© Journal of The Royal Society of New Zealand,
Volume 32, Number 4, December 2002, pp 571–585

Invertebrate species richness and density in relation to size of the New Zealand shrub *Olearia bullata*

José G. B. Derraik[1]*, Gerard P. Closs[2], Katharine J. M. Dickinson[1†], Barbara I. P. Barratt[3], and Phil J. Sirvid[4]

Abstract This study assessed the effects of host plant volume on invertebrate density and taxon richness on a native New Zealand shrub, *Olearia bullata* (Asteraceae). Specimens were collected by beating during a single summer/autumn sampling event from 30 *O. bullata* plants. The influence of the surrounding environment was also examined by assessing canopy connectivity between *O. bullata* shrubs and their nearest neighbours (*O. bullata* and other shrub species). Linear regression analyses suggested a positive association between invertebrate taxon richness and shrub volume, a relationship that was also apparent at the Order level for Coleoptera, Diptera, and Psocoptera. No significant results were found between shrub volume and invertebrate density at any taxonomic level. Negative associations were obtained between the density of Araneae and Hemiptera against the distance between *O. bullata* shrubs.

Keywords shrubland; *Olearia bullata*; host plant; invertebrates; taxon richness; density

INTRODUCTION

The global importance of New Zealand's fauna has been widely acknowledged. Myers et al. (2000) placed it among the 25 biodiversity hotspots of the world. Holloway & Stork (1991) went further to emphasise the importance of this country's biodiversity, stating that the loss of New Zealand's fauna and flora would be devastating to global diversity. New Zealand's invertebrate fauna is unique and diverse, with a level of endemism of at least 90% at the species level (Patrick 1994; Klimaszewski 1997), one of the highest levels in the world for a discrete area (Dugdale 1988). Despite its international importance, little is known of New Zealand's invertebrates. It is consequently necessary to increase our knowledge of invertebrate ecology.

The effect of island size on faunal diversity was first analysed in depth by MacArthur & Wilson (1967) resulting in the prediction that the number of species on an island would be proportional to its size. An island can be considered as any particular habitat that to some degree is isolated from other similar habitats. Connor & McCoy (1979) and Strong (1979)

---

[1]Ecology, Conservation & Biodiversity Research Group, Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.
[2]Ecology, Conservation & Biodiversity Research Group, Zoology Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.
[3]AgResearch, Private Bag 50 034, Mosgiel, New Zealand.
[4]Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand.
*Present address: Ecology and Health Research Centre, Department of Public Health, Wellington School of Medicine & Health Sciences, University of Otago, P.O. Box 7343, Wellington, New Zealand.
†Author for correspondence.

R02004 Received 20 February 2002; accepted 2 September 2002; published 26 November 2002

provided reviews of the species-area relationships for arthropods in plant patches and the mechanisms involved. Strong et al. (1984) proposed that clumps or patches of plants could be seen as "islands" surrounded by other vegetation, and they found that larger patches harboured more species of insect herbivores. However, to examine the effect of patch scale is problematic, as it varies according to several biological factors concerning a particular invertebrate species, such as mobility, home range, and size of the individual. Therefore, it is difficult to assess when the gap between stands of a particular plant may be large enough to create isolated patches. Individual plants nonetheless can be viewed as discrete patches of habitat, and Strong et al. (1984) pointed out that Janzen (1968, 1973) was probably the first to apply MacArthur & Wilson's (1967) theory to insect-plant relationships treating host plants as islands. According to Janzen (1968) a shrub can be considered to be an island (a contiguous habitat that is to some degree isolated from other similar habitats), at least to the individual insects that feed on it.

Host plants also affect the invertebrate fauna through the size and structural complexity of their above-ground parts (referred to as "plant architecture" by Lawton & Schröder (1977) and Lawton (1983)), which has a pronounced effect on the diversity of phytophagous insect communities (Lawton 1983, 1986). Larger and more complex host plants have a higher species richness of herbivorous insects (Strong 1977; Gilbert & Smiley 1978; Lawton 1978; Southwood 1978a; Strong & Levin 1979; Strong et al. 1984; Denno & Roderick 1991).

The present study examines the relationship between invertebrates and their host plant in a modified native New Zealand shrubland. More precisely, it aims to test whether the diversity and density of invertebrates change with an increase in size of *Olearia bullata* H.D. Wilson & Garn.-Jones (Asteraceae) host plants.

METHODS

Invertebrate sampling was carried out in a modified native shrubland at 450 m altitude in the Brookdale Conservation Covenant, on the lower eastern slopes of the Rock and Pillar Range, South Island, New Zealand (45°30′S, 170°03′E). It is a region of extensively modified tussock grasslands, shrublands, and alpine vegetation.

Invertebrate specimens were collected from *O. bullata*, one of the dominant divaricating (*sensu* McQueen 2000) native shrubs in the plant community. The genus is known to harbour a rich invertebrate fauna (Dugdale 1975; Patrick 2000). Thirty *O. bullata* shrubs were selected using random numbers and co-ordinates over a 5-ha area, and sampled by beating (Southwood 1978b; Davies & Stork 1996; New 1998). This sampling method is efficient and useful. As with all techniques, however, it is biased to some extent, and not capable of reliably reflecting the diversity of some groups in the invertebrate community (e.g., flying insects). Sampling was temporally restricted providing a snapshot of communities and relationships in summer/early autumn (March/April 1999). This study is part of a broader project, and is probably the first of its kind in lowland shrubland communities in New Zealand.

Sampling was conducted when the vegetation was dry and on windless days. Each plant received 10 downward strokes with a 1.5-m-long metal probe, and falling material was collected on a polythene sheet, 1.0×1.3 m, placed underneath. Once the material was on the sampling mat, the latter was quickly folded to prevent flying insects from escaping. The material was then sealed in a plastic bag, labelled, and frozen. Invertebrates were initially sorted into morphospecies using a low-power binocular microscope. Examples of each morphospecies were sent to specialist taxonomists for confirmation of identification.

