Beetle assemblages of kahikatea forest fragments in a pasture-dominated landscape

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Abstract: Fragments of kahikatea (*Dacrycarpus dacrydioides*) forest provide a major opportunity for conservation of indigenous biodiversity in the heavily deforested landscape of the Waikato Basin, New Zealand. However, there is little documented information on what indigenous fauna survives in these fragments. Using Malaise traps set 20 m and 50 m into fragments and 20 m and 50 m into the adjacent pasture, we analysed the beetle (Coleoptera) assemblages associated with two such kahikatea forest fragments in the south Waikato Basin in order to determine the scope of biotic invasion by adventive species and use of the surrounding pasture by indigenous species. A total of 3706 beetles were caught, encompassing 37 families and 206 recognisable taxonomic units. The forest fragments had a sharply defined edge, and were dominated by indigenous beetle species, with only a few adventive species present. Beetle assemblages sampled in the surrounding pasture were numerically dominated by adventive species. Despite no indigenous plant species being present in the pastures, 55 indigenous beetles species (61% of total species sampled in the pasture) were recorded in this habitat. Traps in the pasture of greatest floral diversity caught the most indigenous beetle species. Beetles of the detritivore guild dominated the samples from forest, but in samples from pasture, detritovores and predators were co-dominant. Indigenous herbivore species were poorly represented in samples from pasture compared to other guilds. The kahikatea fragments have a rich indigenous beetle fauna and represent important refuges in the pastoral landscape of the Waikato. Many indigenous species are utilising the pasture to some degree, although their abundance and species richness declines with distance from the forest edge. This may have implications for successful dispersal to new patches. Species that could potentially be used as indicators of kahikatea forest fragment community structure and its resistance to invasion are suggested.

Keywords: Coleoptera; forest fragments; edge effects; pasture; community structure; biological diversity; indicator species.

Introduction

Fragmentation of indigenous ecosystems is of global concern for the conservation of indigenous biodiversity and ecosystem processes. Forest fragmentation has been linked to the loss of species from forest systems and alteration of ecosystem function due to loss of microhabitats, changes in the physical and chemical environment, invasive alien species, and changes in metapopulation dynamics (de Souza and Brown, 1994; Didham, 1998; Didham *et al.*, 1998). The effects of forest decline on invertebrates are not always obvious and not all species are affected equally (Darveau *et al.*, 1997; Didham *et al.*, 1998). One result of fragmentation is that remnant forest becomes surrounded by new ecosystems. At the boundary of the remnant forest and the new ecosystem the physical conditions are altered and the changed conditions can extend into the forest (Candenasso *et al.*, 1997; Burke and Nol, 1998; Didham

and Lawton, 1999). This has flow on effects for the biotic community, for example, causing tree dieback and reduced seedling abundance (Laurance *et al.*, 1997; Benitezmalvido, 1998), allowing weed invasion (Burke and Nol, 1998), altering decomposition rates (Didham, 1998), and altering species composition and guild sturcture of the insect community (Golden and Crist, 1999; Didham *et al.*, 1998). As a result, communities at the fragment edge may be intermediate between the fragment and the surrounding habitat. Small fragments can become all "edge" without any of the original miroclimates remaining resulting in greater species loss than for larger fragments (Didham *et al.*, 1998).

Although edge effects are widely accepted as impacting on the health and composition of forest fragments (Murcia, 1995), the scale of the impact on the fauna will be largely influenced by the structural integrity of the vegetation, the composition of the surrounding vegetation, and the resistance of the biotic

community to disturbance (Webb *et al.,* 1984; Camargo and Kapos, 1995; Didham and Lawton, 1999).

The Waikato basin of the North Island of New Zealand has largely been in pastoral production since the indigenous cover of forest and scrub was cleared and wetlands drained in the latter half of the 19th and early part of the 20th century (Ministry for the Environment, 1997). Before deforestation, *Dacrycarpus dacrydioides* (A. Rich.) Laubenf. (kahikatea) forest occurred on swamp-land (reflecting kahikatea's tolerance of waterlogged soils) and alluvial plains subject to flooding (reflecting a regeneration niche requiring high light and humidity) (Wardle, 1974; Duncan, 1991; 1993). In the Waikato basin, remnant forest fragments are almost all kahikatea-dominated. These fragments are of relatively even age (75-125 years old) and appear to have established around a few surviving older trees (200-450 years old) soon after the period of land clearance (Burns *et al.,* 2000). As a result of the formation or expansion of the kahikatea-dominated fragment after clearing for farming, plant species associated with the fragment are often species of moderately well-drained soils (e.g., *Beilschmiedia tawa* (Cunn.) Kirk, *Alectryon excelsus* Gaertner, *Knightia excelsa* R. Br.; Burns *et al.,* *in press*), and not necessarily wetland species, a feature exacerbated by drainage of the surrounding land (Champion, 1988).

