SHORT COMMUNICATION

Invertebrate diversity on *Olearia bullata* and *Coprosma propinqua* in a modified native shrubland, Otago, New Zealand

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Abstract: Despite the global importance of New Zealand's invertebrates, relatively little is known about them and their relationships with plants and plant communities in native habitats. Invertebrate diversity was examined by beating randomly chosen shrubs of the species *Olearia bullata* (Asteraceae) and *Coprosma propinqua* (Rubiaceae). Invertebrate taxon richness was assessed initially using morphospecies, which were identified subsequently by expert taxonomists. Though the taxon richness of invertebrates recorded from *O. bullata* was not significantly higher than that on *C. propinqua* (except for the orders Diptera and Hemiptera), there was a clear indication that *O. bullata* hosts a higher diversity of invertebrates. Mean number of taxa per shrub for *O. bullata* was higher in all cases (except Coleoptera), and so was the maximum number of taxa per shrub. Overall, *O. bullata* yielded 115 invertebrate taxa compared with 93 for *C. propinqua*. Moreover, 50 invertebrate taxa were restricted to *O. bullata* compared with 28 for *C. propinqua*. Since at least ten species of *Olearia* are threatened or uncommon, this could be cause for concern with respect to the maintenance of invertebrate diversity. Therefore, sites where *Olearia* species are still present are likely to be of significance for invertebrate conservation.

Keywords: biodiversity; Coprosma propinqua; invertebrates; Olearia bullata; shrubland; taxon richness.

Introduction

New Zealand's invertebrate fauna is unique and diverse, and at least 90% of its members are endemic at the species level (Watt, 1975; Patrick, 1994a; Klimaszewski, 1997), one of the highest percentages in the world for a discrete area (Dugdale, 1988). Despite the consequent international importance of New Zealand's invertebrates, when reserves are set aside, they are very seldom specifically for the protection of an invertebrate community. Selection of areas for protection is predominantly based on the presence of charismatic large vertebrates, or through ecological surveys based on native vegetation condition. In most rapid ecological surveys, such as New Zealand's Protected Natural Areas (PNA) Programme, the underlying assumption is that preserving the best habitat (botanically) will also preserve the fauna, an implicit assumption that has not been tested thoroughly (Crisp et al., 1998). Historically, protected areas in New Zealand have been established over rugged landscapes, areas of scenic beauty with few conflicting land uses. The protected areas system in this country is still not representative of the full range of ecosystems, with gaps associated particularly with non-forest habitats and low-mid altitude areas. With a shift in focus to the conservation of indigenous biodiversity (Department of Conservation & Ministry for the Environment, 2000), the intensification of land use at lower altitudes, combined with the current tenure review of pastoral leasehold land (20% of the South Island land area), it is urgent that these largely unprotected ecosystems are better understood.

Modified native habitats with a prominent exotic

plant component may still harbour a significant indigenous invertebrate fauna (Crisp *et al.*, 1998) as they do for birds (McLay, 1974). The relationship between degree of modification and indigenous faunal biodiversity in general is little understood (Derraik, 2001). In this study, we examined plant-invertebrate relationships for two native shrub species, *Coprosma propinqua* (Rubiaceae) and *Olearia bullata* (Asteraceae). They are structurally similar shrubs, both being small-leaved and divaricating. Wardle (1991) referred to both species as being "filiramulate", meaning a long leaf internode length in relation to the leaf size (Wardle and McGlone, 1988).

The two species sampled are ecologically important shrubs in New Zealand, since Coprosma and Olearia are two of the most speciose indigenous angiosperm genera with 47 and 38 species, respectively (Wilton and Breitwieser, 2000). All species are endemic, with the exception of two Coprosma species (Wilton and Breitwieser, 2000). Coprosma propingua is a common and widespread endemic woody shrub, whereas O. bullata has a much more restricted distribution. The genus Olearia has been recognised as being significant for its rich invertebrate fauna (Dugdale, 1975; Patrick, 2000), particularly of Lepidoptera (Patrick, 1994b; Patrick, 2000). Our study compared the invertebrate fauna of the two species to assess whether or not they differ as reservoirs of invertebrate diversity. The degree of size similarity of the shrubs was tested and the taxon richness of invertebrates compared.

