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Toward an optimal sampling protocol for Hemiptera on understorey plants

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Abstract

There are no standardised sampling protocols for inventorying Hemiptera from understorey or canopy plants. This paper proposes an optimal protocol for the understorey, after evaluating the efficiency of seven methods to maximise the richness of Hemiptera collected from plants with minimal field and laboratory time. The methods evaluated were beating, chemical knockdown, sweeping, branch clipping, hand collecting, vacuum sampling and sticky trapping. These techniques were tested at two spatial scales: 1 ha sites and individual plants. In addition, because efficiency may differ with vegetation structure, sampling of sites was conducted in three disparate understorey habitats, and sampling of individual plants was conducted across 33 plant species. No single method sampled the majority of hemipteran species in the understorey. Chemical knockdown, vacuum sampling and beating yielded speciose samples (61, 61 and 30 species, respectively, representing 53, 53 and 26% of total species collected). The four remaining methods provided species-poor samples (<18 species or $<16\%$ of total species collected). These methods also had biases towards particular taxa (e.g., branch clipping and hand collecting targeted sessile Hemiptera, and sticky trapping were dominated by five species of Psyllidae). The most time-efficient methods were beating, sweeping and hand collecting (200 minutes of field and laboratory time yielded >7 species for each technique). By comparison, vacuum sampling, sticky trapping, branch clipping and chemical knockdown yielded <5 species for the same period. Chemical knockdown had further disadvantages; high financial cost and potential spray drift. The most effective methods for a standardised sampling protocol to inventory Hemiptera from the understorey are beating and vacuum sampling. If used in combination, these methods optimise the catch of understorey hemipteran species, as their samples have high complementarity.

Introduction

Inventorying global biodiversity is critical for conservation (Hawksworth and Kalin-Arroyo 1995). Given the inadequacy of resources for this task, efficient sampling procedures are needed (Colwell and Coddington 1995; Longino and Colwell 1997). Additionally, there is a pressing need to standardise invertebrate sampling protocols (New 1996; Majer et al. 1997) to allow comparisons between different biomes (Colwell and Coddington 1995; Kitching et al. 2001). These exist for some invertebrates (Spiders – Coddington et al. 1991; Termites – Jones and Eggleton 2000;

Ants – Agosti and Alonso 2000; Carabid beetles – Niemela et al. 2000), but are lacking for the majority of invertebrate taxa. User-friendly protocols may also encourage greater consideration of arthropods by land managers (Andersen et al. 2002). Determining which collecting techniques to use in an optimal and standardised sampling protocol requires consideration of the following criteria: ability to easily repeat the protocol's methods; time efficiency (preparation, fieldwork and laboratory time); and ability to maximise species richness and/or abundance of organisms. Determining optimal protocols for different spatial scales is also important. Intercontinental comparisons, plus the patterning of diversity along altitudinal and latitudinal gradients, are often made at the scale of one hectare plots (e.g., Coddington et al. 1991; Kitching et al. 2001). At a smaller spatial scale, estimates of global biodiversity are often reliant upon the proportion of host-specific species on individual plants (Ødegaard et al. 2000). It is imperative that protocols be tested widely, as the optimal combination of methods will vary depending on the ecosystem (e.g., rainforest, desert or heathland), target habitat (e.g., canopy, understorey or leaf litter) and target fauna (e.g., sessile or mobile, hyperdiverse or depauperate taxa) (see Basset et al. 1997; Kitching et al. 2001).

There are no widely applicable, standardised sampling protocols for inventorying the diversity of Hemiptera within non-agricultural systems. This is surprising given their major contribution to global species diversity (one of the five most speciose insect orders: Gaston 1991), functional importance, and sensitivity to disturbance. Phytophagous Hemiptera are economically important in agriculture, and are also important in natural ecosystems as both herbivores and prey. Perhaps due to their functional importance, previous studies have found that Hemiptera are useful indicators of other taxa present, and/or disturbances (i.e., Ingham and Samways 1996; Nickel and Hildebrandt 2003). For example, within this order, heteropteran species richness is strongly correlated with beetle and vascular plant species richness (Southwood et al. 1979; Virolainen et al. 2000). Other workers have found that Auchenorrhyncha abundance and species richness is more responsive than plant diversity to an alteration in grazing pressure (Vickery et al. 2001; Kruess and Tscharntke 2002).

There are few comparisons of methods for sampling Hemiptera (notable exceptions include Wilson and Room 1982; Buffington and Redak 1998; Standen 2000). Choice of sampling methods depends on the purpose and location of the study. Typically, when inventorying biodiversity, more than one sampling method is necessary to collect a large proportion of species present and limit bias towards particular taxa (New 1984, 1998; Cranston and Trueman 1997). Many techniques are recommended for collecting different hemipteran families (Upton 1991). Utilising numerous techniques, however, is time-consuming, particularly if adequate replication is required (see Hurlbert 1984; Azarbayjani and Richardson 1999). This is especially so for hyperdiverse taxa (Longino and Colwell 1997). That said, an exhaustive sample of all species is impossible unless a study is tightly confined spatially and temporally (Novotný and Missa 2000). Thus, determining which techniques most rapidly accrue species when used in combination (i.e., high complementarity *sensu* Colwell and Coddington 1995) is vital to maximise inventory completeness.

The aims of this paper were to determine an optimal sampling protocol for inventorying hemipteran biodiversity from understorey plants (including heathlands, scrublands, grasslands, and other systems with no tree overstorey) by comparing the efficiency of different collecting methods. The seven techniques were sweeping, vacuum sampling, beating, chemical knockdown, branch clipping, hand collecting and sticky trapping. The techniques considered most efficient were those that maximised the number of species for minimal time invested in the field and laboratory. For sites, techniques were used across three disparate understorey structures: low and open; tall and dense; and intermediate in structure. For individual plants, techniques were tested across 33 plant species. Additionally, techniques were assessed for their degree of bias, and when used in combination, their degree of complementarity (*sensu* Colwell and Coddington 1995).

Methods

Study area

Sampling was conducted by the first author in April 2000 for 16 days from a global biodiversity

hotspot, the South-west Botanical Province of Western Australia (Myers et al. 2000). Sites were located in jarrah (*Eucalyptus marginata*) forest at Jarrahdale, 50 km SE of Perth (32° 14′S 116° 05′E), where mining for bauxite is a prominent activity. The jarrah forest understorey is low and open, and typically dominated by the Proteaceae (*Banksia*, *Hakea*, *Grevillea*), Papilionaceae (*Hovea*, *Chorizema*, *Daviesia*), Myrtaceae (*Melaleuca*, *Calothamnus*), Xanthorrhoeaceae (*Xanthorrhoea*) and Zamiaceae (*Macrozamia*) (Havel 1975). Within the forest, mining and/or burning causes marked changes in understorey structure and floristics. The understorey of rehabilitated mine pits is tall and dense, and often dominated by Mimosaceae (*Acacia*) and Papilionaceae (*Bossiaea*, *Mirbelia*) (Clark 2000). The understorey of rehabilitated mine pits that have been burnt is floristically similar to unburnt pits, but is intermediate in structure between forest and rehabilitated mine pits. Six sites were sampled, representing the three different understorey structures (two jarrah forest sites and four bauxite mine pits rehabilitated in 1989, two of which had been burnt in 1997). Sites were approximately 1 ha and were sampled by methods designed to collect Hemiptera at this scale. Techniques were beating, vacuum sampling, hand collecting, sweeping and sticky trapping. The understorey at any site was only sampled once by any method.

