Insect assemblages in a native (kanuka – *Kunzea ericoides*) and an invasive (gorse – *Ulex europaeus*) shrubland

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Abstract: In New Zealand, the European shrub gorse (*Ulex europaeus*) is becoming the initial post-disturbance shrub, replacing the native myrtaceous manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) scrub in this role. Change in the dominant vegetation is likely to affect the native invertebrate community. To quantify these changes, we compared the assemblages of four selected insect taxa (Coleoptera, Lepidoptera, and two groups of Diptera, the Tachinidae and the fungus gnats, represented in New Zealand by the families Ditomyiidae, Keroplatidae and Mycetophilidae) in neighboring stands of kanuka and gorse using Malaise and pitfall traps set during December. We sorted 34 387 specimens into 564 recognisable taxonomic units. Ordinations showed that insect assemblages associated with each habitat were distinct for all four insect groups. The gorse habitat was species rich compared with kanuka for tachinids, fungus gnats and Malaise-trapped beetles, and both habitats contained few adventive species. Many species were unique to each habitat. Some species loss might occur if the kanuka-dominated community continues to be replaced by gorse, but gorse is nevertheless considered to be valuable as a habitat for native invertebrates.

Keywords: Coleoptera; community composition; Diptera; Ditomyiidae; indicator species; Keroplatidae; Lepidoptera; Mycetophilidae; Tachinidae; weed impacts.

Introduction

Where adventive plant species have invaded, or largely replaced, native vegetation, an increasing number of studies demonstrate significant changes to native invertebrate communities (e.g. Breytenbach, 1986; Samways *et al.*, 1996; Crisp *et al.*, 1998; Standish, 2003), although this is not always the case (e.g. Hedge and Kriwoken, 2000; Toft *et al.*, 2001). The degree to which the native invertebrate community will be restructured may vary with the degree of change to the vegetation structure. For example, exotic shrubland and native heathland of similar structure in Australia had similar litter invertebrate assemblages (French and Eardley, 1997), whereas adventive shrub communities and native grassland in South Africa had markedly different assemblages (Samways *et al.*, 1996). In contrast, native *Quercus agrofolia* and adventive *Eucalyptus globulus* woodland in California had similar total species richness but large differences in species composition for a range of disparate species assemblages (Sax, 2002).

The extent of documented differences in community assemblages also depends on the species sampled, which vary with the location and method of sampling. For example, invasion of forest remnants by *Tradescantia fluminensis* in New Zealand resulted in minimal changes to the assemblages of beetle and fungus gnats sampled using Malaise traps (Toft *et al.*, 2001), no detectable differences in the abundance or species richness of soil nematodes (Yeates and Williams, 2001), but a clear change in species composition of invertebrates sampled using pitfall traps (Standish, 2003). These studies of *Tradescantia* all sampled the same remnants at the same time.

In New Zealand lowlands, a spiny European shrub, gorse (*Ulex europaeus*), is replacing native manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) scrub as the initial post-disturbance shrub. Gorse scrub covered 53 000 ha and manuka/kanuka scrub 155 000 ha when last mapped on a national scale (Blaschke *et al.*, 1981). Gorse has high reproductive potential, resists grazing and recovers rapidly after fire, thereby enabling it to occupy sites in areas where native shrubs are absent (Druce, 1957). Gorse fixes atmospheric nitrogen (Eugunjobi, 1971) and is often succeeded by native shrubs after several decades in suitable climates (reviewed by McQueen, 1993). This has led to it being valued as a precursor to native forest in revegetation projects (Porteous, 1993; Wilson, 1994), as are a number of other alien shrubs (De Pietri, 1992). Derraik *et al.* (2001) suggested remnant native

shrublands are important habitat for native insects in a modified landscape, but such opinions are of little value unless based on quantitative comparisons of native invertebrate species in habitats dominated by native and adventive flora, respectively.

The high species richness of the invertebrate fauna means that it is seldom possible to sample the total fauna of a site. Therefore, selected taxa are used as indicators of general effects on invertebrates, of biodiversity patterns, or to reflect landscape patterns or ecosystem health (e.g. Jansen, 1997; Ferris and Humphrey, 1999; Tshiguvho, *et al.*, 1999). Although individual groups are generally used, some authors have questioned the validity of extrapolation from one group to another (Hilty and Merenlender, 2000; Reyers *et al.*, 2000) or even between closely related taxa (Ricketts *et al.*, 2002).

Our aim was to sample four selected insect groups in neighbouring stands of kanuka and gorse to determine whether there were differences in species richness, abundance, assemblage composition and guild structure between habitat types. We also aimed to assess whether the insect groups sampled responded similarly, and to estimate the possible extent of species loss if kanuka-dominated communities continue to be replaced by gorse. The four insect groups were beetles (Coleoptera), moths and butterflies (Lepidoptera), bristle flies (Diptera: Tachinidae) and fungus gnats (Diptera: Ditomyiidae, Keroplatidae and Mycetophilidae). Beetles were chosen since they represent a large component of non-microbial biodiversity (Southwood, 1978), account for about 50% of New Zealand's described insect species (Watt, 1982; Kuschel, 1990), and include representatives of all trophic groups. Further, beetle species assemblages have been shown previously to be sensitive to changes in the vegetation (Hutcheson, 1990, 1996). Diptera are quoted as the second most species-rich insect order in New Zealand (Dugdale, 1988; but see Emberson, 1998), and within the order, gnats are a diverse and abundant dipteran group which have been used as indicators of disturbance and temperate forest integrity (Okland, 1994, 1996). Bristle flies are another species-rich dipteran family and are all parasitoids; this is the only guild not represented by the other taxa selected. Lepidoptera, New Zealand's third most species-rich insect order (Dugdale, 1988), contains many herbivores that are likely to show preferences for different plant species. Lepidoptera have often been used as indictors of habitat quality in urban or fragmented areas, as indicators of effects of land management practices, or as surrogates for the richness of insects in general (e.g. Hammond and Miller, 1998; Kerr *et al.*, 2000; Rosch *et al.*, 2001).