An estimate of shrub volume was used in this study as a surrogate for island size. It was calculated as shrub height multiplied by projected foliage cover (shrub area in cross-section). The surrounding environment is also likely to influence the association between each shrub and its invertebrate fauna. Three additional environmental variables were measured in the field to estimate the isolation of each shrub from the surrounding vegetation, an important factor in recolonisation and reproduction for invertebrates:

Distance to nearest shrub, i.e., shortest distance between the base of the sampled shrub and the base of the nearest shrub of any species;

Distance to nearest *O. bullata* shrub, i.e., shortest distance between the base of the sampled shrub and the base of the nearest *O. bullata* plant;

Canopy connectivity, i.e., the presence/absence of canopy connection between the sampled shrub and an adjacent shrub regardless of the species.

As we intended to assess how invertebrate richness and density varied in relation to shrub size, the following dependent invertebrate variables were calculated:

Log taxon richness, i.e., $\log_{10}$ of the number of different taxa collected from each shrub, identified to the lowest taxonomic level possible;

Log density, i.e., $\log_{10}$ of the density of the number of individuals found per sampled shrub volume. Density was calculated as: (no. of individuals)/(shrub height × S), where S is the sampled shrub area given by the projected foliage cover (PFC) of the sampled shrub or the area of the sampling sheet (S_S), whichever was smaller.

The data were log transformed and checked to ensure they were normally distributed. Correlation analyses were initially performed between the above variables and the $\log_{10}$ of volume, distance to nearest shrub, and distance to nearest *O. bullata* shrub to screen for potentially interesting relationships. Linear regressions were then run for the significant correlations. For canopy connectivity (a discrete variable), two-sample *t*-tests were used to compare community density and taxon richness between shrubs whose canopy touched adjacent individuals and those which were isolated.

To assess whether similar relationships occurred within invertebrate Orders, the same set of analyses was performed for density and taxon richness of each. This was, however, only possible for the Orders present in a sufficient number of shrubs to allow meaningful statistical analyses. Only relationships between shrub variables and those Orders with specimens present in more than three-quarters of the sampled shrubs (23 or more) were analysed statistically. For taxon richness, it was also determined that the Order should have an average of one or more taxon per shrub. All tests were conducted at a significance level of $P < 0.05$.

RESULTS

Community description and analyses

The maximum distance between any two shrubs sampled was c. 488 m, while the minimum was 0.6 m. A wide range of shrub sizes was sampled, from very small and slender shrubs just over 1 m tall, to large and dense shrubs almost 3 m in height. There was a linear increase in shrub volume for most of the size range, until the upper volume range when there was an exponential increase in size. One shrub was over 40 m^3, another was 17 m^3, and all others were equal to or less than 10 m^3 (Fig. 1).

The 30 *O. bullata* shrubs sampled yielded a total of 5507 invertebrates in 156 taxa, including 2 Phyla, 3 Classes, and 16 Orders (Appendix). The invertebrates sampled are listed in the Appendix to the lowest taxonomic level to which they were identified. The Phylum Arthropoda included (in the Class Arachnida) Acari, Araneae, and Pseudoscorpionida; and (in the Class Insecta) Blattodea, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera, Thysanoptera, and Trichoptera. The other Phylum collected was Mollusca, more specifically Class Gastropoda, Order Stylommatophora. Specialist taxonomists were not available at the time to identify specimens of Acari,

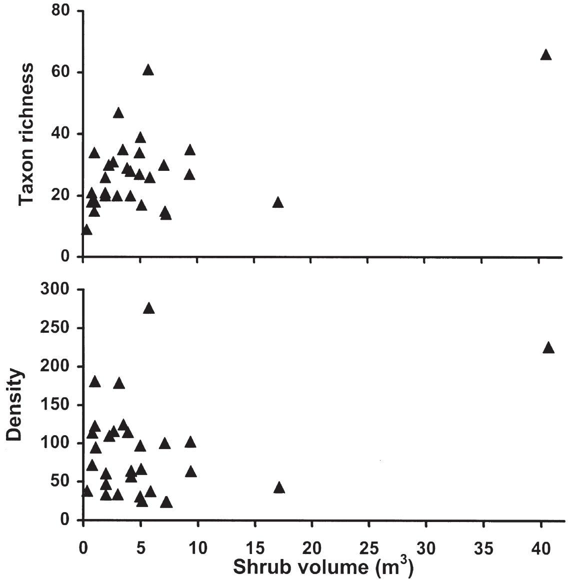

Fig. 1 Scatter plot of invertebrate taxon richness and density against volume (m^3) for each sampled *Olearia bullata*.

Collembola, Psocoptera, Thysanoptera, and most Hemiptera, therefore differentiation of those taxa are based on the initial sorting to morphospecies alone.

The mean number of taxa recorded per shrub was 27.7 species (SD = 12.1), while an average of 183.6 specimens (SD = 159.0) per shrub was collected. With the exception of two shrubs in the upper volume range from which particularly large numbers of specimens and taxa were collected, and one in the lower range that was relatively bare (Fig. 1), all values fell within one standard deviation of the mean volume.

For the overall invertebrate community, the linear correlation analysis between shrub volume and taxon richness was significant ($P = 0.006$) (Table 1). A linear regression analysis was performed, and, despite the small P value, the positive association between volume and taxon richness was weak ($r^2 = 0.24$) (Fig. 2A). The regression for taxon richness appears to have been strongly influenced by the two samples at either end of the scale. The influence of these extreme points was tested by removing them from the data analyses and performing regressions on the remaining 28 sample points, and, as expected, the association became non-significant ($P = 0.386$). There were no significant associations between taxon richness and the three environmental variables measured (Table 1).