The efficiency of collecting techniques was also evaluated at a smaller spatial scale. This is particularly important for Hemiptera, as many show high host-specificity to individual plants. Thirty-three plant species were sampled to determine the effectiveness of each technique on individual plants (Table 1). Plants were sampled by beating, vacuum sampling, chemical knockdown and branch clipping. Some species (e.g., ground covers, grasses) were not sampled by beating or chemical knockdown, as the plant structure was too low to allow the placing of sheets beneath them. Sampling of individual plant species was located outside the 1 ha sites.

Table 1. Plant species sampled.

Cyperaceae	*Cyathochaeta avenaceae* (R.Br.) Benth
	Lepidosperma squamatum Labill.
	Lepidosperma tenue Benth.
	Tetraria capillaris (F.Muell.) Black
Dasypogonaceae	*Lomandra sonderi* (F.Muell.) Ewart
Dennstaedtiaceae	*Pteridium esculentum* (G.Forst.) Cockayne
Dilleniaceae	*Hibbertia commutata* Steud.
Epacridaceae	*Leucopogon capitellatus* DC.
	Leucopogon nutans E.Pritz.
	Leucopogon verticillatus R.Br.
Haemodoraceae	*Conostylis serosa* Lindl.
Mimosaceae	*Acacia drummondii* Lindl.
	Acacia extensa Lindl.
	Acacia puchella R.Br.
	Acacia lateriticola Maslin
	Acacia urophylla Lindl.
Papilionaceae	*Bossiaea aquifolium* Benth.
	Bossiaea ornata (Lindl.) Benth.
	Mirbelia dilatata R.Br.
Poaceae	*Tetrarrhena laevis* R.Br.
Proteaceae	*Adenanthos barbiger* Lindl.
	Banksia grandis Willd.
	Dryandra lindleyana Meisn.
	Grevillea wilsonii A.Cunn.
	Hakea lissocarpha R.Br.
	Persoonia longifolia R.Br.
Restionaceae	*Loxocarya cinerea* R.Br.
Rhamnaceae	*Trymalium ledifolium* Fenzl
Rutaceae	*Boronia fastigiata* Bartl.
Sterculiaceae	*Lasiopetalum floribundum* Benth.
Xanthorrhoeaceae	*Xanthorrhoea gracilis* Endl.
	Xanthorrhoea preissii Endl.
Zamiaceae	*Macrozamia riedlei* (Gaudich.) Gardner

Collecting techniques

Sweeping involves using a net to sweep invertebrates from vegetation, which are then removed using an aspirator or forceps. At each 1 ha site, sweeping occurred along three, 20 m transects arranged in a triangular formation. Sweeps were conducted once per metre, with a 48 cm diameter net.

Vacuum sampling was performed along five quadrats of 1×5 m in each 1 ha site. Vegetation within quadrats was sampled from approximately 5 to 200 cm above ground with a modified garden vacuum (Smith 1999). Five individual plants of each chosen understorey species were also vacuumed. Vacuumed material was placed in a plastic bag and frozen, with all debris examined under a microscope to remove Hemiptera, including sessile fauna attached to leaves.

Beating, using a stick, dislodged Hemiptera onto a white 1 m^2 beating tray. Hemiptera were collected from the tray with forceps or a paintbrush dipped in ethanol. Debris on the tray was examined for sessile fauna. The five most conspicuous

understorey plant (non-tree) species were beaten at 1 ha sites. Five plants of each chosen understorey species were beaten for individual plant sampling.

Chemical knockdown, or fogging, uses insecticide to dislodge and kill invertebrates. In this case, pyrethrum was applied to understorey plants from a handheld pump spray. The fauna fell on to white sheets placed below vegetation. The sheets were left for 1 h. Sampling was limited to calm days to reduce spray drift. Five individual plants of each chosen understorey species were sampled.

Branch clipping involved the collection of a branchlet (< 25 cm in length) in a plastic bag and killing all invertebrates inside by freezing. All debris was examined under a microscope to remove Hemiptera, including sessile fauna attached to leaves. Five individual plants of each chosen understorey species were sampled in this way.

Hand collecting required identification in the field to order. Thirty minutes per site was allocated to hand sampling. All parts of understorey plants were examined including leaves, flowers, galls and under bark. Hemiptera were removed with forceps and a paintbrush dipped in ethanol.

Sticky trapping has been used to monitor populations of Hemiptera (Aphididae – Kennedy et al. 1961; Aleyrodidae – Steiner et al. 1999; Cicadellidae – Mensah 1996; Psyllidae – Adams and Los 1989). Sticky traps consisted of yellow plastic sheets (24 cm×100 cm) mounted on 1 metre high posts and coated in Tangle-trap®. A trap was left standing in each site for two periods of 7 days. One large trap was placed in the middle of each site to reduce the likelihood of attracting Hemiptera from outside the site. Traps were collected at the end of each 7-day period and specimens removed in the laboratory.

A number of other methods were considered, but not used in this study, as they did not specifically target understorey fauna. These included light traps, pitfall traps, Tullgren funnels, soil core samples and bark traps.

Sorting and identification of specimens

All methods were standardised by time on a per site or per plant basis to allow valid comparison between sampling methods. Laboratory cleaning and sorting time were included, as excess plant debris collected by methods such as vacuum sampling (see Wright and Stewart 1992) may slow down the sorting of catches. Specimen mounting and identification were not timed, as the expertise of the first author increased with time, thereby decreasing the time spent on each specimen. All specimens were stored in 70% ethanol, prior to identification. Specimens were identified to morphospecies by the first author and the reference collection validated by specialists. Juveniles were excluded from analysis, an exception being Aleyrodidae nymphs (puparia), as their taxonomy is based on characteristics present in sessile juveniles (Martin 1999). Voucher specimens were lodged at the Western Australian Museum.

Statistical analysis

Two-way analysis of variance (ANOVA) (type 3 sums-of-squares) was used to test for significant differences in hemipteran species richness and abundance between sampling techniques. For the 1 ha sites, a two-way ANOVA with replication was used. Factors were 'understorey structure' (with levels low and open, high and dense, and intermediate) and 'technique' (with levels vacuum sampling, beating, hand collecting, sticky trapping and sweeping). Dependent variables were 'species richness' and 'abundance'. *Post-hoc* means comparisons between the techniques in the 1 ha sites used Scheffé's S (Day and Quinn 1989).

For individual plants, differences between collecting techniques and plant species were analysed using a two-way ANOVA without replication (see Zar 1984). Plant species were clumped into a group of five plants per method, owing to few Hemiptera per sample. Factors were 'plant species' (for levels refer to Table 1) and 'technique' (with levels being vacuum sampling, beating, chemical knockdown and branch clipping). Dependent variables were 'species richness' and 'abundance'. No *post-hoc* means comparisons were possible for individual plant species. Analyses were performed using the statistical package SuperANOVA (Abacus Concepts Inc. 1992).

Smoothed species accumulation curves (400 randomisations) were constructed using species abundance data for each technique. Curves were constructed using EstimateS 6.0b1 (Colwell 1994–2000) and graphed in Prism 4.0 (Graphpad Software Inc. 2003).

Table 2. *F*-ratios from ANOVA results performed on hemipteran species richness and abundance of all techniques applied at two spatial scales: 1 ha sites (two-way ANOVA) and on individual plant species (two-way ANOVA without replication).