Methods

Study sites

The study was conducted in the Wakapuaka Valley near the city of Nelson, northern South Island, New Zealand. The gorse and kanuka sites were in close proximity, 41°12.3'S, 173°25.5'E and 41°11.9'S, 173°25.7'E respectively. The pre-European vegetation on hill slopes was dominated by *Nothofagus truncata-Weinmannia racemosa* forest, with scattered podocarps (Williams and Karl, 2002). This vegetation was burned, cleared, and grazed over the last 100 years, resulting in a mosaic of forest remnants and secondary scrub dominated by kanuka, manuka or gorse, as well as *Pinus radiata* plantations and introduced pasture.

The two adjacent kanuka sites were in the main Wakapuaka valley at 180–205 m a.s.l., on a mid-slope (25–37°) with a north-west aspect. The vegetation at these sites developed after secondary kanuka forest was cleared for firewood. The two gorse stands were on a tributary of the main valley slightly more inland at 60–120 m a.s.l., on a lower to mid slope (20–37°) with a north-west aspect. They were in an area burned at least twice in the last 30 years to encourage deer from the forest to feed on the new growth (K. Anderson, landowner, Nelson, N.Z., *pers. comm.*). For both vegetation types, the canopy plants were about 14 years old when sampling was conducted. We could not select sites with an identical history because differences in management practices, in this case fire frequency, are necessary for the formation of gorse- and kanuka-dominated vegetation. However, the sites are similar in aspect and topography. A mixture of infrequently grazed pasture, other scrub types, *P. radiata* plantations and beech (*Nothofagus* spp.) forest remnants surrounds the sites. Gorse has never occupied the kanuka site. Sheep (*Ovis aries*) occur in the vicinity, but they do not wander beneath dense kanuka where our invertebrate traps were located, and they cannot penetrate the gorse. Wild pigs (*Sus scrofa*) were present in both the kanuka and gorse stands (Williams and Karl, 2002). Rabbits (*Oryctolagus cuniculus*) were sparse in the kanuka, and absent from the gorse. Possums (*Trichosurus vulpecula*) and rats (*Rattus rattus*) were sparse throughout, and mice (*Mus musculus*) were significantly more abundant in the gorse (Williams and Karl, 2002).

Data collection

Three randomly placed Malaise traps (Towns, 1972) were set within each site (two kanuka and two gorse) and a pitfall trap was set 2 m north and south of each Malaise trap. Minimal access tracks were cut through the gorse to avoid creating paths for animals or conduits for flying insects from neighbouring vegetation.

Malaise traps were set with the collecting container facing north, and the central screens pinned to the ground (Hutcheson, 1990). Traps were set for a 4-week period from 1 to 29 December 1997. During this period, Malaise trapping in New Zealand forests can be expected to sample a high proportion of the beetle community present (Hutcheson, 1990, 1996; Hutcheson and Kimberley, 1999; Hutcheson *et al.*, 1999) and the other selected insect groups (e.g. Toft *et al.*, 2001; Dugdale and Hutcheson, 1997). The collecting container fixed to the Malaise traps contained 70% alcohol as a killing and preservative agent. The pitfall traps were similar to those used by Moeed and Meads (1985) (75 mm diameter with an inner cup), except that a tin cover was added to keep out rain and litter. The traps contained Gault's solution (Walker and Crosby, 1988).

Malaise traps were cleared weekly and pitfall traps fortnightly, the samples being stored in 70% alcohol before sorting, pinning and identification. Adults were identified to species level when possible, and to recognisable taxonomic units (RTUs) when not. (Collections have been deposited at Landcare Research, Nelson.) Species were categorised as indigenous or adventive, principally with reference to Kuschel (1990), Dugdale (1988), and Evenhuis (1989). Only beetles were identified from the pitfall traps. Beetle data obtained with the Malaise and pitfall traps were analysed separately (with the two pitfall trap samples associated with each Malaise trap combined), and together.

Lepidoptera collected from Malaise traps and beetles from Malaise and pitfall traps were also classified into functional groups [for Lepidoptera — herbivores, detritivores, and "others" (predators and seed, hair, spore, and fungus feeders); for beetles — herbivores, detritivores, and predators] at family or subfamily level using the classifications of Klimaszewski and Watt (1997), Hutcheson (1996), Didham *et al.* (1998), and Dugdale and Hutcheson (1997).

The composition and structure of vegetation within a 20 m × 20 m area centred on each Malaise trap were described by estimating the foliage cover of all vascular plant species in fixed height tiers following the method of Allen (1992). All vascular plant species present were recorded and their relative abundances scored within height tiers (0–0.3 m, > 0.3–2 m, > 2–5 m, > 5 m). Species were categorised as indigenous or adventive, as indicated by Allan (1961), Moore and Edgar (1970), Healy and Edgar (1980), and Webb *et al.* (1988).