No correlation analyses performed yielded significant results for invertebrate density. The P values were large (Table 1) indicating that density was not significantly associated with shrub volume and the measured environmental variables.

Community taxonomic composition

Acari was by far the most abundant taxon collected, comprising 2044 of the 5507 specimens collected (c. 37.1% of overall abundance) (Appendix). It was followed by Araneae with 1572 specimens (28.5%). Another 1788 invertebrates were included in the Orders Hemiptera with 526 specimens (9.6%), Coleoptera 258 (4.7%), Stylommatophora 249 (4.5%), Psocoptera 243 (4.4%), Hymenoptera 178 (3.2%), Thysanoptera 145 (2.6%), Diptera 109 (2.0%), and Pseudoscorpionida 80 (1.5%). The remaining 103 specimens (equivalent to 1.9% of the overall abundance) were from the Orders Blattodea, Collembola, Ephemeroptera, Lepidoptera, Neuroptera, and Trichoptera.

Of all Orders, only Araneae and Hemiptera were recorded from all 30 *O. bullata* shrubs sampled (Appendix). Acari, Coleoptera, and Hymenoptera were recorded on 27 shrubs, Diptera on 25, Psocoptera on 24, Stylommatophora on 23, and Thysanoptera on 21. Lepidoptera and Pseudoscorpionida had more restricted distributions, and were recorded on 16 and 10 shrubs, respectively. Remaining Orders were collected from relatively few shrubs: Collembola in 7 shrubs; Blattodea 4; Neuroptera and Trichoptera 2; and Ephemeroptera 1.

Within Orders certain taxa were numerically dominant, while others were quite uncommon (Appendix). For example, of the 1320 spiders identified to Family or to a lower taxonomic level, 682 were *Dolomedes* sp. (51.7%). Some Families within the Araneae were extremely rare, such as Mimetidae, Cycloctenidae, and Orsolobidae with only 6 specimens of each being recorded. Among the Hemiptera, 1 species (*Trioza* sp.) made up 205 of the 603 specimens found (34.0%). For Coleoptera, the distribution was more even at the species level, and the most abundant taxa, aleocharine species, represented only 16.7% of the total number of individuals (43 specimens) collected (Appendix). At the Family level, however, 3 Families of the 13 recorded, Coccinellidae, Corticariidae, and Staphylinidae, made up 76.4% of the total comprising 197 individuals. In contrast, Pseudoscorpionida, Blattodea, and Trichoptera consisted of one single species, while Neuroptera and Stylommatophora of two.

Individual analyses were not carried out for all invertebrate Orders. Due to the small number of specimens and low frequency of occurrence on the shrubs, the Orders Blattodea, Collembola, Ephemeroptera, Lepidoptera, Neuroptera, Pseudoscorpionida, Thysanoptera, and Trichoptera were not included. Analyses for density were performed for all the remaining

Table 1 Statistical analyses for the invertebrate community in Brookdale. Linear correlation analyses were performed for volume, distance to nearest shrub, and distance to the nearest *Olearia bullata*. The results from canopy connectivity are from a two-sample *t*-test. *P* values are shown and the significant results at the 95% level are in bold.

	Dependent variable	Volume	Distance to nearest shrub	Distance to nearest *O. bullata*	Canopy connectivity
Community	Taxon richness	**0.006**	0.666	0.189	0.520
	Density	0.930	0.692	0.076	0.440
Order					
Acari	Taxon richness	–	–	–	–
	Density	0.090	0.074	0.312	0.054
Araneae	Taxon richness	0.760	0.574	0.114	0.730
	Density	0.161	0.296	**0.045**	0.160
Coleoptera	Taxon richness	**0.001**	0.270	0.616	0.210
	Density	0.079	0.390	0.924	0.260
Diptera	Taxon richness	**0.035**	0.448	0.579	0.780
	Density	0.897	0.351	0.650	0.490
Hemiptera	Taxon richness	**0.009**	0.501	0.133	0.970
	Density	0.429	0.816	**0.025**	0.460
Hymenoptera	Taxon richness	0.506	0.785	0.533	0.940
	Density	0.118	0.610	0.364	0.590
Psocoptera	Taxon richness	**0.030**	0.524	0.555	0.390
	Density	0.493	0.611	0.611	0.830
Stylommatophora	Taxon richness	–	–	–	–
	Density	0.768	0.492	0.492	0.860