	Sites			Plant species	
	Technique x Understorey structure $df_{8, 19}$	Technique $df_{4, 19}$	Understorey structure $df_{2, 19}$	Technique $df_{3, 93}$	Plant species $df_{30, 93}$
Species richness	0.64	23.45***	2.74	45.26***	10.46***
Abundance	1.94	12.31***	2.36	5.78**	1.35

* denotes $p < 0.05$, ** denotes $p < 0.0l$, *** denotes $p < 0.001$.

Ordinations were performed on a site and plant species basis to examine the differences in hemipteran species composition and potential sampling biases of techniques. A similarity matrix was constructed using the Bray–Curtis measure (Bray and Curtis 1957) on the abundance of hemipteran species in samples. To assist in interpretation, non-metric multidimensional scaling (MDS) (Shepard 1962) was performed on the Bray–Curtis matrix (50 restarts). Analyses of similarities (ANOSIMS) (Clarke 1993) were used to test for significant differences in hemipteran species composition between sampling techniques. A two-way crossed ANOSIM (999 permutations) was used on data from the 1 ha sites to test for the influence of technique and understorey structure. Factors were as given previously for site analysis using two-way ANOVA. Interaction effects cannot be determined directly using ANOSIMs, so values must be plotted manually and the interaction effect determined informally (see Clarke 1993). The presence of an interaction effect between vegetation structure and technique was tested using this method. A two-way crossed ANOSIM2, with no replication (999 permutations) was used on data derived from individual plant species. Factors were those described previously for plant species analysis with ANOVAs. All multivariate analyses were undertaken using Primer 5 (PRIMER-E Ltd. 2001).

Results

Abundance and species richness

A total of 3945 specimens were collected, representing 115 species from 28 families (Appendix 1). The most abundant families were Aleyrodidae, Diaspididae and Psyllidae (1549, 1004 and 530 specimens, respectively), and the most speciose families were Cicadellidae and Psyllidae (25 and 21 species, respectively) (Appendix 1). Singletons (species represented by a single individual) accounted for 41% (47 species) of the total species captured (Appendix 1).

Mean hemipteran abundance differed significantly between techniques at sites and on plant species (Table 2). At sites, vacuum sampling collected significantly higher abundances than other techniques (Table 3). For individual plants, branch clipping recorded the highest number of specimens (2329), and beating the lowest (111).

Mean hemipteran species richness differed significantly between techniques at sites and on plant species (Table 2). Chemical knockdown, vacuum

Table 3. Significance levels from *Post-hoc* comparisons using Scheffé's S, after two-way ANOVAs on hemipteran species richness and abundance sampled at the 1 ha sites.

	Vacuum	Beat	Sweep	Hand		Vacuum	Beat	Sweep	Hand
Species richness					Abundance				
Beat	***					***			
Sweep	***	–				***	–		
Hand	***	–	–			**	–	–	
Trap	***	–	–	–		*	–	–	–

Abbreviations for collecting techniques are given in Figure 1.
* denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$.

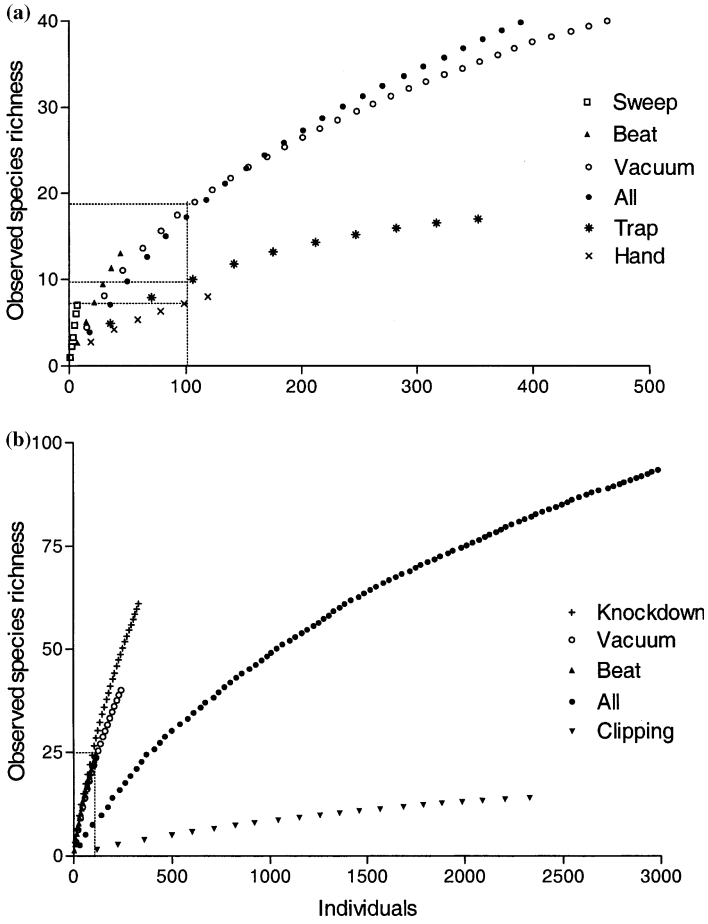

Figure 1. Smoothed species accumulation curves for increasing numbers of individuals (with standardisation line at 100 individuals) at sites (a) and on plant species (b). Abbreviations: Hand – hand collecting, Clipping – branch clipping, Beat – beating, Knockdown – chemical knockdown, Vacuum – vacuum sample, Sweep – sweeping, Trap – sticky trapping, All – all techniques combined.

sampling and beating produced the most speciose collection (a total of 61, 61 and 30 species, respectively, representing 53, 53 and 26% of the total species richness). However, for mean species richness, *post-hoc* comparisons for sites showed vacuuming yielded significantly more species than other techniques (Table 3).

Chemical knockdown, vacuum sampling, beating and sweeping rapidly accrued species as the number of individuals increased. Species accumulation curves for these techniques were very steep (Figure 1). At sites, when a standardised number of individuals were collected (100), 19 species were sampled by vacuuming (Figure 1a). It was not possible to compare beating or sweeping at 100 individuals owing to the low number of individuals captured by these techniques at sites. That said, the initial trajectory of their curves was steeper than vacuuming (Figure 1a). The remaining methods of sticky trapping and hand collecting yielded fewer species for the standardised 100 specimens (10 and 7 species, respectively) and had shallower curves. Sticky trapping was beginning to reach an asymptote (Figure 1a), indicating that the most species that could be sampled by this technique were collected in sites during the sampling period. On plants, with 100 standardised individuals, approximately 25 species were captured by beating, vacuuming and knockdown (Figure 1b). Branch clipping yielded fewer species for the standardised 100 specimens (2 species) and was beginning to reach an asymptote (Figure 1b), indicating that the most species that could be sampled with this