Study Area

Invertebrates were collected from a modified native shrubland at 450 m altitude (45° 30' S, 170° 03' E) in the Brookdale Conservation Covenant (private land protected under the Reserves Act 1977) on the lower eastern slopes of the Rock and Pillar Range, South Island, New Zealand. Located 50 km inland, the mountain range rises to an altitude of 1450 m a.s.l. (Talbot *et al.*, 1992) and experiences annual rainfall of approximately 600 mm at the study site (Knight Frank N.Z. Ltd., 1995). The Range is one of several rolling, block-faulted schist ranges running NE-SW, inland from coastal Otago, that form the distinctive Central Otago tor landscape (McCraw, 1965).

The native vegetation of the South Island has been altered dramatically since human occupation approximately 800 years ago (McGlone and Wilmshurst, 1999). In the region of the Rock and Pillar Range, continued human disturbance has restricted lower-elevation shrubland to gullies that have been protected from fire (and often also from heavy grazing) by the topography. These shrublands probably do not represent the original pre-human vegetation (McGlone, 2001), but are still dominated by native woody species that have survived various disturbance processes and management regimes. The shrubland area where our study was undertaken is protected because its vegetation is representative of the Rock and Pillar Range and has botanical value (Knight Frank N.Z. Ltd., 1995). The covenant is protected in perpetuity in the land title, and while limited grazing is allowed, the use of fire as a management tool is not (Reserves Act 1977, S.77).

Methods

To assess invertebrate diversity in one season (late summer/early autumn), 30 *O. bullata* and 30 *C. propinqua* shrubs were selected using random numbers and co-ordinates from within a 5 ha area on the southfacing (shady) aspect of the main gully that bisects the covenant. The south-facing aspect was chosen as its vegetation cover was most suitable for the wider research programme of which the present study was part (Derraik, 2001; Derraik *et al.*, 2001). Moreover, the shady slopes were predicted to have higher soil moisture and more favourable conditions for invertebrates than the drier, northerly (sunny) faces.

Sampling was carried out when vegetation was dry and on windless days, to avoid bias. Invertebrates were collected by beating each plant with 10 downward strokes of a 1.5 m long metal pole. The fallen material was collected on a polythene sheet, 1.0 m x 1.3 m, placed beneath the plant. The collected material was sealed in a plastic bag, labeled and frozen. Invertebrates were sorted initially into morphospecies by JGBD, using a low-power binocular microscope. Vials containing the morphospecies were then sent to specialist taxonomists for identification or verification (Derraik *et al.*, 2002).

Of the 30 *C. propinqua* sampled, only 15 could be used in the analyses, since the remaining samples were heavily fruited and the resulting stickiness seriously impaired the separation and identification of invertebrates. As a result, though all 30 *O. bullata* samples were examined, 15 of those were selected randomly so a valid comparison could be made. The sizes of individual *O. bullata* and *C. propinqua* plants were established using an estimate of sampled shrub volume. Volume was derived from shrub height multiplied by its projected foliage cover (based on the two longest shrub diameters in cross section). A twosample t-test was used to test whether or not there was a significant difference in mean shrub volume between species.

In order to test whether one shrub species harboured higher invertebrate diversity than the other, analyses of covariance (ANCOVA) were performed, with taxon richness as the dependent variable and shrub volume as the independent covariate (Sokal and Rohlf, 1995). Variables were square root +0.5 transformed to stabilise the variance. The significance level used in all analyses was P < 0.05.

Results

A two-sample t-test for shrub volume showed no significant difference (P = 0.90) between *Olearia bullata* and *Coprosma propinqua*, with means of 6.15 m³ (range 0.34-40.64 m³) and 6.58 m³ (range 0.09-35.32 m³), respectively. As various size classes were represented in the samples (from seedlings to large and presumably old shrubs) (Fig. 1), the standard deviation in both cases was large (9.92 and 8.53, respectively). The size distributions of the sampled plants of both species were similar however (Fig. 1). Most plants of both species were less than 10 m³ volume, with only three shrubs being larger.