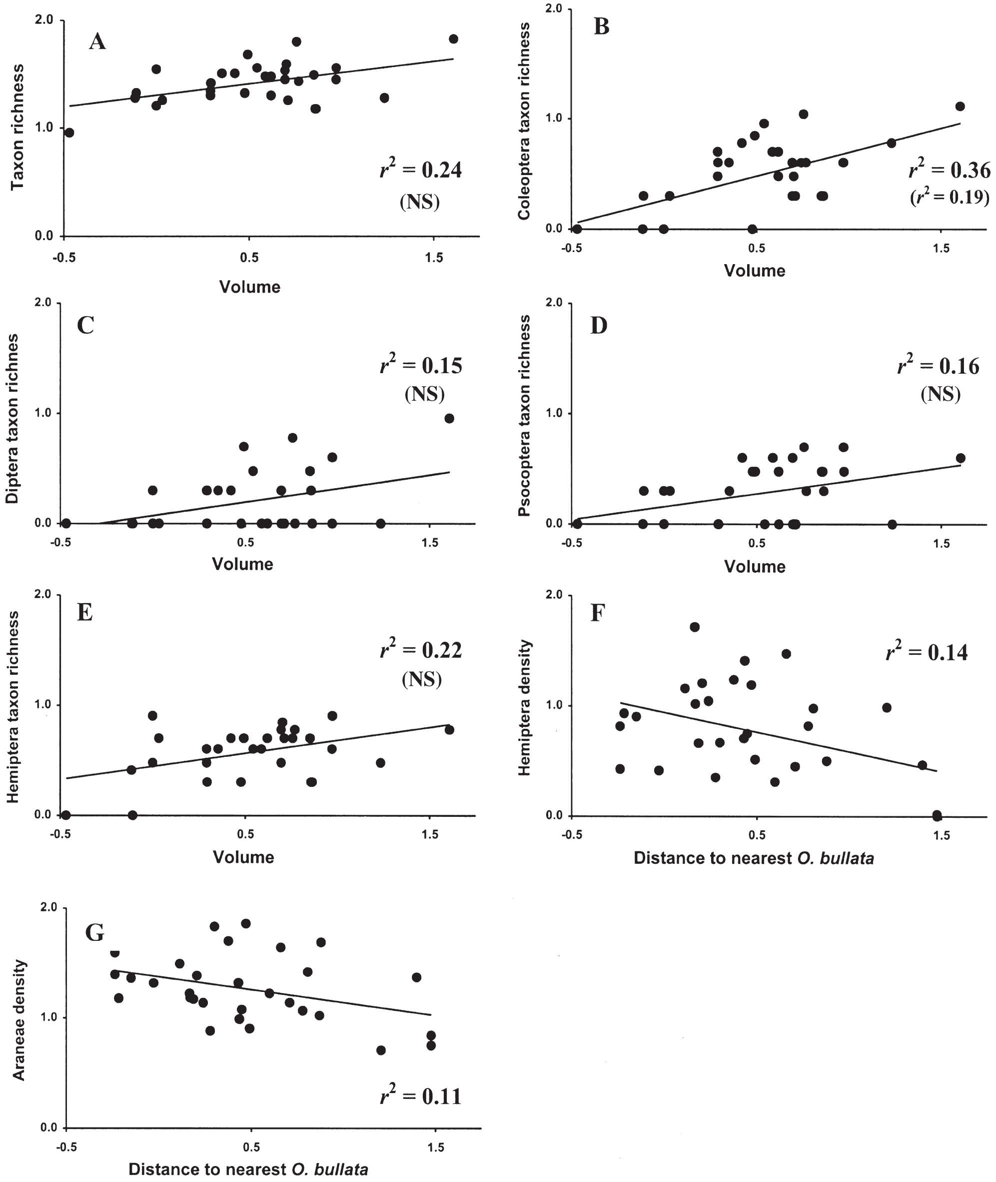

Fig. 2 Linear regression plots for the significant relationships in the invertebrate community on *Olearia bullata*. The r^2 values are shown, and those in brackets refer to analyses excluding the smallest and largest shrubs. All data are logged, the distance being measured in metres and volume in cubic metres.

Orders. For taxon richness, however, Acari and Stylommatophora were also excluded due to their small number of taxa (8 and 2, respectively).

There were no significant associations between the density of invertebrates in any Order and shrub volume (Table 1). For the variables referring to the surrounding environment, most results were non-significant (Table 1). The exceptions were the significant negative associations between the densities of Araneae and Hemiptera and the distance to the nearest *O. bullata* shrub (P = 0.045 and 0.025, respectively). There was, however, considerable scatter in the data (Fig. 2F,G) and the association seems rather weak (r^2 = 0.11 and 0.14, respectively). A possible explanation for the significant negative associations could be a co-linearity between shrub volume and distance to the nearest *O. bullata* shrub. A linear correlation analysis was therefore performed between those two independent variables and it was found to be not significant (P = 0.350).

There was a significant association between taxon richness and shrub volume in four Orders: Coleoptera, Diptera, Hemiptera, and Psocoptera (Table 1). The associations, however, were weak, especially for Diptera and Psocoptera, as shown by the low r^2 values (Fig. 2C,D). The two extreme data points seem to drive most of the relationships, and the regressions were performed again with those excluded. Only the association between Coleoptera taxon richness and shrub volume remained significant (Fig. 2B–E), with r^2 reduced from 0.36 to 0.19. As almost half of the hemipterans collected belonged to an undescribed *Trioza* species, additional analyses were performed excluding the latter, yielding no significant results. For the remaining Orders there were no positive associations between taxon richness and shrub volume (Table 1). There were also no significant results in any of the Orders for taxon richness in relation to the three variables associated with the surrounding habitat (Table 1).

DISCUSSION

Community level analyses

The randomly selected shrubs encompassed a wide variety of size classes. One shrub was exceptionally small, a seedling 90 cm tall with a PFC of 0.38 m^2. The largest shrub was 267 cm tall with a PFC of 15.22 m^2. The seedling produced 9 taxa and 11 specimens, while the largest shrub supported 53 taxa and 761 specimens (Fig. 1), thus supporting the main hypothesis of a positive association between shrub size and taxon diversity.

Host plant size *per se*, however, is probably not the single factor accounting for the higher richness of invertebrate taxa. What appears to be more important is the fact that a larger shrub will generally lead to an increase in the diversity of resources available, especially for herbivores (Lawton 1983, 1986). Strong et al. (1984) discussed several studies showing that the phytophagous fauna increases with increasing size, structural complexity, and diversity of the above-ground parts of the plant. Southwood et al. (1979) found a positive association between Coleoptera and Heteroptera diversity and the increasing complexity of plant architecture along the successional pathway (in the sequence herb → shrub → tree). For *O. bullata*, although canopy complexity was not measured in this study, it seems to increase with increasing shrub size (J. G. B. Derraik pers. obs.).

