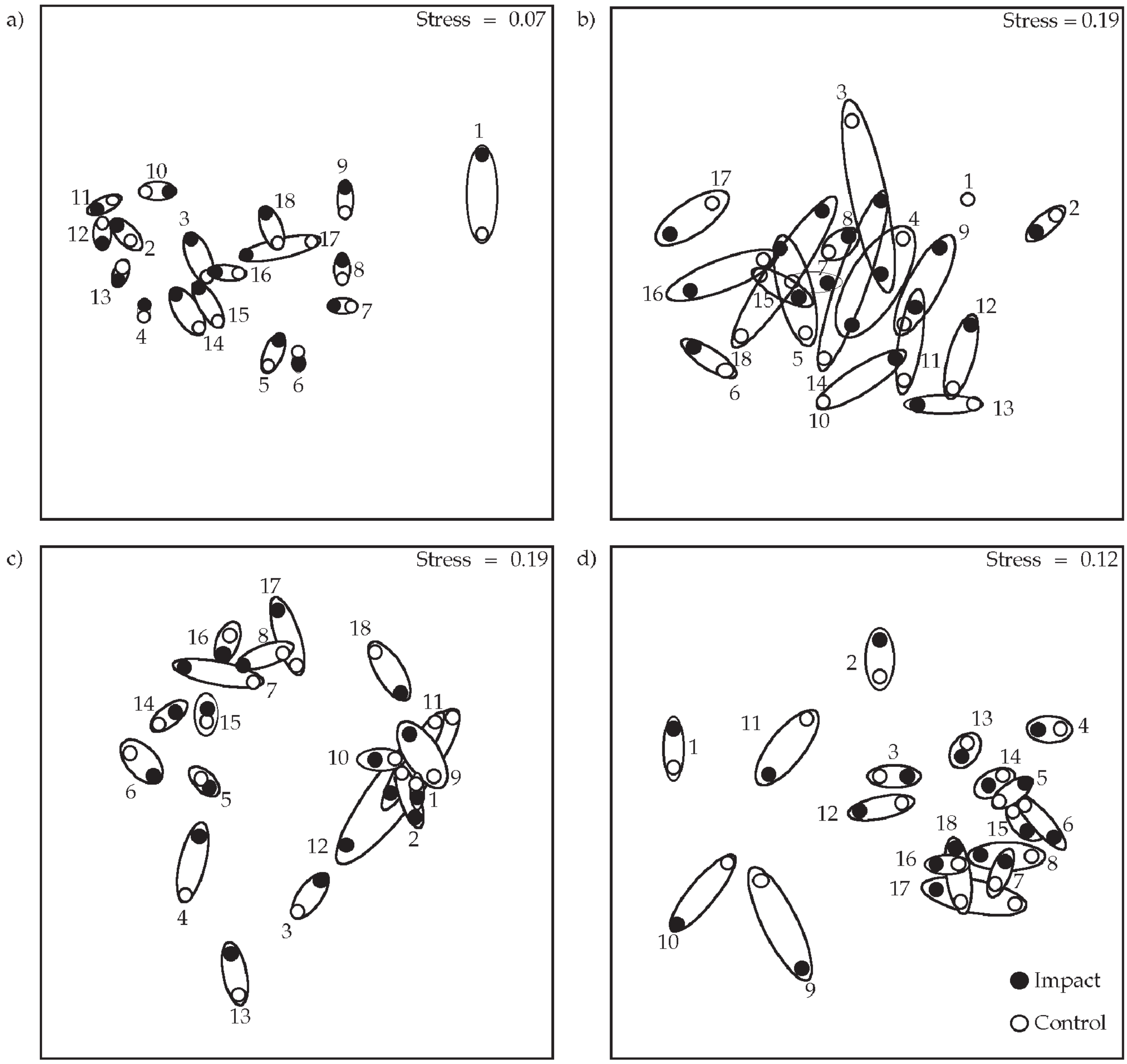

Figure 6. MDS ordination of a) ordinal invertebrate b) Blattodea morphospecies, c) Orthoptera morphospecies and d) Araneae morphospecies abundance in internal controls and impact sites. Impact sites are represented by black circles, while the internal controls are represented by the open circles. Data were transformed by square root. Pre-logging samples = 1-8, post logging samples = 9-18.