Statistical analyses

Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) was used to explore differences in insect assemblages between traps and the vegetation around the traps. DCA arranges groups along ordination axes based on the composition of taxa, and does not force association among groups. Relative to other ordination techniques, DCA has improved performance when data are heterogeneous (Hill and Gauch, 1980). Raw insect abundance and vegetation cover data were transformed by log $(x + 1)$ before ordination, to reduce the impact of very abundant species on the result. DCA eigenvalues cannot be interpreted as proportions of variance explained. An after-the-fact coefficient of determination, represented as a cumulative R^2, is used instead to evaluate the effectiveness of the ordination (McCune and Mefford, 1999). Multi-response permutation procedures (MRPP) with rank transformed distance matrix were used to test the hypothesis of no difference between trap assemblages from the two sites within gorse and kanuka. The test statistic (A) describes the separation between the groups. The program PC-ORD (McCune and Mefford, 1999) was used for these analyses.

Nested ANOVA was used to compare species richness and abundance of insect groups and guilds in gorse and kanuka. Habitat comparisons were between gorse and kanuka, each consisting of two sites with three replicate sampling locations at each site.

Results

Vegetation

The structure and composition of the two plant communities were distinct (Fig. 1, Table 1). The DCA (Fig. 2) clearly separated the vegetation by habitat, and also distinguished between the two gorse sites (MRPP, A= 0.43, P = 0.02), but not the two kanuka sites (Fig. 2a). The two gorse sites differed principally due to the increased presence of two native species, bracken (*Pteridium esculentum*) and mahoe (*Melicytus ramiflorus*) at site A, which also had a more open canopy. Both the kanuka and gorse habitats had a similar percentage of the ground covered in litter. However, a substantial quantity of dead leaves was suspended in the crowns of gorse; some crowns were beginning to senesce, some had died and fallen and were providing a source of rotting wood. In contrast, there was little fallen or standing dead wood at the kanuka sites. Kanuka had a dense canopy and relatively little vegetation in the understorey (Fig. 1).

Insects

The 34 387 insect specimens were sorted into 564 recognisable taxonomic units (RTUs), of which 75% were identified to species. The beetles comprised 191 RTUs in 42 families, with 160 and 65 RTUs captured by Malaise and pitfall traps, respectively. The fungus
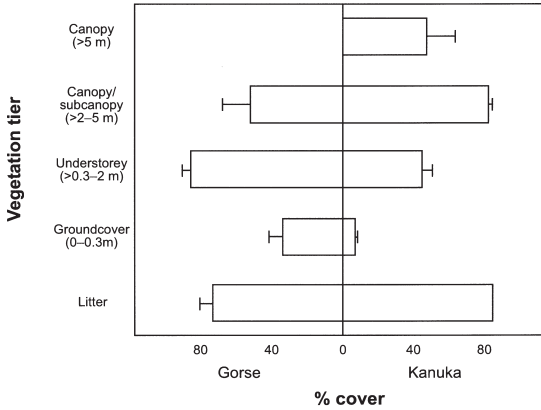
Figure 1. The vegetation structure of gorse and kanuka stands. The width of the boxes represents the percentage cover of the height tiers averaged across vegetation plots, and the variability within height tiers of the six plots in each habitat is indicated by the standard error bars.

gnats were represented by 155 RTUs and the bristle flies by 45 RTUs from eight tribes. The Lepidoptera samples contained 173 RTUs in 27 families, two of which were butterflies and the remainder moths.

Overall, gorse traps had more species than the kanuka traps ($F_{1,2} = 17.4, P = 0.054$, Table 2). Although there were consistently more species in the gorse sites than the kanuka sites for all groups except the pitfall-trapped beetles, differences were not statistically significant, which in part can be attributed to a lack of

statistical power. Gorse and kanuka had similar total abundance of specimens (Table 3). However, this overall similarity in total abundance was largely due to the high abundance of fungus gnats at kanuka site B. *Mycetophila dilatata* (Mycetophilidae) was represented by 3454 specimens in traps in kanuka, and along with *M. minima*, and *Parvicellula ruficoxa*, accounted for 66% (6360 specimens) of all mycetophilids caught in kanuka. The same three species amassed just 395 specimens at the gorse sites (6%). Many other fungus gnats were more abundant in gorse. There were more bristle flies, Malaise-trapped beetles, and Lepidoptera in gorse than kanuka, although differences were not statistically significant (Table 3).

The trend towards greater species richness in gorse than kanuka was not due to a greater number of adventive insect species there (Table 2). At least four adventive fungus gnats are known from New Zealand (Martin, 1983; R. J. Toft, *unpubl.*), but none of these was found. All the species of bristle flies were also native. Of the five adventive beetles identified, only one was unique to gorse. The gorse seed weevil (*Exapion ulicis*), found only in gorse, was the only abundant adventive beetle and made up nearly 25% of the Coleoptera found in gorse. The Lepidoptera included 13 adventive RTUs (7.4% of the total); four were present in the kanuka and 12 in gorse. With the adventives removed, species richness of native Lepidoptera was similar in gorse and kanuka. The adventive Lepidoptera made up 2.7% and 5.3% of the total Lepidoptera present in gorse and kanuka, respectively. The only abundant adventive species

Table 1. Details of the plants (>1 % tier cover), listed in declining order of tier cover abundance, averaged across three 20 x 20m plots within each study site.