In total, 115 invertebrate taxa were collected from

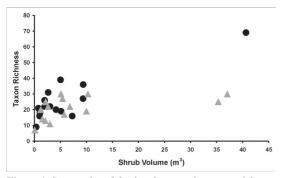


Figure 1. Scatter plot of shrub volume against taxon richness for *Olearia bullata* (\bullet) and *Coprosma propinqua* (\blacktriangle) plants sampled at the Brookdale Covenant.

O. bullata compared with 93 from *C. propinqua*. Mean taxon richness obtained from both shrub species is summarised in Table 1. For the overall community, the mean number of invertebrate taxa per shrub was higher on *O. bullata* (24.8) than on *C. propinqua* (20.8), but this difference was not statistically significant (P = 0.08). All 25 invertebrate orders collected were included in the latter analyses, but only the eight most abundant and speciose ones were examined independently. Mean taxon richness of invertebrates in all orders was higher on *O. bullata* (except for Coleoptera where the opposite was true), but the results were significantly different only for Diptera (P = 0.005) and Hemiptera (P < 0.001) (Table 1).

The maximum number of taxa per shrub was higher on *O. bullata* in all cases, whereas the minimum number was either higher than or equal to that on *C. propinqua*. There was also a large difference in the diversity found on the largest shrub of each species (Fig. 1). These plants stood out as being much larger than the others sampled. Their size was similar, with the largest *O. bullata* being 40.64 m³ and the largest *C. propinqua* 37.04 m³, as were their topographic positions in the shrubland, and their proximity to a creek and surrounding vegetation. However, whereas the *O. bullata* plant yielded 69 invertebrate taxa and 749 specimens, *C. propinqua* yielded only 30 and 178, respectively.

Approximately half the invertebrate taxa recorded were present on both plant species (Fig. 2). Approximately 19% and 13% of Diptera and Lepidoptera taxa, respectively, were shared between the shrub species, with 56% and 63% being restricted to *O. bullata*. In contrast, 75% of the Araneae taxa were taken from both shrub species. Relatively few taxa were restricted to *C. propinqua*, the percentage varying between 10 and 25% among the individual orders (Fig. 2).

Table 1. Invertebrate taxon richness recorded from *Olearia bullata* and *Coprosma propinqua* shrubs sampled in the Brookdale Covenant. Mean and standard deviations are shown, with the minimum and maximum number of taxa per shrub in brackets. The *P*-values from the ANCOVA and the *P*-values for the covariate shrub volume are shown, the latter in brackets. *P*-values in bold indicate significant differences at the 95% level.

	Olearia bullata (n=15)	Coprosma propinqua (n=15)	P-value
Overall Community	24.80 ± 13.56 (9; 69)	20.80 ± 7.28 (7; 30)	0.081 (0.004)
Acari	$2.53 \pm 1.68(0; 6)$	2.33 ± 1.23 (0; 4)	0.619 (0.126)
Araneae	6.47 ± 1.92 (4; 12)	6.07 ± 1.91 (3; 10)	0.390 (0.227)
Coleoptera	3.27 ± 3.49 (0; 14)	3.73 ± 2.19 (0; 8)	0.806 (0.005)
Diptera	$1.80 \pm 2.11(0; 9)$	$0.73 \pm 1.39(0; 5)$	0.005 (0.009)
Hemiptera	3.73 ± 1.83 (1; 7)	$2.07 \pm 1.75(0; 6)$	<0.001 (0.001)
Hymenoptera	1.93 ± 1.75 (0; 6)	$1.40 \pm 1.18(0; 4)$	0.251 (0.108)
Lepidoptera	$0.88 \pm 1.55(0; 6)$	$0.87 \pm 0.91 (0; 3)$	0.879 (0.535)
Psocoptera	$1.93 \pm 1.33 (0; 5)$	$1.73 \pm 1.16 (0; 4)$	0.552 (0.062)

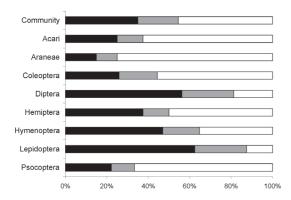


Figure 2. Relative proportion of invertebrate taxa within the eight-most speciose orders recorded: only on *Olearia bullata* (black); only on *Coprosma propinqua* (gray); on both shrub species (white). Community category includes all species recorded in the study. Total number of taxa within each group in brackets.