Discussion

This study has provided information on the composition, diversity, seasonal activity and spatial variability of epigaeic invertebrates in the medium rainfall jarrah forest. Overall, the range of taxa found was similar to that recorded in other regions of jarrah forest (e.g. Majer and Koch 1982; Van Heurck and Friend 1996). Similarly, the seasonal changes in abundance and composition observed here are also well documented (Majer 1980; Majer and Koch 1982; Little and Friend 1993; Van Heurck *et al.* 1998) and are related to the life histories of the different groups, the prevailing climatic conditions and microclimatic factors. The dominance, for example, of ants and collembolans in these communities appears to be directly related to climate, with ants dominating in the drier years.

At the morphospecies level, the spider, cockroach and grasshopper/cricket communities were as diverse as expected. Of the 46 spider families, 338 genera and approximately 1700 species estimated to be present in Western Australia (Main 1981), 31 families and 108 morphospecies were found in this study. CALM subsequently recorded an additional 142 species in this area (Abbott *et al.* 2003). A number of families with Gondwanan affinities have also been reported here and elsewhere (*e.g.* Van Heurck *et al.* 2000).

Similar to the Araneae, the Blattodea and Orthoptera communities were very diverse. Abbott (1995) listed 29 Blattodea species belonging to two families (Blattidae and Blatellidae) and 23 Orthoptera species belonging to seven families (Gryllacrididae, Tettigoniidae, Gryllidae, Eumastacidae, Pyrgomorphidae, Acrididae and Tetrigidae) for the jarrah forest. A larger number of species was recorded in this study. Unfortunately, the inadequate taxonomic knowledge base for these two groups made comparisons to other communities difficult.

Although the spatial variability displayed by these communities was surprising, it appears to be the norm. Little and Friend (1993) reported site differences in the abundance of flies, ants and spiders, while York (1996) found spatial differences in the richness of several taxa. The spatial variability of invertebrate communities has been attributed to changes in short-term climatic conditions and to small-scale differences in their habitat (Campbell and Tanton 1981; Friend 1995). These factors may have also affected the communities in this study.

Timber harvesting had no effects on total invertebrate abundance and richness and none of the taxa believed to be suitable indicators of this type of disturbance (e.g. ants) showed a response in this study. Only five taxa, Blattodea, Coleoptera, Diptera, Hemiptera and Orthoptera, were found to be significantly affected by logging, with Blattodea experiencing the most severe impacts.

Australian Blattodea have been found to be sensitive to grazing (Bromham *et al.* 1999), burning (Abbott 1984; Neumann 1991; Friend 1995), and habitat fragmentation (Abensperg-Traun *et al.* 1996). However, no Australian study to date has reported the response of Blattodea to logging, and existing overseas studies have not found this group to be particularly sensitive to logging (Molina *et al.* 1999: Middleton 1987). As decomposers, cockroaches are closely associated with the humus and the litter layer. Therefore changes to the litter layer may affect these communities. The cockroaches in this study showed a stronger response to logging in those sites that had been more extensively cleared and experienced the largest reduction in litter layer. This indicates that the removal of the litter layer played an important part in the observed response, yet the processes remain less clear. One possibility may be that the removal of the litter layer and the associated microclimatic changes created an unsuitable environment for cockroach survival. The removal of the litter layer may have also reduced the availability of food and increased the risk of predation.

The remaining four taxa have also been found by other workers to be sensitive to environmental disturbance (e.g. Friend 1995; Abensperg-Traun *et al.* 1996; Bromham *et al.* 1999), including logging both in Australia (Neumann 1991, 1992; Michaels and McQuillan 1995) and elsewhere (Bengtsson *et al.* 1997; Watt *et al.* 1997).

The impacts of logging on orthopteran communities were less distinct than those of the Blattodea. Orthopteran abundance decreased at all sites, but the reduction was less at impact sites, suggesting that a small increase in abundance had occurred at logged sites. Increases in Orthoptera abundance following fire (Evans 1988a; Fielding and Brusven 1993) and other disturbances have been reported (Baldi and Kisbenedek 1997). However, the increases observed here were not always significant. It is only when the whole assemblage is examined that the impacts of logging become apparent. These results concur with Andersen *et al.* (2001) and overseas studies (Evans 1984; Evans 1988b; Kemp 1992) which have indicated that Orthoptera species assemblages are sensitive to changes in plant communities.