	Gorse site A	Gorse site B	Kanuka site A	Kanuka site B
Vegetation tiers				
Canopy (>5m)			Kanuka	Kanuka
Canopy/subcanopy (>2–5m)	Gorse[1]	Gorse[1]	Kanuka	Kanuka
	Mahoe	Bracken		Mahoe
Understory (>0.3–2m)	Gorse[1]	Gorse[1]	Kanuka	Kanuka
	Bracken	Bracken		Mahoe
	Mahoe			
	Lemonwood[2]			
Groundcover (0–0.3m)	Bracken	Gorse[2]	Kanuka	Kanuka
	Gorse[2]	Bracken		
Species richness	13	13	10	15
% of total cover:				
gorse	64.6	92.7	0	0
kanuka	0	<0.1	94.2	95.1
% of total cover comprising adventive species	67.0	93.5	1.2	1.0

[1]adventive species

[2]*Pittosporum eugenioides*
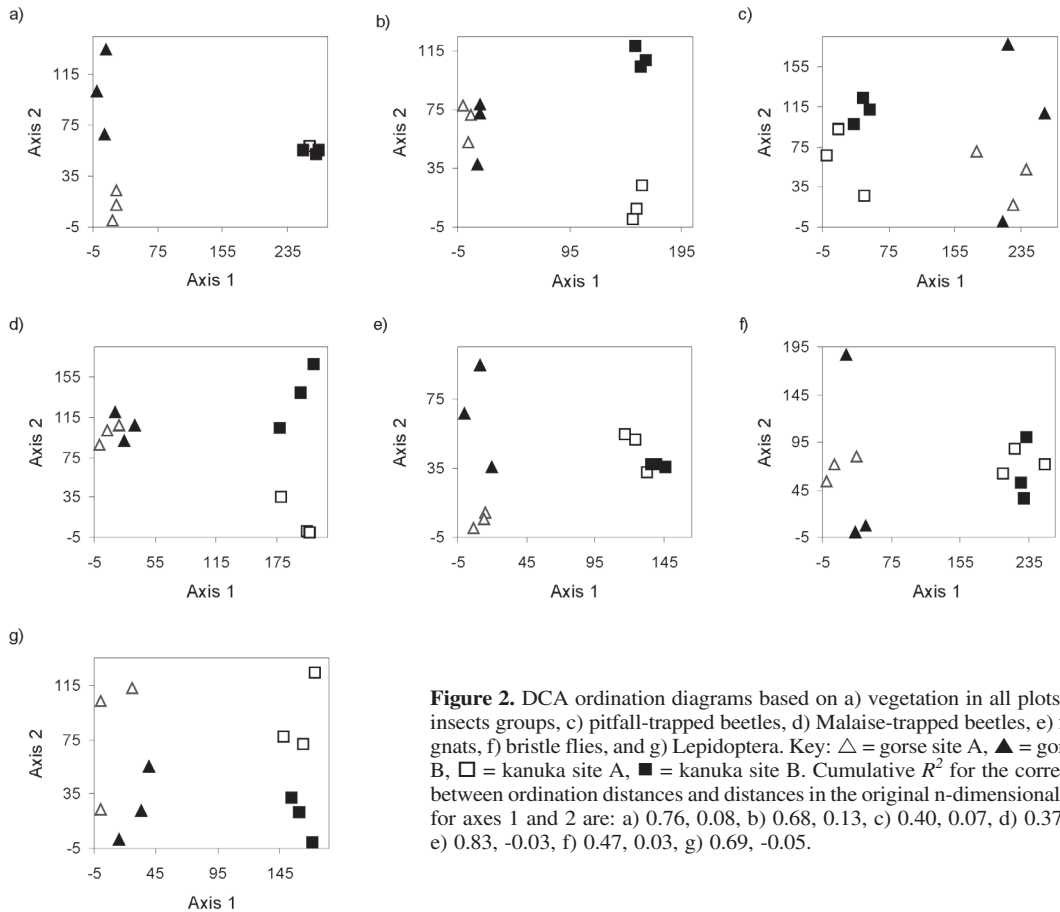
Figure 2. DCA ordination diagrams based on a) vegetation in all plots, b) all insects groups, c) pitfall-trapped beetles, d) Malaise-trapped beetles, e) fungus gnats, f) bristle flies, and g) Lepidoptera. Key: △ = gorse site A, ▲ = gorse site B, □ = kanuka site A, ■ = kanuka site B. Cumulative R^2 for the correlations between ordination distances and distances in the original n-dimensional space, for axes 1 and 2 are: a) 0.76, 0.08, b) 0.68, 0.13, c) 0.40, 0.07, d) 0.37, 0.31, e) 0.83, -0.03, f) 0.47, 0.03, g) 0.69, -0.05.

Table 2. Average (± SE) RTU richness for traps within each site. Numbers in brackets are the number of adventive species. Nested ANOVA results comparing insect faunas between habitats (kanuka v. gorse) and between sites within habitat area also given.