Although common across the landscape (15 fragments per 100 km^2), the kahikatea forest fragments of the Waikato basin are small (mean 1.1 ha) (Burns *et al.*, 2000) and so represent only about 0.2% of the land area. Furthermore, the understorey vegetation of many fragments has been modified by browsing from domestic cattle. Despite their small size and often modified vegetation structure, the fragments provide the major opportunity for conservation of indigenous biodiversity in this pastoral landscape. Yet, with the exception of the flora (e.g., de Lange 1987; 1989; Whaley *et al.*, 1997), there is little documented information on what indigenous biota survives in these forests.

To determine the value of forest fragments as stores of indigenous biodiversity and identify the threats to their conservation and persistence, we need to understand their biotic composition better. In this study, beetles (Insecta: Coleoptera) were chosen for study as they represent a large component of the measurable biodiversity (Southwood, 1978) accounting for about 50% of New Zealand's insect species (Watt, 1982; Kuschel, 1990), have representatives from all trophic groups, and have been shown to associate with habitats (Hutcheson, 1990; 1996). We describe the beetles sampled within two relatively large kahikatea forest fragments and compare these with samples in surrounding pasture ecosystems, in order to determine the scope of biotic invasion by adventive species and the use of the surrounding pasture by indigenous species. Species that could be used as indicators of the current community composition of other kahikatea fragments, or to monitor habitat degradation or restoration over time are suggested.

Methods

Study sites

Yarndley's Bush is 14.5 ha and occupies the bottom of a shallow catchment, 4 km north of Te Awamutu (grid reference NZMS260 S15 135552). The forest is bisected by a drain, and comprises an eastern lobe of about 140 m by 250 m and a larger western lobe of about 250 m by 500 m (from which samples were taken). The forest had previously been browsed by cattle, but was fenced in the summer of 1980-81 (Edmonds, 1982). Kahikatea formed an almost mono-specific canopy up to 30 m over a dense understorey dominated by *Laurelia novae-zelandiae* Cunn. and *Melicytus ramiflorus* Forester et Forester f. Soils are poorly drained Puniu soils, derived from rhyolitic alluvium (M. McLeod, Landcare Research, Hamilton, N.Z., *pers. comm.*).

Pirirakau (listed as "Garrett M.A. & P.M. Open Space Covenant" in Wassilieff and Timmins, 1984) is a 6.8 ha forest 10 km east of Yarndley's (grid reference NZMS260 S15 237537). A farm road bisects the forest. About half the forest was fenced in 1968 to exclude cattle, with further sections fenced in 1981 and 1993. The canopy vegetation is up to 30 m and dominated by kahikatea, but with some *L. novae-zelandiae*. The understorey mostly comprises a dense shrub layer of *L. novae-zelandiae*, *M. ramiflorus*, and *Schefflera digitata* Forester et Forester f., although a strip 20-30 m wide at the forest edge, fenced for only 3 years, had a dense fern understorey of *Hypolepis ambigua* (A. Rich.) Brownsey et Chinnock, *Histiopteris incisa* (Thumb.) J. Smith, and *Diplazium australe* (R. Br.) Wakef. The forest occurs on Puniu silt loam (Wassilieff and Timmins, 1984).

Both forests were surrounded by grassland fields used that were grazed once a month by dairy cows. *Trifolium repens* L. and *Lolium perenne* L. were the dominant forage species amongst a range of grasses and herbs. The herb *Polygonum hydropiper* L. was also abundant. A small ditch with open water passed near the trap located 50 m into the pasture adjacent to Yarndley's Bush.

Beetle sampling

Beetle assemblages were sampled over two seasons using Malaise traps. This sampling methodology has been shown to be most representative of the underlying

beetle communities (Hutcheson, 1990; 1996; Hutcheson and Kimberley, 1999; Hutcheson *et al.*, 1999). In 1995, a line of three Malaise traps was set on the northern aspect of each fragment. These traps were placed 20 m into the fragment, and 20 m and 50 m out from the forest edge in the surrounding pasture. Traps were set with the collecting container facing north, and the screens pinned to the ground (Hutcheson, 1990). The traps were set for 4 weeks between 8 December 1995 and 4 January 1996, and cleared weekly during that period. The Malaise trap 20 m into Pirirakau is sited within the strip of vegetation fenced for only 3 years.

In 1996, Malaise traps were set 20 m into each fragments, at the same location as used in 1995, and an additional trap was placed at 50 m into each fragment. Traps were set for 4 weeks between 3 and 31 December 1996 and cleared weekly.

The collecting container fixed to the Malaise traps contained 70% alcohol as a killing and preservative agent. On return to the laboratory, the samples were stored in 70% alcohol before sorting, pinning, and identification of the beetles. Beetles were identified to species or recognisable taxonomic units (RTUs) and where possible, RTUs were categorised as indigenous or adventive (see Appendix 1), principally by reference to Kuschel (1990). Additionally, beetles were classified into functional groups (herbivores, detritovores, and predators) at family or subfamily level using the classifications of Klimaszewski and Watt (1997), Hutcheson (1996), and Didham *et al.* (1998).