The 20 most abundant invertebrate taxa recorded on *O. bullata* and *C. propinqua* comprised 83.3% and 81.4% of the total abundance, respectively (Table 2). Of the 29 invertebrate taxa listed in Table 2, only one (the spider *Moneta* sp.) was restricted to a single shrub species (*O. bullata*). Eleven taxa were in the top 20 for both shrub species based on rank abundance: five Araneae, four Acari, one Psocoptera, and one Stylommatophora species (Table 2). Acari was the most abundant group on both *O. bullata* (50.9%) and *C.propinqua* (50.1%), whereas Araneae had the highest number of top-20 taxa on both *O. bullata* and *C. propinqua* with eight and six taxa, respectively (Table 2). For the overall community (all taxa recorded), the Acari was not only the most abundant order (43.1% of invertebrates on *O. bullata* and 41.3% on *C. propinqua*), but it also contained the single most abundant taxon present on both shrubs.

The covariate (shrub volume) was positively associated with taxon richness in many cases (Table 1). For the overall community, Coleoptera, Diptera and Hemiptera, the relationship with shrub volume was strong (*P*-values 0.004, 0.005, 0.009 and 0.001, respectively).

Discussion

Despite there being no significant difference in the mean number of taxa per shrub between *Olearia* bullata and Coprosma propinqua in all but two cases, the results of this study provide a clear indication that the richness of invertebrate taxa is higher on O. bullata than on C. propinqua. A total of 115 invertebrate taxa was collected from O. bullata in comparison to 93 from C. propinqua. Moreover, O. bullata was the sole

Table 2. The twenty most abundant invertebrate taxa collected from sampled shrubs of (a) *Coprosma propinqua* and (b) *Olearia bullata*, ranked in order of abundance. Ranks in bold correspond to species ranked in the top 20 for both shrub species; np indicates taxon not recorded on the other shrub species. (?) indicates the family was not determined.

	(a) Coprosma propinqua				
Rank	Order	Family	Species	% Total	Rank on O. bullate
1	Acari	?	morphospecies B	22.43	5
2	Acari	?	morphospecies C	16.55	2
3	Araneae	Pisauridae	Dolomedes sp.	13.77	3
4	Araneae	Araneidae	unidentified sp.	4.25	15
5	Psocoptera	Elipsocidae	Spilopsocus avium	4.18	8
6	Stylommatophora	Punctidae	Laoma sp.	3.17	7
7	Coleoptera	Staphylinidae	aleocharine sp.	1.86	31
8	Psocoptera	Psocidae	morphospecies A	1.70	22
9	Araneae	Stiphidiidae	Cambridgea agrestis	1.55	23
10	Araneae	Thomisidae	Diaea sp.	1.47	18
11	Coleoptera	Coccinellidae	cf. Scymus sp.	1.47	45
12	Hymenoptera	Formicidae	Monomorium antarcticum	1.31	99
13	Coleoptera	Staphylinidae	tachyporine sp.	1.23	35
14	Araneae	Araneidae	Eriophora pustulosa	1.16	30
15	Acari	?	morphospecies A	1.00	1
16	Araneae	Salticidae	salticid n.sp. A	0.93	16
17	Acari	?	morphospecies D	0.85	12
18	Araneae	Theridiidae	Achaearanea sp.	0.85	20
19	Coleoptera	Coccinellidae	coccinelid sp.	0.85	40
20	Araneae	Clubionidae	cf. Clubiona sp.	0.77	43

host of a much larger number of taxa (50) than *C.* propinqua (28), the largest difference occurring amongst the Diptera (9 versus 4, respectively) and Lepidoptera (10 versus 4, respectively). It would be unwise to assume that those species would occur only on these particular plant species however, not only because of the relatively small number of samples taken, but also because other shrub species at the site were not examined. Nevertheless, at least for the Lepidoptera, there is good evidence that several moth species use plants in the genus *Olearia* as single hosts (Patrick, 1994b, 2000). It was also striking that for both Diptera and Lepidoptera very few species were found on both shrub species (19 and 13%, respectively).