Site		Invertebrate group richness					
		Bristle flies	Beetles (pitfall)	Beetles (Malaise)	Lepidoptera	Fungus gnats	Total
Gorse							
A		21.3 ± 2.4	9.8 ± 1.0	61.7 ± 3.8	65.3 ± 3.0	90.3 ± 7.9	247.7 ± 12.2
		(0)	(1.0 ± 0.0)	(2.3 ± 0.7)	(6.7 ± 1.5)	(0)	(9.0 ± 1.2)
B		17.3 ± 3.0	11.3 ± 1.7	55.0 ± 8.1	57.0 ± 8.0	79.7 ± 12.4	221.7 ± 29.7
		(0)	(1.0 ± 0.0)	(1.6 ± 0.3)	(3.3 ± 0.6)	(0)	(5.7 ± 0.9)
Kanuka							
A		12.7 ± 1.9	11.2 ± 1.7	38.3 ± 1.2	55.3 ± 1.9	58.0 ± 5.5	172.0 ± 5.2
		(0)	(1.3 ± 0.3)	(1.0 ± 0.0)	(2.7 ± 0.3)	(0)	(5.0 ± 0.6)
B		7.3 ± 0.7	13.5 ± 0.9	50.7 ± 1.3	45.7 ± 4.7	64.7 ± 3.91	81.7 ± 4.3
		(0)	(0.7 ± 0.3)	(2.0 ± 0.0)	(1.0 ± 0.0)	(0)	(3.3 ± 0.3)
Habitat	$F_{1,2}$	7.8	1.4	3.9	2.8	14.2	17.4
	P	0.107	0.748	0.187	0.237	0.064	0.053
Site (habitat)	$F_{2,8}$	2.4	1.0	2.4	1.7	0.6	0.7
	P	0.152	0.384	0.155	0.250	0.570	0.517

Table 3. The average (± SE) abundance of individuals found in traps within each site. Nested ANOVA results comparing insect faunas between habitats (kanuka v. gorse) and between sites within habitat area also given.

Site		Bristle flies	Beetles (pitfall)	Beetles (Malaise)	Lepidoptera	Fungus gnats	Total
				Invertebrate group (specimens per trap)			
Gorse							
A		378 ± 34	96 ± 41	839 ± 62	629 ± 14	1645 ± 413	3683 ± 351
B		259 ± 70	30 ± 9	587 ± 121	700 ± 142	1129 ± 401	2741 ± 717
Kanuka							
A		118 ± 22	39 ± 5	195 ± 35	361 ± 4	917 ± 325	1670 ± 302
B		73 ± 13	48 ± 3	268 ± 56	475 ± 116	2453 ± 850	3368 ± 723
Habitat	$F_{1,2}$	12.1	0.3	13.5	13.5	0.1	0.5
	P	0.073	0.632	0.067	0.067	0.748	0.551
Site (habitat)	$F_{2,8}$	2.4	2.5	2.1	0.5	2.3	3.0
	P	0.150	0.140	0.189	0.608	0.167	0.120

was the flower-eating generalist *Chloroclystis filata* (Lepidoptera: Geometridae), which occurred in both habitats, with 74% of the 158 specimens being collected in kanuka. Both kanuka and gorse flowered profusely during the sampling period.

Insect assemblages clearly separated by habitat on axis one of the ordination when data from all groups were combined (Fig. 2b). Ordinations of trap catches for each insect group were also separated primarily by habitat on axis one (Fig. 2c–g). Differences in assemblages between sites within each habitat type were less distinct and generally along axis 2 which did not explain much of the total variance. For all groups combined (Fig. 2b; gorse, A= 0.21, P = 0.04; kanuka, A= 0.35, P = 0.03), pitfall beetles (Fig. 2c; gorse, A = 0.21, P = 0.03; kanuka A = 0.37, P = 0.03), Lepidoptera (Fig. 2g; gorse, A= 0.25, P = 0.04; kanuka, A= 0.40, P = 0.03), bristle flies (Fig. 2f; gorse, A = 0.22, P = 0.03; kanuka, A = 0.10, P = 0.05), and Malaise trapped beetles in kanuka only (Fig. 2d; A = 0.10, P = 0.02) traps within a habitat were separated statistically by site. These results often do not correspond with the visual groupings of traps on axis one and two of the ordination.

Table 4. Recognisable taxonomic units unique to the gorse and kanuka plots. Numbers in brackets are confirmed adventive species. For beetles, Malaise and pitfall catches are combined. Only species with > 4 specimens in the data set are included.

Group	RTUs		
	Unique to gorse	Shared	Unique to kanuka
Tachinids	9	20	1
Beetles	14 (1)	70 (1)	12
Lepidoptera	13 (2)	61 (1)	4
Fungus gnats	17	81	4
Total	53 (3)	232 (2)	21

a)