Vegetation sampling

In both years, the vegetation composition and structure within each 20 x 20 m plot was described by estimating the foliage cover of all vascular plant species in fixed height tiers following the method of Allen (1992), with the collecting pottle of the Malaise trap representing the centre of each plot. All vascular plant species present were recorded and their relative abundances scored within height tiers. Species were categorised as indigenous or adventive by reference to Allan (1961), Moore and Edgar (1970), Healy and Edgar (1980), and Webb *et al.* (1988).

Analysis

Sample affinities were assessed using similarity coefficients (Bray and Curtis, 1957) and polythetic diversive classification (TWINSPAN; Hill, 1979). For the vegetation, presence-absence data from the vegetation plots was used to calculate similarity coefficients while the estimated vegetation cover was used for TWINSPAN analysis (Allen, 1992). For the beetles, the four weekly samples for each trap were combined for analysis. Similarity coefficients were calculated and TWINSPAN analysis conducted for quantitative species-abundance data and similarity coefficients also calculated for presence-absence data. Presentation of numbers of RTU's unique to habitats or sites was restricted to the most abundant RTUs, that is, those species represented by more than five specimens in the total data set.

The guild data were classified by habitat (forest and pasture) for the two sites combined and separated into an indigenous and adventive component (origin) to form a three way contingency table (habitat x guild x origin). Log-linear modelling was then used to determine whether the proportions in each guild and origin category were dependent on habitat. Differences in the total catch and number of species between Malaise trap were presented graphically. No analysis is preformed due to the non-random trap placement.

Table 1. Bray-Curtis similarity coefficients of vascular plants in 20 x 20 m plots, presence-absence data. Range from 0 for plots with no shared species to 1 for plots with identical composition. Values < 0.25 are in bold, values > 0.75 are underlined.

			Yarndley's Bush					Pirirakau				
			pasture		forest			pasture		forest		
			50m	20m	20m (1995)	20m (1996)	50m	50m	20m	20m (1995)	20m (1996)	50m
Yarndley's Bush	pasture	50m	-									
		20m	0.56	-								
	forest	20m (1995)	**0.11**	**0.13**	-							
		20m (1996)	**0.10**	**0.13**	<u>0.97</u>	-						
		50m	**0.06**	**0.08**	0.50	0.48	-					
Pirirakau	pasture	50m	0.48	0.62	**0.14**	**0.14**	0.00	-				
		20m	0.49	0.45	**0.11**	**0.10**	0.05	0.67	-			
	forest	20m (1995)	**0.02**	**0.00**	0.49	0.49	0.44	**0.00**	**0.00**	-		
		20m (1996)	**0.03**	**0.00**	0.48	0.45	0.34	**0.00**	**0.00**	<u>0.90</u>	-	
		50m	**0.00**	**0.00**	0.43	0.49	035	**0.00**	**0.00**	0.62	0.63	-

Table 2. Bray-Curtis similarity coefficients of beetle species in Malaise traps set in 20 x 20 m plots, abundance data. Range from 0 for plots with no shared species to 1 for plots with identical composition. Values < 0.25 are in bold.

| | | | Yarndley's Bush | | | | | Pirirakau | | | | |
| | | | pasture | | forest | | | pasture | | forest | | |
			50m	20m	20m (1995)	20m (1996)	50m	50m	20m	20m (1995)	20m (1996)	50m
Yarndley's Bush	pasture	50m	-									
		20m	0.65	-								
	forest	20m (1995)	**0.04**	**0.13**	-							
		20m (1996)	**0.05**	**0.14**	0.55	-						
		50m	**0.06**	**0.16**	0.49	0.64	-					
Pirirakau	pasture	50m	0.40	0.37	**0.03**	**0.04**	**0.06**	-				
		20m	0.42	0.46	**0.04**	**0.07**	**0.10**	0.66	-			
	forest	20m (1995)	**0.10**	**0.21**	0.34	0.35	0.33	**0.09**	**0.13**	-		
		20m (1996)	**0.05**	**0.14**	0.31	0.34	0.31	**0.07**	**0.07**	0.46	-	
		50m	**0.05**	**0.14**	0.44	0.49	0.64	**0.05**	**0.08**	0.44	0.41	-

Results

Vegetation

As expected, the Bray-Curtis similarity coefficients indicated that the vascular plant assemblages of the forest and pasture were very different (Table 1). The recently grazed plot 20 m into the fragment at Pirirakau was not dissimilar from the other forest plots based on presence absence data. However, it was structurally different with little vegetation in the subcanopy above two metres, and with an understorey dominated by ferns[1].

From 12 to 36% of the vascular plant species recorded in the plots within the forest fragments were adventive, but generally occurred only in low abundance. Only one forest plot had an adventive species with more than 5% cover (the succulent groundcover herb *Tradescantia fluminensis* Vell. which had a restricted distribution within Yarndley's Bush). Few of the adventive species recorded within the forests also occurred in the nearby pasture plots.