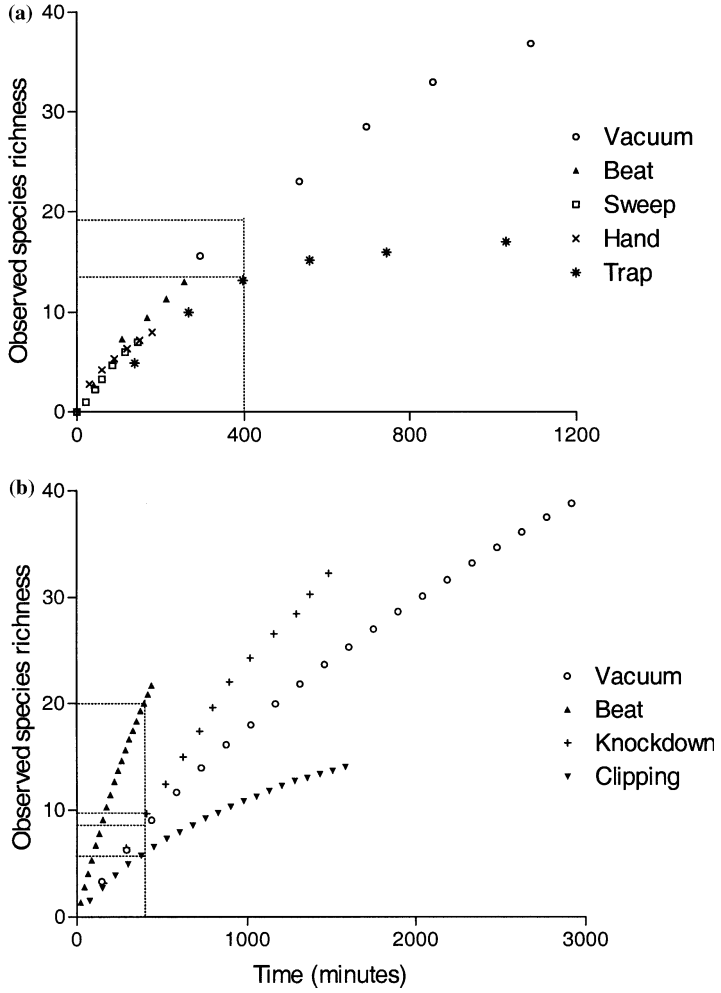

Figure 2. Smoothed species accumulation curves for increasing sampling time (with standardisation line at 400 minutes) at sites (a) and individual plant species (b). Abbreviations are given in Figure 1.

technique were collected on plant species during the sampling period.

Time efficiency

The efficiency of the various techniques differed (number of species captured per minute of field-work and laboratory time). At sites, beating was the most efficient technique for short periods of sampling, as more species were collected over the least time (Figure 2a). Given a longer period, such as standardising for 400 minutes, vacuum sampling had the steepest curve and yielded the most species (19). Sticky trapping began to reach an asymptote suggesting that few additional hemipteran species were captured after 600 min. For individual plants, beating was the most time-efficient technique when time was standardised at 400 min; it collected 20 species, whereas other techniques caught < 10 species (Figure 2b). Chemical knockdown was second most efficient, with vacuum sampling third and branch clipping the least (Figure 2b).

Combinations of techniques and complementarity

When combinations of techniques were considered, the steeper species accumulation curves for combinations of techniques compared to individual techniques indicated that there was little similarity in hemipteran species composition. In other words, there was high complementarity between techniques (see Longino and Colwell 1997). For

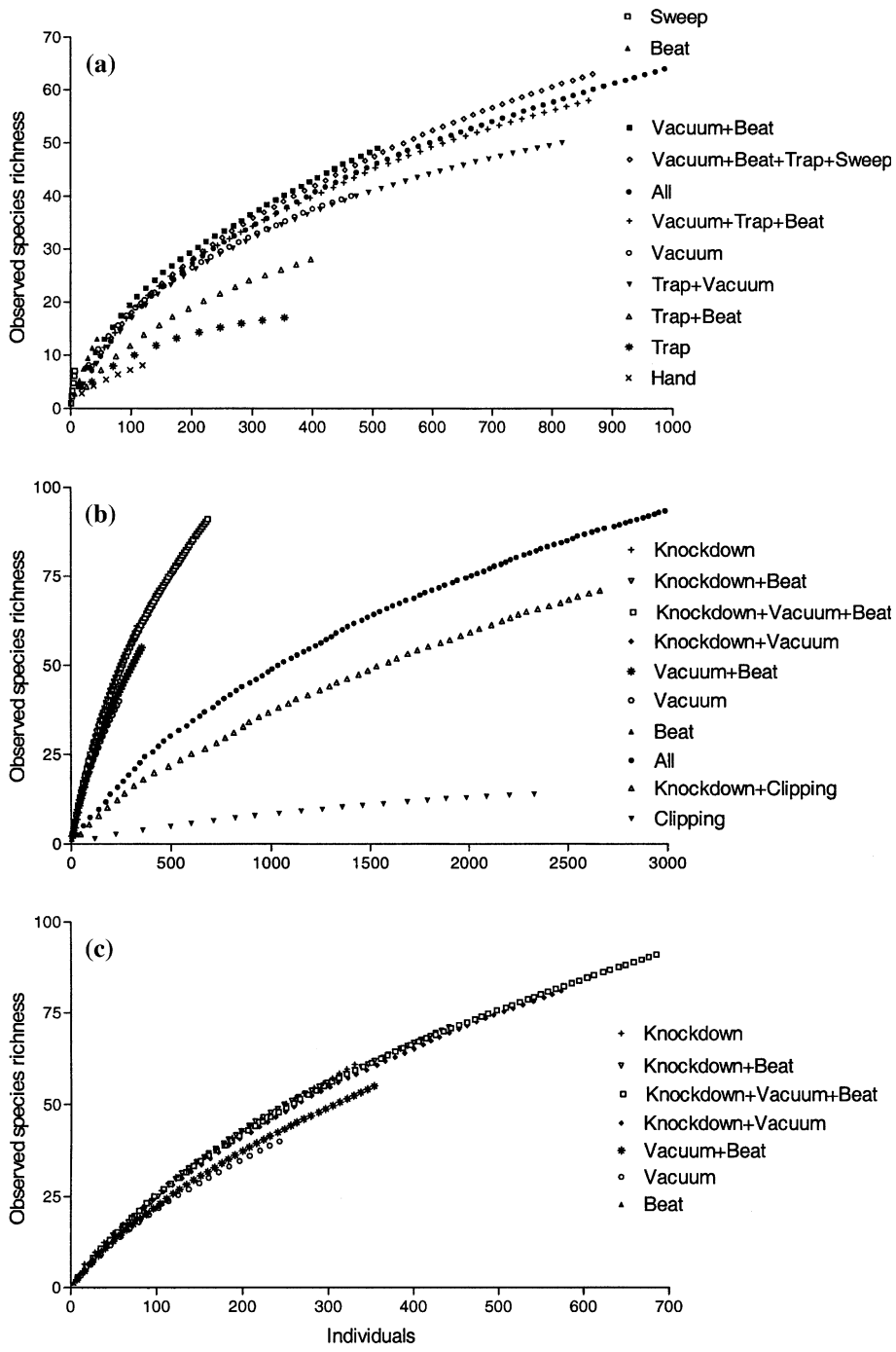

Figure 3. Species accumulation curves for combinations of techniques plotted against individuals at sites (a), for plant species (b) and for plant species excluding branch clipping (c). Abbreviations are given in Figure 1 and are in order of highest to lowest curve.

sites, the pairwise combination with the steepest species accumulation curves was beating plus vacuum sampling (Figure 3a). The best combination of three techniques was beating, vacuum sampling plus sticky trapping for sites. For individual plants, chemical knockdown plus beating gave the best pairwise combination of techniques (Figures 3b and c). The curve for a combination of