b)
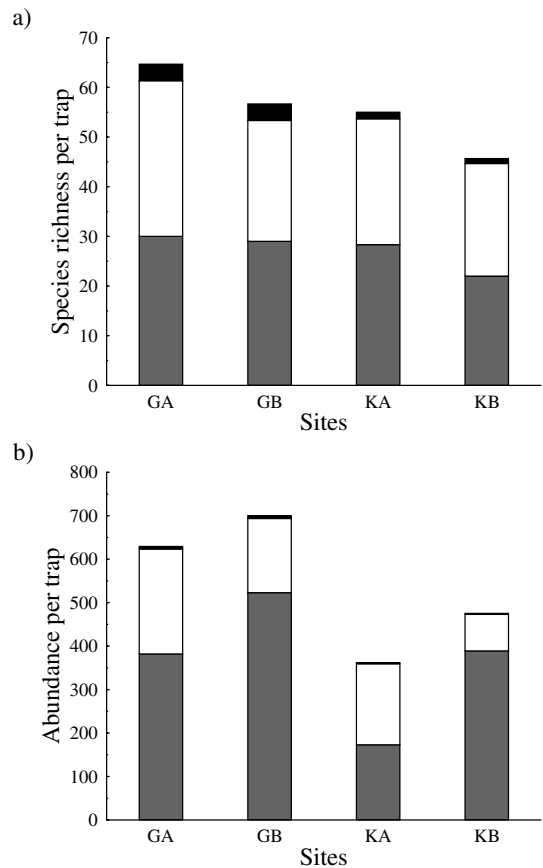
Figure 3. Guild structure of Lepidoptera: a) species in each guild; b) abundance of individuals in each guild. GA, GB = gorse sites, KA, KB = kanuka sites. ■ = detritivores, □ = herbivores, ■ = others. Data averaged across traps at each site. "Others" includes, seed, hair, spore and fungus feeders and predators.

Table 5. Nested ANOVA results comparing Coleoptera and Lepidoptera guilds between habitats (kanuka v. gorse) and between sites within habitat.

		Lepidoptera			Beetles		
		Detritivores	Herbivores	Other	Detritivores	Herbivores	Predators
Species richness							
Habitat comparison	$F_{1,2}$	1.8	1.0	169.0	1.2	0.1	324.0
	P	0.309	0.414	0.006	0.391	0.793	0.003
Sites within habitat	$F_{2,8}$	2.2	1.4	0.1	16.1	2.8	0.04
	P	0.179	0.304	0.936	0.002	0.121	0.963
Abundance							
Habitat comparison	$F_{1,2}$	1.8	1.3	144.0	3.9	259.5	2.3
	P	0.315	0.373	0.007	0.188	0.004	0.271
Sites within habitat	$F_{2,8}$	2.9	2.8	0.1	9.3	0.04	9.9
	P	0.110	0.116	0.948	0.008	0.960	0.007

Over half (52.8%) the species collected were unique to either gorse or kanuka, although 64.7% of them were taken rarely (< 5 specimens). About a quarter (24.2%) of species with > 4 specimens were unique to one habitat or the other, and few were adventive species (< 1%) (Table 4). Of the 202 species taken in both habitats and represented by > 4 specimens, over half (53.0%) were predominantly (> 80%) in one or other habitat.

The species richness and abundance of individuals within each feeding guild of Lepidoptera were similar, with the exception of the relatively small "other guild" category, that was more abundant and species-rich in gorse (Fig. 3, Table 5). There was a significantly higher abundance of herbivorous beetles, and significantly more species of predatory beetles in the gorse than kanuka. However, if the gorse seed weevil (the only abundant adventive beetle) is removed from the comparison, then significantly more herbivorous beetles were taken in kanuka than gorse ($F_{1,2} = 55.6$, $P = 0.02$). Ordinations of each guild of Lepidoptera and Coleoptera (not shown) all had a similar primary separation into gorse and kanuka groups.

Discussion

The insect assemblages sampled in gorse- and kanuka-dominated scrub were distinct, despite their geographical proximity. Many species were unique to, or much more abundant in, one habitat or the other. Gorse also contained at least as many, or more, native species than did the kanuka in all insect groups sampled, indicating the value of this adventive weed as habitat for native invertebrates.

Specific host associations

For many species, particularly among the Lepidoptera, bristle flies and beetles, larval-host associations are known (e.g. Spiller and Wise, 1982; Dugdale, 1969, 1975, 1996; Dugdale and Hutcheson, 1997). These associations may result in strong habitat preferences. Within the sampled taxa there were specialist herbivores that are strongly associated with gorse or kanuka, species that feed on other vegetation found only in one or other habitat, and specialist predators of species found in only one habitat (Table 6). Some of the species collected may occur primarily in other habitats nearby rather than the two habitats being studied (Table 6).

**Influence of habitat structure on insect assemblages**

Habitat structure rather than plant species *per se* may be of primary importance for determining the range of microhabitats present and the suitability of a habitat for particular insects (Samways and Moore, 1991). Table 6 presents some possible examples. The structure of gorse and kanuka create very different physical environments. Kanuka was taller, with a dense, even canopy that created a shaded interior. By comparison, the margins of the gorse stand were armoured, and there were large canopy gaps within the stand where light penetrated to ground level. The diverse, but generally higher-light environment of gorse may support a mix of insect species that inhabit forest and open areas. Kanuka stems are hard and tough (Roy *et al.*, 1998) and are likely to take many more years than gorse stems to break down. Its litter layer may therefore provide less suitable habitat for detritivorous insects. Species usually associated with the forest interior are more likely to occur in the low-light kanuka habitat.

Table 6. Examples of species that show strong habitat preferences between gorse and kanuka, and likely reasons for insect-plant associations.