The vegetation in pasture plots at Yarndley's Bush was compositionally more diverse (32 and 18 species) than in pasture plots adjacent to Pirirakau (13 and 14 species). No indigenous vascular plant species were recorded in any of the pasture plots.

The TWINSPAN classification separated the vegetation plots at first into forest and pasture (Fig. 1a). The forest plots then classified by site. For the pasture, the plot with the ditch on its edge classified out separately to the other plots.
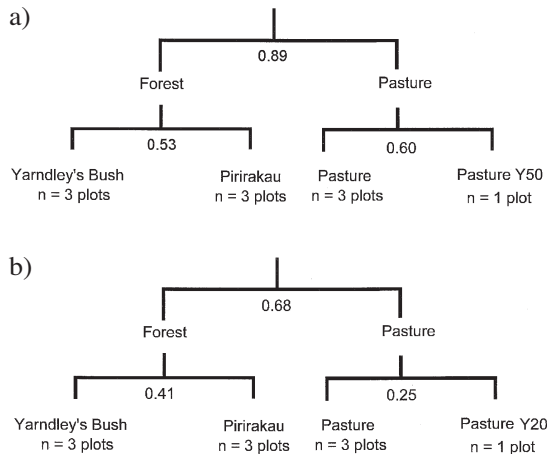
[1]List of vascular plant species recorded and beetles sampled are available on request from RJH.

Figure 1. Dendrogram of meaningful TWINSPAN divisions of a) vegetation plots and b) beetles captured in Malaise traps. The eigenvalue is a measure of the variance accounted for by the division.

Beetles

A total of 3706 beetles were captured, comprising 37 families and 206 RTUs (referred to hereafter as species)[1]. Ninety species were represented by more than five specimens. The most species-rich families in samples were Staphylinidae, Curculionidae, Corticariidae, and Corylophidae (all represented by more than 15 species). The species list obtained is clearly a sample from a much larger pool of beetle species, as evidenced by 61 (30%) of the species being represented by only a single individual in the total data set. Of these, 47 (77%) were captured from within the fragments.
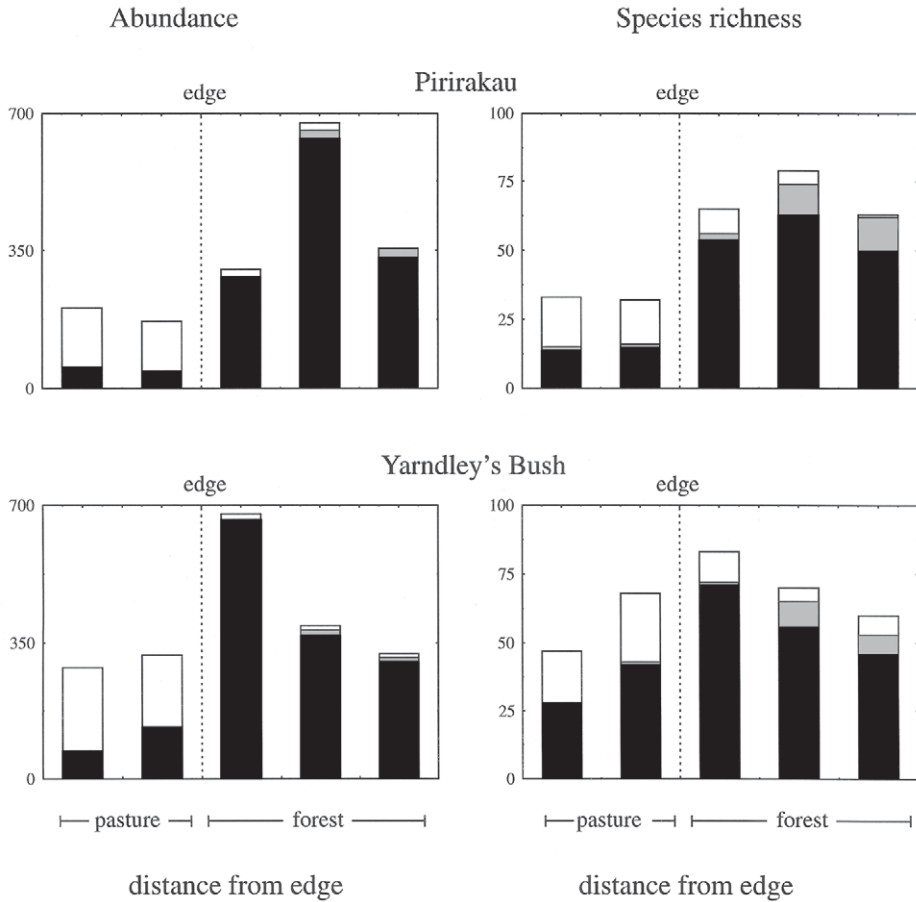
Figure 2. Abundance and species richness of beetles in Malaise traps set 20 and 50 m from the edge of the forest and adjacent pasture at Pirirakau and Yarndley's Bush. □adventive species, ▨undetermined, ■indigenous species. The number in brackets for the 20 m traps into the forest is the year of sampling.