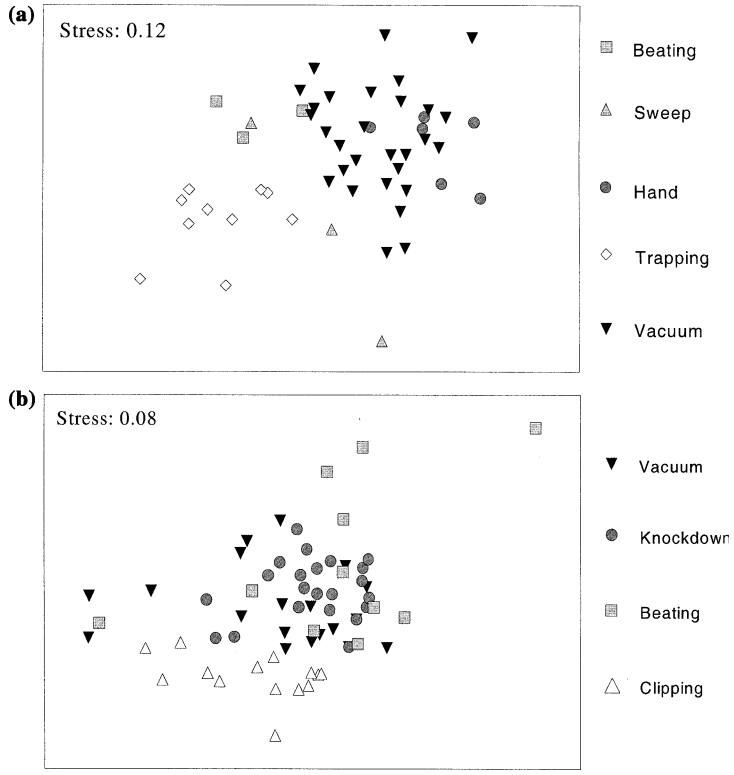

Figure 4. Ordination of Hemiptera species sampled by different techniques at sites on plant species (a) and (b). Each point represents the hemipteran composition of a particular plant or site sampled by a particular technique. Outliers (4 site samples from a total of 55 samples and 12 plant samples from a total of 78 samples) were excluded. Abbreviations are given in Figure 1.

vacuum sampling plus chemical knockdown was lower than chemical knockdown in combination with beating (Figure 3c). Therefore, vacuum and chemical knockdown samples were more similar in composition than those from beating. The best combination of three techniques for individual plants was chemical knockdown, vacuum sampling plus beating (Figure 3c). Curves were shallower when utilising three methods in combination than the two best combinations (Figure 3). Therefore, efficiency was greater by utilising two techniques, rather than three combined.

Hemipteran composition

Different techniques collected different suites of species. At sites, sticky traps differed significantly in species composition from the remaining techniques ($R = 0.518$ to 0.906, $p < 0.01$); sticky trap samples clustered together and were distinct from other techniques (Figure 4a). Sticky traps had greater proportions of mobile Sternorrhyncha, predominantly Psyllidae (Figure 5a). The high complementarity noted above for beating and vacuum samples was supported with ANOSIMs, as they were significantly different ($R = 0.55$, $p < 0.001$) in species composition (Figure 4a). This indicates that they were sampling different suites of species. Beating yielded no Auchenorrhyncha and high proportions of Heteroptera in samples when compared to vacuum sampling, which in turn had moderate proportions of Auchenorrhyncha and Heteroptera (Figures 5b and c, respectively).

On individual plants, the various techniques also differed in the species they collected ($R = 0.121$, $p < 0.05$) (Figure 4b). When compared to other techniques, branch clipping samples were biased towards sessile Sternorrhyncha (100% of all samples), especially Aleyrodidae and Diaspididae (Appendix 1). In contrast, vacuum sampling and chemical knockdown clustered loosely together, indicating high similarity in species composition (Figure 4b), despite the fact that they

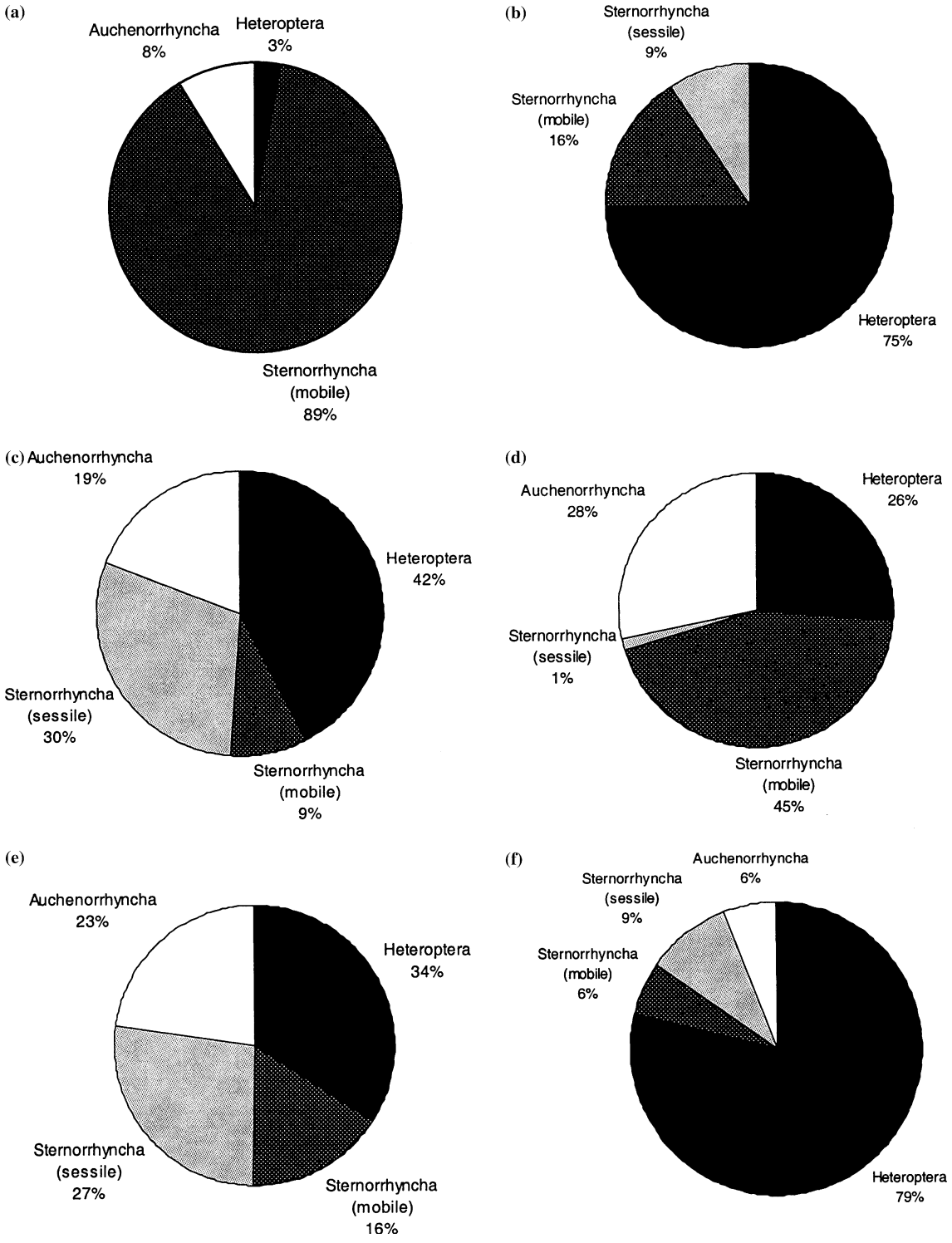

Figure 5. Percentage abundance of Heteroptera, Auchenorrhyncha, Sternorrhyncha (mobile) and Sternorrhyncha (sessile) for sticky trapping (a), beating (b) and vacuuming (c) at sites, and chemical knockdown (d), vacuuming (e) and beating (f) on plant species.

were significantly different ($R = 0.092$, $p < 0.01$). Knockdown and vacuum samples consisted of relatively even proportions of hemipteran suborders (Figures 5d and e, respectively), although there were few sessile Sternorrhyncha in knockdown samples. On the ordination, beating samples were more highly dispersed in ordination space when compared to other techniques (Figure 4b). This suggests greater heterogeneity in species composition for beating samples. Beating samples mainly consisted of Heteroptera (Figure 5f).