The diversity of microhabitats increases with shrub size (Lawton 1983, 1986), but the results here indicate that the density of invertebrates per unit area may not. Non-significant results were obtained at the community level and for all Orders subjected to density analysis. Despite the increase in the variability of resources per unit area, there was apparently no increase in the carrying capacity, which means that the maximum number of invertebrates that a certain volume of the shrub could hold remained relatively unaltered. Other factors apart from shrub size alone may be at play. It is possible, for instance, that competition may also increase, and, as has been observed in other studies (Lawton 1978), it might be limiting the number of invertebrates able to explore the available niches.

Analyses at the Order level

Most studies cited here have focused on phytophagous invertebrates. The results discussed so far are not necessarily comparable to those in the literature since the community was an amalgamation of various arthropod groups from at least three trophic levels.

The Araneae was the only closely examined Order made up solely of predators. There seems to be a positive association between species richness/abundance of orb-weavers and other web-builders, and plant canopy complexity (Stratton et al. 1979; Hatley & MacMahon 1980; Greenstone 1984). The same pattern has also been found among hunting spiders (free-living or vagrants) (Duffey 1962a,b; Uetz 1991). In our study there was no significant association between shrub size and spider taxon richness, which contradicts the previously cited literature.

The Coleoptera comprised the largest number of taxa (at least 29) recorded from *O. bullata*, and showed the strongest association between taxon richness and shrub volume (Table 1). Larger, older shrubs have more food resources (e.g., prey, algae, and lichens) and are able to support a more diverse fauna than smaller shrubs. Some coleopteran species that use pheromones to attract mates require prominent vantage points and some wood-boring beetles need wood of a certain diameter for larval development, so both communities are positively influenced by the size of the host plant.

At least 16 different dipteran species (all adults) distributed over 10 families were collected from *O. bullata*. Different dipteran families present distinct life histories and habitat requirements, some using the shrubs as a direct food source, others for reproduction and prey capture. Larger shrubs are, therefore, not only likely to provide more suitable sites, but also be more conspicuous and likely to attract more flies, which might explain the positive association between dipteran taxon richness and the volume of *O. bullata* shrubs.

The Order Hemiptera is an amalgamation of insects with rather dissimilar families (Sharell 1971), and while most hemipterans feed on plants and fruit, a few (i.e., members of the Families Berytidae and Reduviidae collected here) are predators. A positive (though weak) association between shrub size and taxon richness was observed, as larger shrubs may provide a greater range of plant parts that benefit species that otherwise are unable to settle on smaller plants.

Nearly all Hymenoptera recorded (95.5%) were wasps, parasitoids of various groups such as aphids, spiders, beetles, caterpillars, scale insects, and fly pupae (J. Early pers. comm. 2000). One could expect that an overall increase in insect diversity would lead to an increase in parasitoid-host diversity, and, therefore, Hymenoptera diversity. Nonetheless, there was no significant association between *O. bullata* volume and hymenopteran taxon richness, which could also be a result of the sampling method, inadequate for properly inventorying this Order.

The Psocoptera is probably the least known Order of small insects (New 1974), being grazers on microepiphytes (fungi, algae, and lichens) that grow on bark and leaves and in the litter (New 1974; Thornton 1985). Although some species show little food discrimination, many species show marked food and habitat preferences (New 1974; Thornton 1985). The availability of suitable microhabitat for Psocoptera would most likely increase in larger shrubs, and the observed positive association between the taxon richness of psocids and shrub size could be expected.

There were no significant results between taxon richness or density of any Order and habitat connectivity (Table 1). Many spider species are highly mobile and are able to move freely between shrubs, some species dispersing over large distances as juveniles by ballooning (Forster & Forster 1999), and hunting spiders are not tied to fixed structures such as snares, moving about freely, including from shrub to shrub. Many Coleoptera species are able to fly over long distances (Crowson 1981), therefore isolation at the scale measured within the shrubland is unlikely to be a barrier. Although a few families recorded here were comprised entirely of flightless beetles (e.g., Tenebrionidae), these are able to walk across large distances, as would the larger Carabidae (Crowson 1981). Hemipterans, apart from the predatory bugs, are typically confined to the host plant (Dolling 1991). During their lifetime, many species have both flightless and winged morphs (Sharell 1971; Speight et al. 1999), the latter capable of migrating to other host plants to establish new colonies (Sharell 1971). All species in the Orders Diptera, Hymenoptera, and Psocoptera collected were mostly comprised of active flying adults.

There were only two significant results for the density analyses, which showed negative associations (though weak) between the density of Hemiptera and Araneae and the distance to the nearest *O. bullata* shrub. The relationships indicate that the closer the shrubs were, the more spiders and hemipterans per unit volume were present. Some studies have shown that the density of host specific insects increases with increasing host plant density (Bach 1984a,b), and a similar pattern could be occurring here. However, since spiders are not host specific and the other analyses gave non-significant results, it is difficult to explain the significant associations.

CONCLUSIONS

Our results indicate that invertebrate taxon richness increases with increasing host plant size. We should point out, though, that these results are conservative, as the sampling efficiency of beating is likely to decrease with increasing shrub size. Consequently, the difference between the diversity of small and large shrubs is probably higher than that obtained in this study.

This positive association between invertebrate diversity and shrub size seems likely to be related to the ecology of the invertebrate species in question. No association between shrub size and the density of invertebrates was found, though some inconclusive results were obtained in relation to the distance between shrubs. Different sampling procedures and further sampling events may be required to effectively test the significance of the shrub size for the invertebrate community.