Table 3. Bray-Curtis similarity coefficients of beetle species in Malaise traps set in 20 x 20 m plots, presence-absence data. Range from 0 for plots with no shared species to 1 for plots with identical composition. Values < 0.25 are in bold.

| | | | Yarndley's Bush | | | | | Pirirakau | | | | |
| | | | pasture | | forest | | | pasture | | forest | | |
			50m	20m	20m (1995)	20m (1996)	50m	50m	20m	20m (1995)	20m (1996)	50m
Yarndley's Bush	pasture	50m	-									
		20m	0.64	-								
	forest	20m (1995)	**0.21**	0.40	-							
		20m (1996)	**0.14**	0.30	0.60	-						
		50m	**0.18**	0.34	0.52	0.64	-					
Pirirakau	pasture	50m	0.47	0.47	**0.17**	**0.15**	**0.21**	-				
		20m	0.46	0.42	**0.10**	**0.12**	**0.19**	0.66	-			
	forest	20m (1995)	0.34	0.42	0.53	0.49	0.50	0.29	0.27	-		
		20m (1996)	**0.22**	0.38	0.50	0.52	0.53	**0.23**	**0.16**	0.64	-	
		50m	**0.18**	0.27	0.41	0.66	0.48	**0.19**	**0.17**	0.53	0.56	-

The total abundance and species richness of beetles caught in Malaise traps over the month long sampling period were similar between the two sites (Fig. 2). Malaise traps in the forest caught more beetles than those in the pasture. The total abundance of indigenous beetles was consistently high in the forest and low in the pasture. Adventive beetles were four-times more abundant in the pasture traps than in the forest traps.

The composition of the beetle assemblages in the forest and pasture differed, with dissimilarity being greatest for abundance data (Tables 2, 3). The two plots within each fragment sampled in two consecutive years showed large variation in the total abundance of beetles caught between years (Fig. 2).

The TWINSPAN classification of the beetles from traps was very similar to the vegetation, separating first by habitat (pasture verses forest) then between sites for traps within the forest (Fig. 1b). The composition of the beetle assemblage sampled at the recently browsed plot 20 m into the fragment at Pirirakau was more similar to that sampled at other forest plots than those sampled in the pastures. In the pasture the trap at Yarndley's Bush 20m from the fragment (which had the highest diversity of indigenous beetles) separated from the other traps in the pasture.

Species richness was higher in samples from forest than in samples from pasture (Fig. 2). Species richness among indigenous beetles was higher within the forest while species richness among adventive beetles was higher in samples from the pastures. Few adventive beetles were recorded in Malaise trap samples within the forest and their richness and abundance tended to decrease from 20 to 50 m into the fragment (Fig. 2). Likewise, indigenous species richness and abundance was considerably lower 20 m outside the fragments

compared with 20 m into the fragment, and species richness tended to be further reduced at 50 m compared with 20 m.

Abundant species

Forest fragments were numerically dominated by indigenous species (Table 4). Of the abundant indigenous species (n > 5), 52 were recorded in samples from both fragments, with Pirirakau and Yarndley's Bush having only three and six unique species respectively.

Samples from the pasture were numerically dominated by adventive species, but several indigenous species were also abundant (Table 5). Three abundant indigenous species were only recorded in pasture plots. The traps in pasture plots at Yarndley's Bush and Pirirakau had similar numbers of adventive species (Fig. 2). Of the abundant adventive species, 16 occurred in samples from both pastures, and three were present in samples at only one site or the other. The main difference between the beetle assemblages in pasture at Yarndley's Bush, compared with those in pasture at Pirirakau, was the greater number of abundant indigenous species with at least one individual in the pasture (28 verses 13 species).

Of the 62 abundant indigenous species recorded within forest fragments, 48% were also recorded in the surrounding pastures, but this decreased with distance into the pasture habitat (41% at 20 m, 29% at 50 m).

Guild structure

The only analysis which fitted the data well was a saturated model, including a three-way interaction

Table 4. The ten most abundant beetle species from Malaise trap samples 20 and 50 m into Pirirakau and Yarndley's Bush (mean ± SE) and the comparative catch of those species in pasture 20 and 50 m from the forest edge.