Species	Native/ adventive	Number in gorse	Number in kanuka	Reasons and comments	Reference
Specialist herbivores					
Pyronota sp. (Coleoptera: Scarabaeidae)	Native	0	9	Feeds on kanuka/manuka leaves	Crow (2002)
Sharpius brouni (Sharp) (Coleoptera: Anthribidae	Native	65	1	Reared from gorse and *Cosprosma robusta* (only present in gorse plots)	Holloway (1982)
Exapion ulicis (Coleoptera: Brentidae)	Adventive	1259	0	Feeds on gorse seed	Hill and Gourlay (1989)
Pyroderces anarithma Meyrick (Lepidoptera: Cosmopterigidae)	Native	138	0	Feeds on bracken (present only in gorse plots)	NZAC[1] specimen label
Eutorna phaulocosma Meyrick (Lepidoptera: Depressariidae)	Native	32	2	*Rubus* specialist (recorded only in gorse plots)	NZAC specimen label
Holocola zopherana Meyrick (Lepidoptera: Torticidae)	Native	1	378	Feeds on kanuka	NZAC specimen label
Musotima nitidalis Walker (Lepidoptera: Crambidae)	Native	14	1	Feeds on bracken (present only in gorse plots)	NZAC specimen label
Pseudocoremia lupinata Felder & Rogenhofer (Lepidoptera: Geometridae)	Native	0	16	Feeds on kanuka	Spiller and Wise (1982)
Sestra humeraria Walker (Lepidoptera: Geometridae)	Native	177	13	Feeds on bracken, (present only in gorse plots)	NZAC specimen label
Specialist predators					
Proscissia cana Hutton (Diptera: Tachnidae)	Native	1112	0	Predator of *C. zealandica* (only found in gorse traps)	Valentine (1967)
Indirect associations					
Glyphipterix spp. (Lepidoptera: Glyphipterigidae)	Native	246	37	Feeds on sedges that did not occur in either habitat but were predominantly found adjacent to gorse	Spiller and Wise (1982)
Xanadoses nielseni, gen. nov., sp. nov., (Lepidoptera: Cecidosiidae)	Native	13	0	Mines frequently encountered on kamahi (*Weinmannia* spp.) that occurred nearer kanuka plots than gorse plots	Hoare and Dugdale (2003)
Habitat structure					
Costelytra zealandica (White) (Coleoptera: Scarabaeidae)	Native	14	0	Species preferring more open habitat with larvae a pasture pest and adult a generalist herbivore	Ferro (1976), Crow (2002)
Chiasmoneura fenestrata (Edwards) (Diptera: Keroplatidae)	Native	0	42	Associated with moist and sheltered microhabitats	Toft *et al*. (2001)
Isoneuromyia spp. (Diptera: Keroplatidae)	Native	381	41	Favour open canopy, scrubby habitat	RJT *pers. obs*.
Tinea fagicola Meyrick (Lepidoptera: Tineidae)	Native	0	40	Forest species reared from bark of margarodid-infested *Nothofagus*	NZAC specimen label
Elachista archaeonoma Meyrick (Lepidoptera: Elachistidae)	Native	330	20	Generalist miner of grasses found mostly at gorse sites	NZAC specimen label
Gymnobathra omphalota Meyrick (Lepidoptera: Oecophoridae)	Native	971	55	Detritivore probably utilizing gorse trunks	JSD *pers. obs*.
Trachypepla ocneropis Meyrick (Lepidoptera: Oecophoridae)	Native	226	9	Detritivore probably utilizing detritus in gorse	JSD *pers. obs*.
Capua intractana (Walker) (Lepidoptera: Torticidae)	Adventive	25	1	Detritivore probably utilizing dead leaves in gorse canopy	JSD *pers. obs*.

[1]NZAC = New Zealand arthropod collection

a)

b)
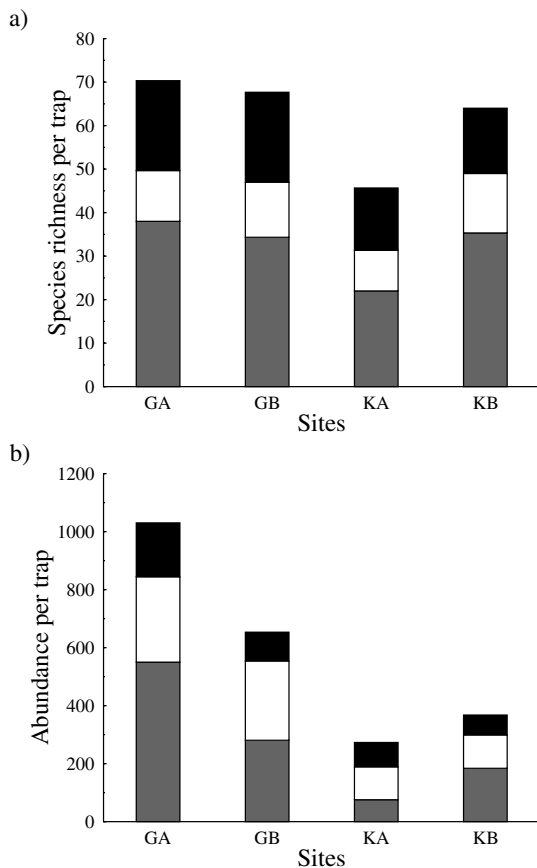
Figure 4. Guild structure of Malaise trapped beetles: a) species in each guild; b) abundance of individuals in each guild. GA, GB = gorse sites, KA, KB = kanuka sites. ■ = detritivores, □ = herbivores, ■ = predators. Data averaged across traps at each site.