ACKNOWLEDGMENTS

We are grateful for the financial support from the Miss E. L. Hellaby Indigenous Grasslands Research Trust. Thanks to Bill and Alison Howell who permitted access to their covenanted land, Nicola Derraik and Fiona Harris for spending long hours helping in the field, Cathy Rufaut for advice on the design of this project, and two anonymous reviewers for comments on the manuscript. Special thanks must go to the taxonomists who kindly gave us their time towards the identification of specimens: Gary Barker, Pam Dale, John Early, Alan Eyles, Mark Harvey, Rosa Henderson, Peter Johns, Rod MacFarlane, and Brian Patrick.

REFERENCES

Bach, C. E. 1984a: Plant spatial pattern and herbivore population dynamics: plant factors affecting the movement patterns of a tropical cucurbit specialist (*Acalymma innubum*). *Ecology 65*: 175–190.

Bach, C. E. 1984b: Host plant growth form and diversity: effects on abundance and feeding preference of a specialist herbivore, *Acalymma vittata* (Coleoptera: Chrysomelidae). *Oecologia 50*: 370–375.

Connor, E. F.; McCoy, E. D. 1979: The statistics and biology of the species-area relationship. *American Naturalist 113*: 791–833.

Crowson, R. A. 1981: The biology of the Coleoptera. London, Academic Press.

Davies, J.; Stork, N. 1996: Data and specimen collection: invertebrates. *In*: Anon. *ed*. Biodiversity assessment—a guide to good practice. Field manual 2—data and specimen collection of animals. London, HMSO. Pp. 1–56.

Denno, R. F.; Roderick, G. K. 1991: Influence of patch size, vegetation texture, and host plant architecture on the diversity, abundance, and life history styles of sap-feeding herbivores. *In*: Bell, S. S.; McCoy, E. D.; Mushinsky, H. R. *ed*. Habitat structure: the physical arrangement of objects in space. London, Chapman & Hall. Pp. 169–196.

Dolling, W. R. 1991: The Hemiptera. London, Oxford University Press.

Duffey, E. 1962a: A population study of spiders in limestone grassland: description of study area, sampling methods and population characteristics. *Journal of Animal Ecology 31*: 571–599.

Duffey, E. 1962b: A population study of spiders in limestone grassland, the field-layer fauna. *Oikos 13*: 15–34.

Dugdale, J. S. 1975: The insects in relation to plants. *In*: Kuschel, G. *ed*. Biogeography and ecology in New Zealand. The Hague, Dr. W. Junk. Pp. 561–589.

Dugdale, J. S. 1988: Lepidoptera annotated catalogue, and keys to family-group taxa. *Fauna of New Zealand 14*.

Forster, R. R.; Forster, L. M. 1999: New Zealand spiders and their worldwide kin. Dunedin, University of Otago Press.

Gilbert, L. E.; Smiley, J. T. 1978: Determinants of local diversity in phytophagous insects: host specialists in tropical environments. *Symposium of the Royal Entomological Society of London 9*: 89–104.

Greenstone, M. H. 1984: Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. *Oecologia 62*: 299–304.

Hatley, C. L.; MacMahon, J. A. 1980: Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology 9*: 632–639.

Holloway, J. D.; Stork, N. E. 1991: The dimensions of biodiversity: the use of invertebrates as indicators of human impact. *In*: Hawksworth, D. L. *ed*. Biodiversity of microorganisms and invertebrates: its role in sustainable agriculture. Wallingford, CAB International. Pp. 37–61.

Janzen, D. H. 1968: Host plants as islands in evolutionary and contemporary time. *American Naturalist 102*: 592–595.

Janzen, D. H. 1973: Host plants as islands II: competition in evolutionary and contemporary time. *American Naturalist 107*: 786–790.

Klimaszewski, J. 1997: Biodiversity of New Zealand beetles (Insecta, Coleoptera). *Memoirs of the Museum of Victoria 56*: 659–666.

Lawton, J. H. 1978: Host plant influences on insect diversity: the effects of space and time. *In*: Mound, L. A.; Waloff, N. *ed*. Diversity of insect faunas. Oxford, Blackwell Scientific Publications. Pp. 105–125.

Lawton, J. H. 1983: Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology 28*: 23–39.

Lawton, J. H. 1986: Surface availability and insect community structure: the effects of architecture and fractal dimension of plants. *In*: Junniper, B.; Southwood, T. R. E. *ed*. Insects and the plant surface. London, Edward Arnold. Pp. 317–331.

Lawton, J. H.; Shröder, D. 1977: Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature 265*: 137–140.

MacArthur, R. H.; Wilson, E. O. 1967: The theory of island biogeography. Princeton, Princeton University Press.

McQueen, D. R. 2000: Divaricating shrubs in Patagonia and New Zealand. *New Zealand Journal of Ecology 24*: 69–80.

Myers, N.; Mittermeier, R. A.; Mittermeier, C. G.; da Fonseca, G. A. B.; Kent, J. 2000: Biodiversity hotspots for conservation priorities. *Nature 403*: 853–858.

New, T. R. 1974: Psocoptera. Handbooks for the identification of British insects. Vol. I, Part 7. London, Royal Entomological Society of London.

New, T. R. 1998: Invertebrate surveys for conservation. Oxford, Oxford University Press.

Patrick, B. 1994: The importance of invertebrate biodiversity: an Otago Conservancy review. *Conservation Advisory Science Notes 53*. Wellington, Department of Conservation.

Patrick, B. 2000: Lepidoptera of small-leaved divaricating *Olearia* in New Zealand and their conservation. *Conservation Advisory Science Notes 168*. Wellington, Department of Conservation.

Sharell, R. 1971: New Zealand insects and their story. Auckland, Collins.