Family	Taxon	Guild[1]	Origin	Abundance			
				Pasture		Forest	
Corylophidae	*Sacina oblonga* Broun	P	indigenous	2.5 ± 2.5		109.5 ± 24.9	
Corticariidae	*Bicava illustrus* (Reitter)	D	indigenous	0.8 ± 0.8		33.0 ± 21.7	
Chrysomelidae	*Eucolaspis* spp.	H	indigenous?	9.5 ± 3.0		30.3 ± 4.7	
Corticariidae	*Melanophthalma zelandica* Belon	D	indigenous	1.8 ± 1.4		21.7 ± 15.1	
Corylophidae	*Holopsis nigellus* Broun	P	indigenous	0.0 ± 0.0		16.7 ± 4.4	
Elateridae	*Panspoeus guttatus* Sharp	H	indigenous	0.3 ± 0.3		14.3 ± 7.5	
Coccinellidae	*Rhyzobius ?acceptus* (Broun)	P	indigenous	1.3 ± 0.9		14.3 ± 10.1	
Leiodidae	*Paracatops lugubris* (Sharp)	D	indigenous	0.0 ± 0.0		11.0 ± 5.4	
Curculionidae	*Andracalles horridus* (Broun)	H	indigenous	0.0 ± 0.0		10.3 ± 3.7	
Corticariidae	*Melanophthalma* sp. 1	D	indigenous?	0.0 ± 0.0		7.2 ± 2.3	
Cryptophagidae	*Micrambina obscura* Broun	D	indigenous	0.3 ± 0.3		7.2 ± 2.5	
			Contribution to total sample (%)	6.6		60.5	

[1]P= predator, D = detritovore, H = herbivore.

Table 5. The ten most abundant beetle species from Malaise trap samples 20 and 50 m into pasture from the edge of Pirirakau and Yarndley's Bush (mean ± SE) and the comparative catch of those species for traps 20 and 50 m into the forest fragments.

Family	Taxon	Guild[1]	Origin	Abundance Pasture			Forest		
Corticariidae	*Cortinicara hirtalis* (Broun)	D	adventive	31.5	±	3.2	0.7	±	0.7
Elateridae	*Conoderus exsul* (Sharp)	H	adventive	28.5	±	10.3	0.7	±	0.5
Carabidae	*Notagonum submetallicum* (White)	P	adventive	25.8	±	10.9	0.0	±	0.0
Staphylinidae	*Philonthus pyropterus* Kraatz	P	adventive	13.3	±	2.9	0.0	±	0.0
Corticariidae	*Cortinicara meridiana* Johnson	D	adventive	11.8	±	7.4	1.0	±	0.6
Brentidae	*Exapion ulicis* (Forster)	H	adventive	11.8	±	4.2	0.3	±	0.2
Coccinellidae	*Adalia bipunctata* (L.)	P	adventive	11.0	±	2.8	0.0	±	0.0
Mordellidae	*Zeamordella monacha* Broun	P	indigenous	9.5	±	3.8	0.0	±	0.0
Chrysomelidae	*Eucolaspis* spp.	H	indigenous?	9.5	±	3.0	30.3	±	4.7
Corylophidae	*Anisomeristes thoracicus* (Erichson)	P	adventive	8.3	±	4.2	1.5	±	0.7
			Contribution to total sample (%)	66.5			7.6		

[1]P= predator, D = detritovore, H = herbivore.

term (habitat*guild*origin) (χ^2 = 17.82, d.f. = 2, *P* = 0.0001). This indicates that not only were there different proportions of each guild and origin categories in the two habitat types, but also that different proportions of indigenous and adventive beetles occurred in the two habitats (Table 6). Within the forest remnants, detritivores were more abundant than herbivores and predators (Table 6). The adventive species present in samples from forest were also predominantly detritivores. In pasture, there were fewer detritivores and higher relative abundance of predators (Table 6). Indigenous species of all guilds were present in the pasture, but they were least represented by herbivores.

Discussion

Very low numbers of adventive beetle species were sampled within the forest fragments, even at Pirirakau where the trap at 20 m was in an area retired from cattle browse only 3 years before sampling. This suggests that the indigenous beetle communities of these

Table 6. Comparison of guild structure of indigenous and adventive beetles in Malaise trap samples from a) pasture and b) forest plots. Pirirakau and Yarndley's Bush total abundance data combined. Values represent means across all traps within that habitat.

Habitat	Guild	% Composition Endemic	Adventive
Pasture	Predators	9.3	28.3
	Herbivores	5.2	16.7
	Detritivores	15.4	25.1
Forest	Predators	12.4	0.3
	Herbivores	20.7	0.5
	Detritivores	64.0	2.1

fragments have a high resistance to invasion and/or the forests were not suitable habitat for the adventive species that were dominant in the samples from the adjacent pasture. A feature of these forests that may have contributed to the maintenance of an indigenous-dominated beetle assemblage is the intact, closed canopy of these even-aged kahikatea stands and the presence of branches and foliage down to low levels on the edge of the stands. This structure apparently kept light levels within the forest low and may have helped prevent the invasion of pasture plant species beyond the forest edge. Murcia (1995) reported that edges with the least lateral protection exhibit the greatest changes in microclimate (air temp, humidity, soil moisture, light intensity) within the fragment. There was very little commonality in the adventive plant species recorded in the forest and pasture plots, and so it follows that there has been little movement of any of the host-specific component of the adventive beetle assemblage associated with the pasture into the fragment.