Discussion

This study demonstrates that collecting techniques differ in their efficiency at inventorying biodiversity when measured in terms of time and the number of individual hemipterans sampled. These results support earlier comparisons of: hand collecting vs. branch clipping vs. sweeping (Wilson and Room 1982); vacuum sampling vs. sweeping (Buffington and Redak 1998); and pitfall traps vs. sweeping/vacuum sampling (Standen 2000). Moreover, like others we have shown that because all techniques are biased towards particular suites of species, no single technique can adequately inventory biodiversity (New 1998; Buffington and Redak 1998; Standen 2000). The key question is, which combinations of the available techniques maximise complementarity and therefore are most efficient? This optimal combination should comprise the protocol for inventorying Hemiptera. We approach this question by discussing in turn the performance and merits of each technique. Our optimal protocol is then detailed and future areas for research outlined.

Beating had high complementarity with vacuum sampling and chemical knockdown. When used in combination with either method, beating gave efficient sampling of hemipteran species per individuals for both sites and on individual plant species. In addition, beating was efficient when measured by time and yielded speciose samples at both spatial scales. However, beating appeared biased against highly mobile organisms (see New 1984) and small or well camouflaged species. This explains why beating had high complementarity with techniques that were good at sampling mobile fauna (i.e., vacuuming and chemical knockdown). Beating did sample small sessile fauna provided that there was close inspection of debris on the beating tray. However, future studies should examine the influence of body size when elucidating biases between techniques. A further advantage of beating was its ability to collect Hemiptera in dense foliage that are hard to obtain using other methods, for example, species found deep within *Xanthorrhoea* foliage (Fletcher and Moir 2002).

Vacuum sampling collected diverse and abundant samples of Hemiptera at sites and on plant species, and was relatively time efficient in comparison to all methods except beating. Vacuum samples on individual plants had low complementarity with those from chemical knockdown, but high complementarity with beating samples. Previously, vacuuming has been shown to be more successful in collecting Hemiptera than pitfall traps in grasslands (Standen 2000), and sweeping in scrubland (Buffington and Redak 1998). Vacuuming has also been found to be efficient and less laborious in agricultural lands. In these situations, it is less biased towards nymphs and brachypterous adults when compared to sweeping and visual searches (Perfect et al. 1983).

Chemical knockdown provided an abundant and speciose catch from individual plants, but undersampled sessile Hemiptera. Majer and Recher (1988) supplemented chemical knockdown with branch clipping. They found this combination estimates abundance and diversity of all Hemiptera adequately, especially when compared to other techniques such as beating (see Fauvel 1999). However, we found the combination of chemical knockdown plus branch clipping was not as successful at accruing species as other combinations, such as beating plus knockdown. Furthermore, when compared to other techniques, chemical knockdown was less efficient in the rate of species captured when measured in terms of time. Chemical knockdown is curtailed by three logistical factors, the first being possible loss of specimens to wind drift (Basset 1990; Majer et al. 1996). In the present study, this problem was avoided by careful selection of sampling days. Secondly, there is the problem of the availability of clean ground sheets for subsequent samples. In the present study, Hemiptera were removed by the first author from sheets at night to provide sheets for the following day's sampling. For other studies, the number of hours required for specimen removal will be dependent upon the number of field workers available. Thirdly,

some countries prohibit the use of chemical knockdown in national parks (N. Gunawardene pers. comm.). The greatest problems with chemical knockdown, however, are its high financial cost and potential spray drift on to neighbouring plants.

Branch clipping was not adequate for sampling taxa other than sessile organisms. Samples yielded a less diverse fauna than other techniques (and see Majer and Recher 1988). Although branch clipping contributed some unique species, when used in combinations of techniques complementarity between samples was low, and efficiency in the rate of species capture decreased. Furthermore, branch clipping was time consuming in the laboratory, as it required spraying or freezing, and inspection of branches under a dissecting microscope to remove arthropods. These constraints have also been noted by others (Wilson and Room 1982; Peeters et al. 2001).

Sweeping must be complemented with other methods to ensure abundant samples of Hemiptera (and see Wilson and Room 1982). Sweeping did not sample sessile fauna (as noted by previous workers – Abbott and Van Heurck 1985; Fowler 1993), Heteroptera or brachypterous fauna. Sweeping has been found to be successful when supplemented by a second technique (Schwab et al. 2002). However, we found sweeping had low complementarity with other techniques. Unlike grasslands, in which sweeping has been very successful (Southwood and Henderson 2000), the South-west Botanical Province of Australia is dominated by understorey plants with structural defences to deter grazing by large native herbivores (Bell 1994). These structures are usually spines or serrated leaves, which present an additional problem, as sweep nets often become tangled or torn on understorey vegetation. As some ecosystems on other continents have similar vegetation, incorporating sweeping into a standardised sampling protocol would hinder attempts to inventory global hemipteran biodiversity.

Hand collecting had the disadvantages of low species richness and bias towards highly visible and easy-to-collect organisms. It collected a narrow suite of species, consisting mainly of sessile fauna. No species were unique to hand collecting, causing samples to have low complementarity with other techniques and not contributing towards species diversity in combinations. Furthermore, Bishop and McKenzie (1982) found visual searches significantly underestimated species in high abundance (although see Elder and Mayer 1990).

Sticky traps tend only to sample hemipteran species attracted to the colour of the trap (Meyerdirk and Oldfield 1985; De Barro 1991). In this study, the yellow traps attracted mainly aphids and six species of Psyllidae, and underestimated the sessile organisms present. Sticky traps had low complementarity with other techniques and, when used in combination, lead to poor overall performance. Moreover, specimens were easily damaged, as the sticky material inhibited removal of specimens (and see Fauvel 1999). Sticky trapping is also unsuitable for inventorying Hemiptera of specific understorey plants, as the origin of specimens remains unknown.

The methods utilised here are relatively comprehensive in terms of inventorying understorey hemipteran species when applied in combination. Additional sampling at the same site over 18 months for other studies has collected over 26,000 Hemiptera (M. Moir unpublished data). However, there were still species that were not captured. These were generally species from other strata, and included ground-dwelling taxa such as Gelastocoridae and Cydnidae, or those living in cryptic habitats, such as nocturnal feeders that live in ant nests (i.e., Eurymelidae: Pogonoscopini) (Day and Pullen 1999). Hand collecting may be required to sample such cryptic fauna. Other species inhabiting the understorey but not captured in the present study were large, highly alert and active species such as *Pauropsalta encaustica* (Cicadidae), *Mictis profana* (Coreidae) and *Poecilometis apicalis apicalis* (Pentatomidae). The problems of capturing such species are well documented (Wilson and Room 1982; New 1984). For these species, intercept traps may be required.