Southwood, T. R. E. 1978a: The components of diversity. *Symposium of the Royal Entomological Society of London 9*: 19–40.
Southwood, T. R. E. 1978b: Ecological methods with particular reference to the study of insect populations. London, Chapman & Hall.
Southwood, T. R. E.; Brown, V. K.; Reader, P. M. 1979: The relationship of plant and insect diversities in succession. *Biological Journal of the Linnaean Society 12*: 327–348.
Speight, M. R.; Hunter, M. D.; Watt, A. D. 1999: Ecology of insects: concepts and applications. Oxford, Blackwell Scientific Publications.
Stratton, G. E.; Uetz, G. W.; Dillery, D. G. 1979: A comparison of the spiders of three coniferous tree species. *Journal of Arachnology 6*: 219–226.
Strong, D. R. 1977: Rolled-leaf hispine beetles (Chrysomelidae) and their Zingiberales host plants in middle America. *Biotropica 9*: 156–169.
Strong, D. R. 1979: Biogeographical dynamics of insect-host plant communities. *Annual Review of Entomology 24*: 89–119.
Strong, D. R.; Levin, D. A. 1979: Species richness of plant parasites and growth form of their hosts. *The American Naturalist 114*: 1–22.
Strong, D. R.; Lawton, J. H.; Southwood, T. R. E. 1984: Insects on plants: community patterns and mechanisms. Oxford, Blackwell Scientific Publications.
Thornton, I. W. B. 1985: The geographical and ecological distribution of arboreal Psocoptera. *Annual Review of Entomology 30*: 175–196.
Uetz, G. W. 1991: Habitat structure and spider foraging. *In*: Bell, S. S.; McCoy, E. D.; Mushinsky, H. R. *ed*. Habitat structure: the physical arrangements of objects in space. London, Chapman and Hall. Pp. 325–348.
Walter, D. E.; Behan-Pelletier, V. 1999: Mites in forest canopies: filling the size distribution shortfall? *Annual Review Entomology 44*: 1–19.

APPENDIX (*over page*)

APPENDIX

Invertebrate taxa collected from the 30 *Olearia bullata* shrubs at Brookdale to the lowest taxonomic level to which they have been identified. For some Orders, only morphospecies information was available at the time the analyses were carried out.

Class	Order	Family	Species	No. of shrubs where spp. were recorded	Total specimen count
Arachnida	Acari	–	morphosp. 1	11	29
			morphosp. 2	18	661
			morphosp. 3	7	25
			morphosp. 4	23	548
			morphosp. 5	6	49
			morphosp. 6	15	730
			morphosp. 7	1	1
			morphosp. 8	1	1
			Total	**27**	**2044**
	Araneae	Araneidae	*Coleranea verutum* (Urquhart, 1887)	2	2
			Eriophora pustulosa (Walckanaer, 1841)	9	20
			Zealaranea crassa (Walckanaer, 1841)	1	3
			–	24	86
		Clubionidae	?*Clubiona* sp.	12	23
			Clubiona convoluta Forster, 1979	1	3
		Cycloctenidae	*Toxopsiella* sp.	2	6
		Desidae	*Laestrygones otagoensis* Forster, 1970	4	13
		Linyphiidae	–	3	55
			Diplocephalus cristatus (Blackwall, 1833)	1	2
		Mimetidae	*Mimetus* sp.	3	6
		Orsolobidae	–	2	6
		Pisauridae	*Dolomedes* sp.	30	682
		Salticidae	n. sp. 1	1	4
			n. sp. 2	14	52
		Stiphidiidae	*Cambridgea agrestis* Forster & Wilton 1973	15	35
		Theridiidae	*Achaearanea* sp.	10	36
			cf. *Episinus* sp.	13	140
			Moneta sp.	10	64
			Phoroncidia spp.	8	10
				2	7
		Thomisidae	*Diaea* sp.	20	65
		–		30	252
			Total	**30**	**1572**
	Pseudoscorpionida	Chernetidae	*Apatochernes* sp. nov.	10	80
Gastropoda	Stylommatophora	Punctidae	*Laoma* sp. (undescribed sp.)	23	220
			Phrixgnathus celia Hutton, 1883	4	29
			Total	**23**	**249**
Insecta	Blattodea	Blattellidae	*Parellipsidion* sp.	4	11
	Coleoptera	Anthribidae	*Sharpius sandageri* (Broun, 1893)	1	2
			Xenanthribus hirsutus Broun, 1893	2	8

APPENDIX (*continued*)

Class	Order	Family	Species	No. of shrubs where spp. were recorded	Total specimen count
		Cerambycidae	*Psilocnaeia* cf. *asteliae* Kuschel, 1990	1	1
		Coccinellidae	*Scymus* cf. *prolongatus* Broun, 1914	2	9
			cf. *Scymus* sp.	14	30
			coccinelid spp.	10	12
			Rhizobius forstieri (Mulsant, 1853)	1	1
			–	4	5
		Corticariidae	*Aridius bifasciatus* (Reitter, 1877)	8	14
			Cortinicaria hirtalis (Broun, 1880)	8	14
			Cortinicaria spp.	12	29
		Corylophidae	*Holopsis* sp. nr. *lawsoni* Broun, 1886	1	1
			Holopsis sp.	2	5
		Cryptophagidae	*Paratomaria crowsoni* Leschen, 1996	3	3
		Curculionidae	cf. *Catoptes* sp.	1	1
			cf. *Peristoreus* sp.	2	2
			Praolepra infusca Broun, 1880	1	6
			–	3	3
		Dermestidae	–	1	1
		Scarabaeidae	*Odontria striata* White, 1884	1	1
		Scirtidae	scirtid sp.	2	2
		Staphylinidae	–	2	2
			aleocharine spp.	10	43
			tachyporine spp.	10	38
		?Tenebrionidae	–	4	7
		Tenebrionidae	*Artystona obscura* Sharp, 1886	1	1
		Trogossitidae	trogossitid sp.	6	8
		Zopheridae	zopherid sp.	2	3
		–		6	6
			Total	**27**	**258**
	Collembola	Tomoceridae	morphosp. 1	2	6
			morphosp. 2	5	44
			morphosp. 3	2	4
			Total	**7**	**54**
	Diptera	?Agromyzidae	–	1	1
		Ceratopogonidae	–	6	8
		Chironomidae	*Chironomus ?zealandicus* (Hudson 1892)	1	1
			Orthocladinea sp. 1	10	20
			Orthocladinea sp. 2	4	15
			–	1	1
		Chloropidae	*Aphanotrigonum nuttoni* (Malloch, 1931)	1	1
			Eutricimbra sp. (n. sp.)	1	1
			Melanum neozelandicum Malloch, 1931	1	1
		Dolichopodidae	*Parentia* sp.	2	2
		Ephydridae	*Hydrellia tritici* Coquillett, 1903	1	1
		Muscidae	–	2	2
		Sciaridae	–	5	7