The kahikatea remnants represent a likely expansion of forest about a few surviving trees after a period of land clearance 80-120 years ago (Burns *et al.,* 2000), and both forest fragments sampled in this study had previously been impacted through cattle browse of the understorey. As a result, these fragments will likely have had beetle species losses, and the fauna resident today may be a mix of those that remained in the fragments after clearance and those that subsequently dispersed to the expanding forest. Comparison with assemblages within larger tracts of forest that have not undergone such fragmentation would be needed to determine those beetle species that may be missing. However, in the Waikato such undisturbed lowland systems do not occur.

Hutcheson (1996) conducted sampling using similar methods in a large tract of *B. tawa* forest in the

Onaia Ecological Area, north of Lake Rotorua in the central North Island. The nine Malaise traps used by Hutcheson at Onaia caught between 140 and 430 individuals and between 52 and 99 RTUs for a 4-week sample period in December. Trap catches from the fragments in the present study were higher, i.e., between 301 and 678 individuals, but numbers of RTUs were similar (between 57 and 83) for a comparable sampling period. If adventive beetles are removed from the data set, the species richness is still comparable to Hutcheson's study (between 54 and 75 RTUs). By contrast, the richness of indigenous species in traps placed a short distance from the fragments edge was much lower (between 13 and 40 RTUs), similar in species richness to samples collected by Hutcheson and Jones (1999) over a comparable sampling period in *Pinus radiata* plantation (< 30 RTUs (adventive and indigenous combined)).

Despite their disturbance history, the Yarndley's Bush and Piririkau fragments appear to have a rich indigenous beetle fauna and represent important refuges of native biodiversity in a landscape dominated by adventive species. The beetle assemblages from the two forest fragments were quite similar, although nine abundant species were unique to one site or the other and many other unique species were only sampled in low abundance. More sampling within these fragments may reveal other unique components within each fragment, increasing their levels of complementarity. Sampling is also needed in smaller, more degraded fragments common throughout the Waikato Basin to determine where along a degradation gradient adventive beetle fauna begin to dominate. In addition, a reduction in vegetation diversity may be concomitant with reduced beetle diversity (Crisp *et al.*, 1998). Sampling in forest remnants dominated by different vegetation associations within the Waikato Basin would indicate if there is a distinctive component of the beetle community associated with kahikatea fragments.

A relatively high proportion of indigenous species recorded within the forest fragments were also recorded in the surrounding pastures, but this decreased with distance into the pasture habitat. Furthermore, abundance of indigenous species was low in pasture relative to that in the forests. Crisp *et al.* (1998) also found low diversity of indigenous beetles in pasture. This means that there are probably no resident populations of many of the indigenous species in the pasture, but dispersal by some beetle species into the surrounding habitat from the fragments occurs. Further sampling at greater distances from fragments and over the entire season is needed to determine the proportion of the indigenous beetle species capable of moving large distances into the pastoral landscape, enabling colonisation of isolated forest habitats. Dispersal limitations will have consequences for the establishment

of beetle species in new habitats (e.g., created through revegetation) and possible the persistence of some species in isolated fragments undergoing disturbance events (Devries *et al.,* 1996; Burke and Goulet, 1998; Haddad, 1999).

Didham *et al.* (1998) found fragmentation significantly changed species composition, but did not result in a reduction in biodiversity. Rather there was a change in species dominance, with species found within dense undisturbed forest becoming rare, and gap specialists and disturbance-tolerant species becoming abundant. The large reduction in the total forested area in the Waikato has likely reduced the total species diversity across the landscape, as reduction in patch size results in species losses, even when the fragments are large (100ha) (Turner 1996; Didham *et al.,* 1998). Those species remaining in small fragments are likely to be less sensitive to edge and area effects (Didham *et al.*, 1998). As a result of the fragmentation process and dispersal limitations, the remaining beetle species assemblages will probably vary between fragments resulting in unique communities worthy of protection (Turner and Corlett, 1996).

Despite a complete lack of indigenous plants in the pasture plots, 54 indigenous beetle species were either resident or dispersing through that habitat. This represents 60% of the species sampled in the pasture, and includes representatives of 43% of the indigenous species recorded (although their abundance was low compared to the fragment). This may mean that many of the species still surviving in the fragments after 80-120 years are either good dispersers, or highly disturbance adapted forest species able to utilise the surrounding habitat, at least to some degree. However, herbivores, which generally exhibit the greatest association with particular plant species, were poorly represented in the Malaise trap catches from the pasture plots. For other guilds, the diversity of the pasture system may dictate how many species of indigenous beetles will move out of the forest, as plots with the greater number of adventive plant species had more indigenous beetles species.