Conclusion: the optimal protocol

The most effective combination of collecting methods for abundant, speciose samples were beating and vacuum sampling. These form the optimal protocol for inventorying understorey Hemiptera assemblages. Samples from beating and vacuum sampling were significantly different in composition to each other, and thus, when used in combination had high complementarity. Additionally, they were relatively time-efficient, as the

cost in adding new species was low. Chemical knockdown also yielded abundant and speciose samples, but knockdown and vacuuming had low complementarity. Thus, combining knockdown and vacuuming would be superfluous. Vacuuming is preferred over chemical knockdown, as the latter has the disadvantages of spray drift and high financial cost.

Our optimal protocol for inventorying understorey Hemiptera from a 1 ha site consists of vacuuming all vegetation within six quadrats (each 1×5 m) and beating 10 individual plants (one plant for each of the 10 most dominant understorey species). More replicates for each sampling technique are proposed in the protocol than were evaluated here, in order to increase abundances and collect more species. For individual plants, the optimal protocol involves sampling from 10 individuals of each plant species (five plants by vacuuming and five plants by beating), as described in the methods.

Although we have described an optimal protocol, further refinements may be necessary. For example, it is important that the efficiency of available techniques, and their complementarity when used in combination, be tested in other ecosystems. In hotter, semi-arid and arid environments, the fauna may be extremely active and therefore difficult to catch whilst beating. Other important questions for future studies aimed at refining the protocol for 1 ha sites are: (1) How many vacuum quadrats should the protocol comprise? This requires knowing, how many extra individuals are needed for species accumulation curves to begin to flatten towards an asymptote; (2) What is the most efficient size and spatial arrangement of quadrats?; (3) Are beating and vacuum sampling the most effective sampling techniques in all seasons?; and (4) Is beating the 10 most dominant plants more efficient than beating vegetation in a quadrat? For individual plants, future workers should also consider levels of replication and seasonality. Additionally, how does the spatial proximity of individual plants for a given species influence the rate at which new species are added? In other words, for a given plant species is it more effective to sample 10 plants from a single stand or is it better to sample 10 widely spaced individuals?

The refinement of a standardised sampling protocol for inventorying invertebrates should be a high priority for conservation biologists. As noted in our introduction, the limited resources available for inventorying global biodiversity demand the development of efficient sampling protocols. Here we have evaluated seven collecting techniques over two spatial scales for sampling Hemiptera from the understorey and proposed an optimal sampling protocol. Most importantly, we calculated complementarity between samples of different combinations of techniques. As Hemiptera are the fifth most speciose insect order, the refinement of our protocol and the standardisation of sampling protocols for Hemiptera in all vegetation strata is critical for inventorying and estimating global biodiversity.

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Table 4. Species list of Hemiptera sampled by this study

Suborder Family	Species	Technique	Undestorey structure/Plant species	Abundance
Sessile Sternorrhyncha			Forest, mine pit, burnt mine pit, *A. barbiger, B. aquifolium, B. ornata, D. lindleyana, G. wilsonii, L. nutans, L. verticillatus, M. dilatata*	828
Aleyrodidae	*Aleurotrachelus stypheliae* (Maskell)	VS, CK, BE, HC, BC		
	Puparium sp. 2	VS, BC	Forest, *M. dilatata*	48
	Puparium sp. 5	VS, BC	Burnt mine pit, *H. lissocarpha*	5
	Puparium sp. 20	BC	*B. grandis*	668
Coccidae	Coccidae sp. 1	VS	*X. gracilis*	2
	Coccidae sp. 6	VS, BC	*H. lissocarpha, P. longifolia, L. sonderi*	28

Appendix 1.

Suborder Family	Species	Technique	Undestorey structure/Plant species	Abundance
Diaspididae	Diaspididae sp. 3	VS, HC, BC	Forest, mine pit, burnt mine pit, *A. extensa, A. pulchella, H. lissocarpha, L. nutans*	52
	Diaspididae sp. 7	CK, BC	*B. grandis, H. communtata*	364
	Diaspididae sp. 8	VS, BC	Forest, *B. fastigata*	534
	Diaspididae sp. 9	VS, HC, BC	Mine pit, burnt mine pit, *A. pulchella*	12
	Diaspididae sp. 13	BC	*A. pulchella, A. lateriticola, A. urophylla*	42
Mobile				
Sternorrhyncha				
Aphididae	Aphididae sp. 60	TP	Mine pit	2
	Aphis craccivora (Koch)	TP, BC	Mine pit, *M. dilatata*	2
	Aphis sp. 3	CK, BE, TP	Forest, mine pit, *B. grandis, L. nutans, M. dilatata, X. gracilis*	20
	Ceriferella dossuaria Carver and Martyn	CK, TP, BC	Forest, *G. wilsonii, L. capitellatus, L. floribundum, L. nutants*	8
	Rhopalosiphum padi (L.)	CK, TP	*B. grandis, B. ornata, M. dilatata*	12
Margarodidae	Margarodidae sp.7	CK	*L. sonderi*	1
	Margarodidae sp.11	BE	Forest	1
	Margarodidae sp.12	BE	Mine pit	1
	Margarodidae sp.13	BE	Burnt mine pit	1
Pseudococcidae	*Dysmicoccus macrozamiae* (Fuller)	VS, CK, BE, BC	Forest, mine pit, burnt mine pit, *L. sonderi, M. reidlei*	15
	Pseudococcidae sp. 2	VS	*T. ledifolium, M. dilatata*	2
	Pseudococcidae sp. 4	CK	*M. reidlei*	1
	Pseudococcidae sp. 5	CK	*M. reidlei*	1
	Pseudococcidae sp.9	CK	*L. floribundum*	9
	Pseudococcidae sp.14	VS	Forest	23
Psyllidae	*Acizzia uncatoides* Ferris and Klyver	CK, VS, HC	Mine pit, *A. extensa, A. pulchella, H. lissocarpha, M. dilatata*	21
	Acizzia sp. 2	VS, CK, BE	Forest, *A. extensa, A. pulchella, A. lateriticola, H. lissocarpha*	79
	Acizzia sp. 5	VS	Mine pit, *M. dilatata*	10
	Acizzia sp. 13	VS, CK	Mine pit, *A. pulchella*	14
	Acizzia sp. 14	VS, CK, TP	Mine pit, *A. pulchella*	248
	Acizzia sp. 15	VS, CK	Mine pit, *A. pulchella*	23
	Acizzia sp. 16	VS, CK	Mine pit, *A. pulchella*	3
	Acizzia sp. 17	CK	*A. pulchella*	1
	Acizzia sp. 18	VS	Mine pit, burnt mine pit	17
	Acizzia sp. 19	VS	Burnt mine pit	1
	Agelaeopsylla sp. 12	VS, TP	Forest, mine pit, *B. aquifolium*	3
	Agelaeopsylla sp. 21	TP	Mine pit	1
	Cryptoneossa sp. 6	VS	*M. dilatata*	1
	Cryptoneossa sp. 8	CK	*M. dilatata*	1
	Glycasp.is sp. 20	TP	Mine pit	1
	Psyllidae sp. 4	VS, BC	*A. pulchella, L. nutans*	24
	Phellopsylla sp. 3	VS, CK, BE	Forest, *G. wilsonii, H. lissocarpha*	6
	Phellopsylla sp. 4	BE, TP	Forest, *P. longifolia*	3
	Phyllolyma sp. 1	CK, BE, TP	Forest, mine pit, burnt mine pit, *A. barbiger, B. ornata, L. nutans, M. reidlei*	67
	Phyllolyma sp. 7	VS, CK	*A. barbiger, H. lissocarpha, P. longifolia*	5
	Phyllolyma sp. 10	CK	*L. cinerea*	1

Appendix 1. Continued.