The abundance of litter and dead wood in the gorse habitat was reflected in a trend towards higher abundance of detritivores in gorse than kanuka (Fig. 3 and 4). In contrast, herbivores (excluding the adventive gorse seed weevil) were more abundant in kanuka and we would predict specialist herbivores to be directly affected by the change in the landscape from kanuka-to gorse-dominated scrub.

Selected taxa as indicators of patterns

Selection of any one of the four insect groups used in this study would have identified the large assemblage differences evident between gorse and kanuka habitats.

However, conclusions about the extent of differences in species richness between habitats, and the extent of assemblage differences between sites within the gorse and kanuka habitats, differed depending on which group had been selected, and whether pitfall or Malaise trap datasets for beetles had been selected. Clearly, it would be difficult to extrapolate the findings of this study to other invertebrate groups, except to hypothesize that there would be marked community differences between the two habitats and that gorse would be suitable habitat for many other native invertebrates. Marked community differences were generally found for soil nematodes, rotifers, and copepods at the same sites (Yeates and Williams, 2001).

The rapid inventory of vegetation in ecological surveys is used in New Zealand to select representative areas worth preserving (Kelly and Park, 1986) and assumes that preservation of these sites will conserve most insects. Crisp *et al.* (1998) used pitfall-trapped beetles to test the validity of this premise and found a positive correlation between native beetle richness and the percentage of native vegetation, although modified habitat still showed relatively high diversity. Our results for a range of insect groups also showed high diversity of native insects within adventive flora, diversity which was as great as in native scrub. Evaluating the value of a site to invertebrates on the basis of high native plant diversity is clearly a flawed approach.

Value of adventive-dominated landscapes

Gorse is likely to continue to replace kanuka and manuka across the landscape due to its high reproductive potential and ability to resist grazing and regenerate rapidly after fire (Druce, 1957). If so, insect community composition is likely to be significantly altered, and species with specialised associations with kanuka scrub can be expected to disappear locally, although many other native species will remain.

Our study sites had a relatively simple vegetation structure with few plant species. Burning, firewood gathering and grazing within the sites, and clearance of the surrounding land provide continuing disturbance. Despite their simple structure and disturbance, these sites support diverse native insect assemblages. To place the species richness of these sites in context, the RTU richness of Malaise-trapped beetles and fungus gnats was compared with other studies where identical methods were used (Harris and Burns, 2000; Toft *et al.*, 2001; R. J. Harris and B. R. Burns, *unpubl.*). The gorse sites were clearly species rich, with the diversity of fungus gnats being considerably higher than in lowland forest fragments in the Manawatu, North Island (Table 7). Sampled beetle richness was similar to that in forest remnants in the Manawatu and Waikato,

Table 7. Species richness (Mean ± SE per trap, *n* in parentheses) of beetles and fungus gnats sampled in Malaise traps in gorse and kanuka habitats, and in studies in native forest remnants that used identical sampling methods and a December sampling period. The same RTU groupings have been used across the data sets.

Region and habitat		Beetles	Fungus gnats	Reference
Nelson region, gorse	Site A (3)	51.0 ± 3.0	90.3 ± 7.9	This study
	Site B (3)	48.7 ± 6.8	79.7 ± 7.9	
Nelson region, kanuka	Site A (3)	33.7 ± 1.2	54.0 ± 5.5	
	Site B (3)	42.7 ± 1.9	64.7 ± 3.9	
Manawatu region, forest fragments	Kirkwell's Bush (6)	30.5 ± 3.4	28.5 ± 3.0	Toft *et al.* (2001)
	Denton's Bush (6)	41.7 ± 5.9	31.0 ± 6.1	
	Rangiawa Bush (6)	58.3 ± 4.9	38.5 ± 1.7	
Waikato region, kahikatea (*Dacrycarpus dacrydioides*) fragments	Grazed understorey, 4 fragments (5)	41.3 ± 5.0	-	Harris and Burns (2000), Harris and Burns (*unpubl.*)
	Ungrazed, 3 fragments (9)	50.0 ± 2.4	-	
Waikato region, Pirongia forest	Kahikatea stands within intact forest (2)	47.0 ± 6.0	-	Harris and Burns (*unpubl.*)

North Island. For the fungus gnats this was surprising, since the damper darker environment of the kanuka and forest remnants was expected to support more species than the drier, more open gorse. The number of species supported by each habitat may change seasonally and over the life of the stand.

The Nelson region, upper South Island, is noted for high plant and animal species richness (Heads, 1997). Therefore, comparisons with forest remnants within the Nelson region would be needed to confirm that the relative richness of native species in our scrub habitats reflects habitat and not regional patterns of diversity. Indeed, Malaise traps set in large tracts of beech forest within the nearby Nelson Lakes National Park do appear to have a high species richness of fungus gnats (R. J. Toft, *pers. obs.*), suggesting either regional patterns may be reflected in our scrub samples, or the isolated forest fragments of the Manawatu and Waikato are in relatively poor condition.

The dominance of an ecosystem by an exotic plant species will not necessarily result in a reduction of species diversity (Sax, 2002), a contention supported by our study. The value of gorse scrub as a habitat for a wide range of native insect species [including the giant weta (Gibbs, 1999)] can be added to its value as a nursery crop that aids forest regeneration. Although some native scrub invertebrate species will be absent, the value of gorse as invertebrate habitat, and as a nursery crop for native forest regeneration, should see it promoted as a beneficial landscape feature.

Acknowledgements

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