Malaise-trapped beetles could potentially be used as indicators of habitat quality in this system. The larger the suite of species that are used as indicators the more powerful will be the ability to discriminate habitats and communities. However, identification and analysis of the entire beetle assemblage captured in a series of Malaise traps is a very time-consuming process and may not be necessary to address a particular hypothesis. For species to be useful indicators they would need to be relatively easy to identify and show strong fidelity for particular ecosystem types. Some potential candidates from the present data set that meet these criteria are suggested in Table 7. These species could be used in combination as indicators of the resistance

Table 7. Visibly distinguishable species of beetle from Malaise trap samples in kahikatea forest and surrounding pasture which could be used together as indicators of habitat resistance and changes in the status of that habitat over time.

Family	Taxon	Guild[1]	Origin	Trapped in pasture (Mean ±SE)			Trapped in forest (Mean ±SE)		
Forest species									
Corylophidae	*Sacina oblonga* Broun	P	indigenous	2.5	±	2.5	109.5	±	24.9
Corticariidae	*Bicava illustrus* (Reitter)	D	indigenous	0.8	±	0.8	33.0	±	21.7
Corylophidae	*Holopsis* spp.	P	indigenous?	0.0	±	0.0	29.0	±	7.2
Coccinellidae	*Rhyzobius* spp.	P	indigenous	1.8	±	1.1	26.7	±	14.6
Elateridae	*Panspoeus guttatus* Sharp	H	indigenous	0.3	±	0.3	14.4	±	7.5
Leiodidae	*Paracatops lugubris* (Sharp)	D	indigenous	0.0	±	0.0	11.0	±	5.4
Anthribidae	*Androporus discedens* (Sharp)	D	indigenous	0.0	±	0.0	6.0	±	1.8
Curculionidae	*Rhopalomerus tenuirostris* Blanchar	H	indigenous	0.8	±	0.5	5.8	±	2.5
Salpingidae	*Salpingus bilunatus* Pascoe	P	indigenous	0.3	±	0.3	5.5	±	1.7
Cerambycidae	*Spilotrogia fragilis* (Bates)	D	indigenous	0.0	±	0.0	3.7	±	0.2
Anobiidae	*Ptinus speciosus* Broun	D	indigenous	0.0	±	0.0	3.3	±	1.5
Anthicidae	*Sapintus pellucidipes* (Broun)	D	indigenous	0.3	±	0.3	3.2	±	1.4
Anthribidae	*Pleosporius bullatus* (Sharp)	D	indigenous	0.3	±	0.3	2.7	±	1.0
Nemonychidae	*Rhinorhynchus rufulus* (Broun)	H	indigenous	0.0	±	0.0	2.3	±	0.9
Curculionidae	*Omoeacalles crisioides* (Broun)	H	indigenous	0.0	±	0.0	2.2	±	1.1
Corticariidae	*Enicmus foveatus* Belon	D	indigenous	0.3	±	0.3	1.8	±	0.5
	% of total catch in that habitat			3.1			56.4		
Pasture species									
Elateridae	*Conoderus exsul* (Sharp)	H	adventive	28.5	±	10.3	0.7	±	0.5
Carabidae	*Notagonum submetallicum* (White)	P	adventive	25.8	±	10.9	0.0	±	0.0
Staphylinidae	*Philonthus pyropterus* Kraatz	P	adventive	13.3	±	2.9	0.0	±	0.0
Brentidae	*Exapion ulicis* (Forster)	H	adventive	11.8	±	4.2	0.3	±	0.2
Coccinellidae	*Adalia bipunctata* (L.)	P	adventive	11.0	±	2.8	0.0	±	0.0
Mordellidae	*Zeamordella monacha* Broun	P	indigenous	9.5	±	3.8	0.0	±	0.0
Coccinellidae	*Coccinella undecimpunctata* L.	P	adventive	4.8	±	0.6	0.0	±	0.0
Nitidulidae	*Carpophilus marginellus* Motschulski	H	adventive	3.3	±	1.8	0.0	±	0.0
	% of total catch in that habitat			44.1			0.2		

[1]P= predator, D = detritovore, H = herbivore.

of a kahikatea forest fragment to invasion. The assumption is that if adventive beetle species (found predominantly in samples from pasture in this study) comprise a significant component of a forest fragment community, then that fragment has lost its resistance to invasion. Alternatively, the success of a restoration project could be judged by the occurrence of the indigenous forest-inhabiting species at the restoration site and corresponding reduction in adventive species. Dispersal limitations could be investigated by determining movement patterns of a subset of forest species. However, reduction of the sample set can lead to misinterpretations (Hutcheson *et al.,* 1999), and further sampling would be needed in a range of intact and degraded fragments to confirm that the suggested subset of the trap catch has general applicability. In other systems where the distinction between habitats is less distinct this approach would be more difficult.

With the dramatic loss of lowland indigenous habitats that has occurred in the Waikato basin, protection of the integrity of those indigenous habitats that remain, and the restoration and creation of new habitats, are of vital importance to protect indigenous biodiversity as the Waikato Basin landscape will continue to be dominated by adventive vegetation. Further research is clearly needed to understand how management of indigenous habitats impacts on the invertebrate community.

Acknowledgements

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