Suborder Family	Species	Technique	Undestorey structure/Plant species	Abundance
Auchenorryncha				
Cicadellidae	*Aneono* sp. 2	BE	*B. grandis*	1
	Austroasca sp. 10	CK	*A. urophylla*	1
	Austrolopa sp. 1	CK	*M. dilatata*	3
	Balclutha incisa (Matsumura)	CK	*A. pulchella*	1
	Batracomorphus sp. 1	VS	*M. dilatata*	2
	Dikraneura sp. 4	VS, CK, SW	Forest, *A. barbiger, X. preissii*	21
	Dikraneura sp. 13	VS	Forest	2
	Dziwneono sp. 11	SW	Mine pit	1
	Idiocerinae sp. 3	VS	Burnt mine pit	1
	Kahaono sp. 7	VS, CK	Mine pit, *M. dilatata*	2
	Linacephalus sp. 3	VS	Forest	1
	*Nesoclutha pallida (*Evans)	VS	Mine pit	1
	Orosius canberrensis (Evans)	CK	*B. aquifolium, L. verticillatus*	2
	Orosius argentatus (Evans)	VS, CK, BE, SW, TP	Forest, mine pit, burnt mine pit, *A. pulchella, A. urophylla, A. barbiger, B. fastigata, D. lindleyana, H. lissocarpha, H. communtata, L. floribundum, L. nutans, L. verticillatus, L. cinerea, P. longifolia, P. esculentum, X. preissii, X. gracilis*	69
	Platyledra monstrosa (Evans)	TP	Mine pit	1
	Tartessinae sp. 1	CK	*A. pulchella*	1
	Thamnophyne sp. 1	CK	*B. aquifolium, M. reidlei, M. dilatata*	3
	Ulopinae sp. 1	BE	*M. dilatata*	1
	Zygina zealandica (Myers)	VS, CK, TP	Mine pit, burnt mine pit, *A. pulchella, B. aquifolium, B. ornate, M. dilatata, T. ledifolium, X. gracilis*	39
	Zygina sp. 1	VS, CK, BE	Mine pit, burnt mine pit, *A. drummondii, A. extensa, A. pulchella, A. lateriticola, A. barbiger, B. aquifolium, D. lindleyana, H. lissocarpha, H. communtata, M. dilatata, T. ledifolium*	52
	Zygina sp. 3	VS, CK	Burnt mine pit, *T. ledifolium, X. preissii*	47
	Zygina sp. 5	VS, CK	*A. barbiger, M. dilatata*	3
	Zygina sp. 6	VS	*M. dilatata*	1
	Zygina sp. 8	CK	*A. pulchella, M. dilatata*	3
	Zygina sp. 12	VS	Forest	9
Cixiidae	Cixiidae sp. 6	CK	*H. lissocarpha*	1
	Gelastocephalus sp. 1	CK, SW	Mine pit, *P. longifolia*	2
Dictyophoridae	Dictyophoridae sp. 1	BE	*M. reidlei*	1
Eurymelidae	Ipoini sp. 1	SW	Burnt mine pit	1
Flatidae	Flatidae sp. 4	CK	*A. barbiger, L. verticillatus, P. longifolia*	4
Issidae	Issidae sp. 1	CK	*M. reidlei*	1
	Issidae sp. 2	VS	*B. ornata*	1
Nogodinidae	Bladini sp. 1	CK	*H. lissocarpha*	1
Ricaniidae	*Epithalamiun aziola* Kirkaldy	VS	Mine pit	1
Heteroptera				1
Alydidae	Alydidae sp. 1	CK	*B. fastigata*	
	Riptortus setripes (Fabricius)	CK	*G. wilsonii*	1
Anthocoridae	*Lasiochilus* sp. 5	VS	Forest, *X. preissii*	5

Appendix 1. Continued.

Suborder Family	Species	Technique	Undestorey structure/Plant species	Abundance
Berytidae	Berytidae sp. 1	BE	*L. nutans*	1
	Berytidae sp. 2	VS, CK, BE	Forest, mine pit, *C. avenacea, D. lindleyana, L. nutans, T. ledifolium*	10
	Berytidae sp. 3	VS	*D. lindleyana*	1
	Berytidae sp. 4	BE	Mine pit	1
Lygaeidae	*Crompus* sp. 8	CK	*M. dilatata*	1
	Nysius vinitor Bergroth	VS, CK, BE, SW, TP	Burnt mine pit, *A. pulchella, A. lateriticola, A. urophylla, B. aquifolium, B. fastigata, L. floribundum. L. verticillatus, M. dilatata, P. longifola*	19
Miridae	*Coridromius* sp. 2	VS, TP	Forest, *M. dilatata*	3
	Zanchius sp. 1	VS, CK, BE, SW, HC, TP	Forest, mine pit, *A. barbiger, L. floribundum. T. ledifolium, X. preissii*	80
Oxycarenidae	*Oxycarenus westraliensis* Malipatil	CK	*M. dilatata*	1
Pachygronthidae	*Stenophyella macreta* Horvath	BE	*L. floribundum*	1
Pentatomidae	*Arniscus humerals* (Dallas)	CK	*X. preissii*	1
	Conspicona privata Walker	CK, BE	*L. verticillatus*	2
	Diaphyta fulvescens (Dallas)	VS	Burnt mine pit	1
	Dictyotus caenosus (Westwood)	BE	*X. preissii*	1
	Dictyotus inconspicuous Dallas	CK	*B. aquifolium*	2
	Everardia picta Gross	BE	*H. lissocarpha*	1
	Poecilometis lineatus (Westwood)	BE	Burnt mine pit, *T. ledifolium*	3
Reduviidae	*Empicoris rubomaculatus* (Blackburn)	CK	*X. preissii*	2
	Gminatus sp. 3	VS, BE	Forest, *A. barbiger, H. lissocarpha, L. nutans*	4
	Oncocephalus sp. 1	VS	*X. preissii*	1
Rhyparochromidae	*Plinthisus* sp. 6	VS	*P. longifolia*	1
	Plinthisus sp. 10	CK	*L. nutans*	1
	Udeocoris sp. 9	VS, CK	*B. fastigata, L. floribundum*	2
Schizopteridae	*Pateena* sp. 1	VS, CK, TP	Forest, mine pit, *A. pulchella, A. urophylla, G. wilsonii, L. nutans*	9
Thaumastocoridae	*Baclozygum brachypterum* Slater	VS, CK	Forest, *X. preissii*	34
	Onymocoris stysi Cassis, Schuh and Brailovsky	BE	Forest, burnt mine pit	9
Tingidae	*Caloloma* sp. 2	VS, CK, BE, AT	Forest, mine pit, *C. avenacea, L. floribundum, T. ledifolium*	216
	Oncophysa vesiculata gracilis Hacker	BE	*L. cinerea*	1
	Radinacantha sp. 4	VS, CK	Mine pit, burnt mine pit, *M. dilatata*	3
	Tinginae sp. 1	VS, CK, BE	Forest, mine pit, burnt mine pit, *A. pulchella, A. lateritocola, B. aquifolium*	38
	Tingis sp. 5	VS	*D. lindleyana*	2

Abbreviations for plant species are given in Table 1.
Abbreviations for techniques are: HC– hand collecting, BC – branch clipping, BE – beating, CK – chemical knockdown, VS – vacuum sampling, SW – sweeping, TP – sticky trapping. Understorey structures are: forest – low and open, mine pit – high and dense, burnt mine pit –intermediate.

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