Despite the significant impacts of timber harvesting on these five invertebrate taxa, the magnitude of change was small and its duration was short, except for the Blattodea. In fact, all five taxa had abundances similar to that of control sites 12 months after logging. This relatively minor response of invertebrates to logging may lead to considerable scrutiny and scepticism of this study. Some may argue that the results were due to deficiencies in the experimental design rather than being a reflection of the resilience of these communities. The sole reliance on only one invertebrate sampling method, for example, may have contributed to the obtained results. As mentioned previously, pitfall traps have a number of limitations (Greenslade 1964; Uetz and Utzicker 1976; Adis 1979; Topping and Sunderland 1992). However, many of these were addressed in the design of the sampling grid (*e.g.* outer PVC sleeve to prevent the "digging in effect", larger sized cups, arrangement of and spacing between cups).

Criticism may also be aimed at the design itself. However, the design used here is one of the more powerful designs described in the literature, containing elements of the BACIP (Stewart-Oaten *et al.* 1986; Stewart-Oaten *et al.* 1992) and "beyond BACI" designs (Underwood 1991; 1992; 1993). In fact, it represents the "ideal scenario" as defined by Underwood (1991, 1992, 1993), with multiple control and impact sites, sampled simultaneously on a number of occasions before and after the disturbance. The only area of concern may be the limited amount of pre-disturbance data. However, the argument of Morris and Williams (1998) that one whole year of pre-disturbance data are sufficient to determine the seasonal cycle of the community is also valid here, especially because the internal and external controls continue to provide additional information of the seasonal cycles of undisturbed populations.

Overall, this design had the power to detect changes of 10% in Araneae, Coleoptera and Blattodea and changes of >50% for all other taxa. While these changes may seem to be large, one needs to acknowledge that invertebrate communities experience large seasonal and interannual fluctuations in their abundance. Collembolla abundances, for example, decreased by nearly 99% in less than a month as a result of season. A change of 10% in such a population may not be biologically significant, although there remains the need to determine what constitutes a biologically significant effect for these communities.

There is a number of possible reasons for the results obtained. The most important may be that this study examined only part of the logging prescriptions (*i.e.* the removal of the trees) and did not include the post logging burns. However, continued monitoring of these populations by CALM has shown that while Blattodea, Araneae and Orthoptera experienced immediate decreases in species richness and total abundance after the fire, these changes were only of a short duration. Similarly, changes in the community structure were only short-lived (Abbott *et al.* 2003). Invertebrates in logged coupes resembled the communities in control sites five years after harvesting and three years after the burn. The results obtained by CALM confirm that timber harvesting practices (including post harvest burns) have only minimal and short term impacts on the jarrah forest's invertebrate populations.

These results agree with a number of recent studies, which have also reported limited impacts of logging on invertebrates (Bird *et al.* 2000; Vanderwoude *et al.* 2000; Vasconcelos *et al*. 2000; Lewis 2001). These studies indicate a higher than expected resilience of invertebrates to disturbance. In jarrah forest invertebrates, this resilience may have evolved in response to the unique climatic changes and the fire history of the south-west region of Australia.

The gradual change from the moist and cool conditions prevailing in Gondwana to the arid mediterranean conditions existing today, the appearance of Aboriginal people in Australia and the subsequent increased incidence of fire resulted in the emergence of more seasonally and fire adapted taxa, which are more resilient to disturbance. The jarrah forest spider communities provide an excellent example. The community was dominated by vagrant taxa such as Corinnidae, Clubionidae, Gnaphosidae, Lycosidae, Zoride and Zodariidae. All of these families were identified by (Main 2001) as "adaptive opportunists", *i.e.* taxa that have responded to ecological changes and have evolved behavioural strategies making them more resilient to change. It is worth noting that the relic invertebrate taxa found in the jarrah forest lack those evolutionary adaptations and their survival is dependent on the persistence of the moist refugia present in the southwest of the state (Main 1996; Van Heurck *et al.* 2000).

The high adaptability to climatic and seasonal changes of jarrah forest invertebrate communities may make them less vulnerable to disturbances. This is more apparent at the species level. The majority of spider, cockroach and grasshopper/cricket species, for example, were active only for very short periods of time, presumably to coincide with periods of favourable environmental conditions for that particular species. These short periods of activity, related to life history, could protect these species from disturbances. Consequently, a community in which each species has different times of activity would be more resilient than one where all species are active at the same time. Moreover, a species-rich community may be more stable and resilient to environmental changes than a species-poor community, because the former is more likely to have a number of species that will be insensitive to that particular disturbance (Walker 1995; Sankaran and McNaughton 1999; Ives *et al.* 2000).