(*continued over page*)

APPENDIX (*continued*)

Class	Order	Family	Species	No. of shrubs where spp. were recorded	Total speci-men count
		Stratiomyidae	*Odontomyia chloris* (Walker, 1854)	1	1
			Zelandoberis sp.	1	1
		Tipulidae	–	7	16
		–		12	30
			Total	**25**	**109**
	Ephemer-optera	Leptophlebiidae	*Austroclima* sp.	1	1
	Hemiptera	Aphididae	morphosp. 1	7	22
			morphosp. 2	8	27
			morphosp. 3	11	40
			morphosp. 4	1	8
			morphosp. 5	3	9
			morphosp. 6	1	1
			Brevicoryne brassicae (Linnaeus, 1758)	9	46
			Drepanosiphum platanoides (Schrank, 1801)	2	2
		Berytidae	*Bezu wakefieldi* (White, 1878)	3	11
		Eriococcidae	*Eriochiton pseudohispidus* (Hodgson & Henderson, 1996)	12	21
		Miridae	Chaetedus reuterianus (White, 1878)	1	1
			Chinamiris punctatus Eyles & Carvalho, 1991	2	3
			Diomocoris maoricus (Walker, 1873)	1	1
			Romna scotti (White, 1878)	9	26
			–	1	2
		Pseudococcidae	*Balanococcus danthoniae* (Morrison, 1925)	1	1
		Psyllidae	*Trioza* sp.	24	205
			Trioza gourlayi Tuthill, 1952	10	22
		Reduviidae	*Empicoris rubromaculatus* (Blackburn, 1889)	1	1
		–		20	77
			Total	**30**	**526**
	Hymenoptera	Bethylidae	–	2	2
		Braconidae	*Ascogaster* sp.	1	1
			–	10	14
		Diapriidae	*Spilomicrus* sp.	1	1
		Encyrtidae	*Microterys flavus* (Howard, 1881)	1	1
			Odiaglyptus biformis Noyes, 1988	1	1
		Eulophidae	species 1	9	13
			species 2	15	22
		Formicidae	*Amblyopone saundersi* Forel, 1892	1	1
			Monomorium antarcticum (Smith, 1858)	3	4
			–	3	3
		Ichneumonidae	–	3	4

APPENDIX (*continued*)

Class	Order	Family	Species	No. of shrubs where spp. were recorded	Total speci-men count
		Megaspilidae	–	5	10
		Platygastridae	*Errolium* sp.	2	2
		Proctotrupidae	*Oxyserphus* sp.	1	1
		Pteromalidae	*Ophelosia australis* Berry, 1995	3	4
			?*Trichomalopsis* sp.	7	48
		Scelionidae	*Baeus* sp.	2	2
			Idris sp.	6	20
			Trissolcus sp.	1	1
			?*Trimorus* sp.	10	15
		–		4	8
			Total	**27**	**178**
	Lepidoptera	Elachistidae	*Cosmiotes ombrodoca* (Meyrick, 1889b)	1	1
		Geometridae	–	1	1
			Declana junctilinea (Walker, 1865)	5	6
		Gracillariidae	*Caloptilia elaeas* (Meyrick, 1911b)	1	1
		Nepticalidae	*Stigmella ilsea* Donner & Wilkinson, 1989	3	3
		Noctuidae	*Tmetolophota* sp.	1	1
		Oecophoridae	–	2	2
			Tingena melanamma (Meyrick, 1905)	3	6
		Tineidae	–	1	1
		Tortricidae	undescribed genus and species	1	2
			Ctenopseutis obliquana (Walker, 1863)	1	1
			–	3	3
		–		2	5
			Total	**16**	**33**
	Neuroptera	Hemerobiidae	*Drepanacra binocula* (Newman, 1838)	1	1
			Micromus tasmaniae (Walker, 1860)	1	1
			Total	**2**	**2**
	Psocoptera	Eliopsocidae	*Interpsocus axillaris* Smithers, 1969	10	45
			Spilopsocus avium Smithers, 1964	14	122
		Myopsocidae	–	13	41
		Peripsocidae	*Ectopsocus briggsi* McLachlan, 1899	1	2
			Pteroaxanium kelloggi (Ribaga, 1905)	6	9
		Trogiidae	–	1	1
		Philotarsidae	morphosp. 1	1	4
			morphosp. 2	4	7
		–	morphosp. 1	1	1
			morphosp. 2	3	4
			morphosp. 3	1	1
			morphosp. 4	3	6
			Total	**24**	**243**
	Thysanoptera	Phlaeothripidae	–	21	145
	Trichoptera	Hydroptilidae	*Oxyethira albiceps* (McLachlan, 1862)	2	2