The listing of taxa in terms of rank-abundance indicates that the bulk of the invertebrate community was made up of abundant species which were probably widespread throughout the shrub community, as indicated by the fact that only one of the 29 species listed in Table 2 was restricted to one shrub species. Therefore, those taxa whose distributions are more restricted (with low abundance and probably locally rare) largely account for the fact that *O. bullata* hosted 23% more taxa than *C. propinqua*.

It is important to point out that the beating method we used is biased to some extent. Though it is a very efficient collection method (Upton, 1991), it does not enable comprehensive collection of some invertebrate groups. As a result, our collections almost certainly underestimated the diversity of some orders, such as Lepidoptera. Moreover, the results from a single sampling need to be considered with caution. Our results indicate that *O. bullata* harbours a more diverse invertebrate community than *C. propinqua*. Also, they add support to view that *Olearia* is of special significance for invertebrates (Patrick, 2000). Since at least ten species of *Olearia* are recognized as threatened or uncommon, and four are classified as endangered or critically endangered (Lange *et al.* 1999), this is cause for concern with respect to the maintenance of invertebrate diversity. We conclude that sites where *Olearia* species are still present are likely to be of conservation significance for invertebrates.

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Table 2b.	See c	caption	on previous	page.

Rank	Order	Family	Species	% Total	Rank in C. propinque
1	Acari	?	morphospecies A	21.23	15
2	Acari	?	morphospecies C	15.29	2
3	Araneae	Pisauridae	Dolomedes sp.	12.63	3
4	Hemiptera	Psyllidae	Trioza n.sp.	5.17	28
5	Acari	?	morphospecies B	4.09	1
6	Araneae	Theridiidae	cf. <i>Épisinus</i> sp.	2.93	21
7	Stylommatophora	Punctidae	Laoma sp.	2.51	6
8	Psocoptera	Elipsocidae	Spilopsocus avium	2.32	5
9	Hemiptera	Aphididae	Aphis sp.	2.24	35
10	Thysanoptera	Thripidae	morphospecies A	2.04	50
11	Pseudoscorpiones	Chernetidae	Apatochernes n.sp.	2.01	49
12	Acari	?	morphospecies D	1.73	17
13	Hemiptera	?	unidentified sp.	1.60	29
14	Araneae	Linyphidae	unidentified sp.	1.51	31
15	Araneae	Araneidae	unidentified sp.	1.20	4
16	Araneae	Salticidae	salticid n.sp. Å	1.04	16
17	Araneae	Theridiidae	Moneta sp.	1.04	np
18	Araneae	Thomisidae	Diaea sp.	0.93	10
19	Hemiptera	Miridae	Romna scotti	0.93	22
20	Araneae	Theridiidae	Achaearanea sp.	0.85	18