Changes in community composition may occur as the species best adapted to the conditions, prevailing during the disturbance, become dominant. However, in this study, changes in community composition occurred in all sites on a yearly basis and could therefore not be attributed to logging. In fact, the invertebrate communities in all treatments (impact, external and internal controls) showed the same synchronized patterns of fluctuations indicating that these communities and their response to disturbance may be influenced by large scale weather variations. Climate therefore, appears to be the main driving force of the Kingston invertebrates, affecting not only the seasonal and yearly changes in abundance, richness and composition, but overshadowing the effects of the disturbance.

Implications for conservation and management

The findings of this study have significant implications for conservation and management. As both areas are intimately linked in forests that are managed for multiple uses, they are discussed together here. One issue with the potential to create difficulties is the presence of a large number of rare species. Usually, rare species are excluded from most studies because their low numbers make meaningful statistical analysis nearly impossible (a fact experienced here). Their presence and responses to disturbance are therefore largely ignored. However, rare species comprise the bulk of the richness of the community. Many of the rare species found in this study are Gondwanan relics and/or are endemic to the south-west of Western Australia. They are therefore of considerable conservation value and need to be considered in the management process. Their distribution, habitat preferences and responses to disturbances need to be determined.

The spatial variability observed in these communities may also pose some problems. Without reliable databases on the distribution of the species and assemblages, the impact of most management practices is difficult to determine. Currently most management practices (especially those related to logging and burning) are undertaken at the landscape scale. In the jarrah forest, it is at the Forest Block scale. However, invertebrates are often responding to changes in microclimate. As the linkages between the landscape and microhabitat scale are not particularly well understood, the conservation of these communities cannot always be ensured. Clearly, a precautionary approach to the conservation of these communities is needed and may require that a large number of existing and potential habitats be set aside for conservation. While it is acknowledged large areas have been protected under the reserve system, significant areas are still used for commercial timber production. In such areas, management should be aimed at creating a mosaic of forests of different age classes and disturbance histories to ensure the survival of both pioneer species and old growth forest specialists.

No adverse long-term effects on the ground dwelling invertebrate fauna were observed as a result of current silvicultural practices in this study. Abbott *et al.* (2003) therefore argue that this indicates that timber harvesting in Western Australia's Jarrah forest is sustainable and that the harvesting techniques currently employed do not need to be modified. However, care should be given that these conclusions are not extended to other parts of the biota. Arboreal invertebrates, for example, may not have responded so well to this disturbance.

The most important finding with significant implications for management and conservation was the influence of climate in determining community composition, seasonality and response to disturbance. Similar climatic influences on invertebrate communities have been documented by Campbell and Tanton (1981) Strehlow (1993) and Friend and Williams (1996). There is a need to include this factor in the management process, especially in view of the threat of global warming.

The threat of global warming impacts on ecosystems and biodiversity is increasingly being acknowledged (*e.g.* Noss 2001). For invertebrates, these climatic changes may have both positive and negative impacts. Some species may experience an accelerated rate of development, leading to extra generations, with a potential risk of an increase in insect outbreaks. However, for other species global warming will have deleterious impacts. Gondwanan relics are likely to be among the most severely affected not only because of their long generation times, low mobility, restricted range, and high specificity but because their moist refuges will disappear. Unfortunately, these are also those species of highest conservation value.

Undoubtedly, global warming alone presents a serious challenge for conservation. Management prescriptions such as fire and harvesting should be scheduled to coincide with times of low invertebrate activity (e.g. autumn) to limit the impacts of these disturbances. Moreover, logging and burning should be avoided in periods of abnormal weather patterns such as droughts.

Finally, management also needs to acknowledge the need for more invertebrate research. CALM discontinued the invertebrate component of the Kingston study because no substantial logging impacts had been identified. The continued data collection might have been used to answer some of the other questions that have arisen from this study, especially that of resilience to logging under shifting climatic regimes. Data published by Abbott *et al*. (2003) show that the invertebrate community of 2000 does not resemble that of 1994. It is obvious that more research is needed before one may conclude that current timber harvesting is sustainable and will remain so in a changing world.

Acknowledgements

The authors thank the following for assistance: Dr. D. Rentz, Ms. J. Waldock, Dr. M. Harvey and Dr. P. Ladd confirmed invertebrate and plant identifications, Mr. M. Williams and Mrs. A. Mellican provided support with the statistical analysis, Mr. F. Salleo, Ms. A. Hepworth and Mrs. McGuire helped with computer problems. The authors acknowledge a debt of gratitude to all the volunteers, especially Mrs. Strehlow and Mr. Croce. The contributions of the Division of Science and Engineering of Murdoch University and the Department of Conservation and Land Management are gratefully acknowledged. The senior author was supported by a Murdoch University Scholarship and a Bursary from the Federation of University Women.

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