References

- Crisp, P.N.; Dickinson, K.J.M.; Gibbs, G.W. 1998. Does native invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation. *Biological Conservation 83*: 209-20.
- Derraik, J.G.B. 2001. *Plant-invertebrate relationships* in a native modified shrubland, Otago, New Zealand. M.Sc. thesis. University of Otago, Dunedin, N.Z.
- Derraik, J.G.B.; Barratt, B.I.P.; Sirvid, P.; Macfarlane, R.P.; Patrick, B.H.; Early, J.; Eyles, A.C.; Johns, P.M.; Fraser, P.M.; Barker, G.; Henderson, R.; Dale, P.J.; Harvey, M.S.; Fenwick, G.; McLellan, I.D.; Dickinson, K.J.M.; Closs, G.P. 2001. Invertebrate survey of a modified native shrubland, Brookdale Covenant, Rock and Pillar Range, Otago, New Zealand. New Zealand Journal of Zoology 28: 273-290.
- Derraik, J.G.B.; Dickinson, K.J.M.; Closs, G.P.; Sirvid, P.; Barratt, B.I.P.; Patrick, B.H. 2002. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera and Lepidoptera. *Conservation Biology 16*: 1015-1023.
- Department of Conservation & Ministry for the Environment 2000. *New Zealand biodiversity strategy*. Department of Conservation and Ministry for the Environment, Wellington, N.Z.
- Dugdale, J.S. 1975. The insects in relation to plants. In: Kuschel, G. (Editor), Biogeography and ecology in New Zealand, pp 561-589. Dr. W. Junk Publishers, The Hague, The Netherlands.
- Dugdale, J.S. 1988. Lepidoptera-annotated catalogue, and keys to family-group taxa. Fauna of New Zealand 14. Science Information Publishing Centre, DSIR, Wellington, N.Z.
- Knight Frank N.Z. Ltd. 1995. Draft proposal to Commissioner of Crown Lands – application for tenure change: Brookdale. File number Po277, available from:

http://www.publicaccessnewzealand.org/files/ otago pastoral lands.html

- Klimaszewski, J. 1997. Biodiversity of New Zealand beetles (Insecta, Coleoptera). *Memoirs of the Museum of Victoria 56:* 659-666.
- Lange, P.J.; Heenan, P.B.; Given, D.R.; Norton, D.A.; Ogle, C.C.; Johnson, P.N.; Cameron, E.K. 1999. Threatened and uncommon plants of New Zealand. *New Zealand Journal of Botany* 37: 603-28.

- McCraw, J.D. 1965. Landscapes of Central Otago. In: Lister, R.G.; Hargreaves, P. (Editors), Central Otago, pp 30-45. Miscellaneous Series No. 5. New Zealand Geographical Society, Dunedin, N.Z.
- McGlone, M.S. 2001. The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology 25:* 1-16.
- McGlone, M.S.; Wilmshurst, J.M. 1999. Dating initial Maori environmental impact in New Zealand. *Quaternary International 59:* 5-16.
- McLay, C.L. 1974. The species diversity of New Zealand forest birds: some possible consequences of the modification of beech forests. *New Zealand Journal of Zoology 1:* 179-196.
- Patrick, B. 1994a. The importance of invertebrate biodiversity: an Otago Conservancy review. Conservation Advisory Science Notes No. 53. Department of Conservation, Wellington, N.Z.
- Patrick, B. 1994b. Valley floor Lepidoptera of Central Otago. Miscellaneous Series 19. Department of Conservation, Dunedin, N.Z.
- Patrick, B. 2000. Lepidoptera of small-leaved divaricating Olearia in New Zealand and their conservation. Science for Conservation 168. Department of Conservation, Wellington, N.Z.
- Sokal, R.R.; Rohlf, F.J. 1995. *Biometry*. W. H. Freeman and Company, New York, U.S.A.
- Talbot, J.M.; Mark, A.F.; Wilson, J.B. 1992. Vegetation-environment relations in snowbanks on the Rock and Pillar Range, Central Otago, New Zealand. New Zealand Journal of Botany 30: 271-301.
- Upton, M.S. 1991. *Methods for collecting, preserving, and studying insects and allied forms*, 4th Edition. Miscellaneous Publications 3. The Australian Entomological Society, Brisbane, Australia.
- Wardle, P. 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge, U.K.
- Wardle, P.; McGlone, M.S. 1988. Towards a more appropriate term for our divaricating shrubs and juvenile trees. *New Zealand Botanical Society Newsletter 11*: 16-18.
- Watt, J.C. 1975. The terrestrial insects. *In*: Kuschel, G. (Editor), *Biogeography and ecology in New Zealand*, pp. 507-535. Dr. W. Junk Publishers, The Hague, The Netherlands.
- Wilton, A.D.; Breitwieser, I. 2000. Composition of the New Zealand seed plant flora. New Zealand Journal of Botany 38: 537-549.