

New Zealand Journal of Forestry Science

Effects of land cover type on carabid beetles (Coleoptera: Carabidae) of the Canterbury foothills, New Zealand

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(Received for publication 27 April 2019; accepted in revised form 23 December 2019)

Abstract

Background: Land cover changes during the recent history of New Zealand have had a major impact on its largely endemic and iconic biodiversity. As in many other countries, large areas of native forest have been replaced by other land cover and are now in exotic pasture grassland or plantation forest. Ground beetles (Carabidae) are often used as ecological indicators, they provide ecosystem services such as pest control, and some species are endangered. However, few studies in New Zealand have assessed the habitat value for carabid beetles of natural forest, managed regenerating natural forest, pine plantation forest and pasture.

Methods: We compared the carabid beetle assemblages of natural forest of *Nothofagus solandri* var *solandri* (also known as *Fuscospora solandri* or black beech), regenerating *N. solandri* forest managed for timber production, exotic pine plantation forest and exotic pasture, using pitfall traps. The study was conducted at Woodside Forest in the foothills of the Southern Alps, North Canterbury, New Zealand, close to an area where the critically endangered carabid *Holcaspis brevicula* was found.

Results: A total of 1192 carabid individuals from 23 species were caught during the study. All but two species were native to New Zealand, with the exotic species present only in low numbers and one of these only in the pasture habitat. Carabid relative abundance and the number of species was highest in the pine plantation, where a total of 15 species were caught; however, rarefied species richness did not differ significantly between habitats. The sampled carabid beetle assemblages were similar across the three forested habitat types but differed significantly from the pasture assemblages based on unconstrained and canonical analyses of principal coordinates. *Holcaspis brevicula* was not detected in this area.

Conclusions: Our results show that managed or exotic habitats may provide habitat to species-rich carabid assemblages although some native species occur only in natural, undisturbed vegetation. Nevertheless, it is important to acknowledge the potential contribution of these land uses and land cover types to the conservation of native biodiversity and to consider how these can be managed to maximise conservation opportunities.

Keywords: biodiversity, Carabidae, community composition, exotic, forest, *Fuscospora*, landscape ecology, native, *Nothofagaceae*, pasture, *Pinus radiata*

Introduction

As in many other parts of the world, forest loss and fragmentation had a considerable impact on New Zealand's forests. Approximately two thirds of the original area of native forest has been lost since human

arrival (McGlone 1989) ca. 750 yr ago (Wilmshurst et al. 2008). Lowland forests that have a particularly rich biodiversity have experienced the greatest losses and are under-represented in the conservation estate, and species of *Nothofagaceae* (southern beech) are now

the most common canopy species, especially at higher elevation (Wardle 1984; Wiser et al. 2011). Today, exotic grassland used for pastoral agriculture covers more than 50% of New Zealand's land area while plantation forests (largely based on *Pinus radiata* D. Don which is native to California) represent ca. 7% (Leathwick et al. 2003). Although there is no further decline in the area of natural forest in New Zealand, globally natural forests are still declining, while the plantation forest area is increasing (Brockerhoff et al. 2013; Payn et al. 2015). New Zealand's plantation forests are the basis of an economically important industry (MPI 2019), they are an important carbon sink (Beets & Garrett 2018) and provide a range of other ecosystem services (e.g. Brockerhoff et al. 2013). New Zealand's native forests are largely protected and part of a large conservation estate, although a small proportion is privately owned and in part managed for timber production (e.g. Allen et al. 2012; Ganivet et al. 2017). With increasing national and international focus on the protection of biodiversity on managed and private land (Norton 2000; Brockerhoff et al. 2001), a greater understanding is required of the role of production land, including managed native forest, plantation forest and agricultural land, in the conservation of native biodiversity.

Although the canopy tree species of New Zealand's plantation forests are exotic in origin, these forests can support a diverse suite of native flora and fauna, including rare species such as kiwi, New Zealand falcon, long-tailed bat and various orchids (Brockerhoff et al. 2003; Pawson et al. 2010). Plantation forests may also support various native invertebrates (Hutcheson & Jones 1999; Berndt et al. 2008; Pawson et al. 2008), including a critically endangered carabid beetle (Brockerhoff et al. 2005). However, there is a paucity of studies that have compared invertebrate biodiversity in a variety of production land uses and managed and unmanaged natural vegetation.

Compared to plantation forests, exotic grassland used for pastoral agriculture appears to be less suitable for native species which are adapted to the previously dominant forest environment (e.g. Kuschel 1990). Some native invertebrates are present or even very abundant in pasture (Crisp et al. 1998; Berndt et al. 2008). In some cases species from adjacent native forest or shrubland may spill over into pasture (e.g. Derraik et al. 2005; Pawson et al. 2008). By contrast, native tussock grasslands support a large suite of native invertebrates, some of which also inhabit improved pasture (Rufaut 2002). In a study in the central North Island, native forest and adjacent pine plantations and exotic grassland were found to have approximately similar species richness of native beetles (including Carabidae and two other families) but native forest had by far the lowest proportion of non-native species (Pawson et al. 2008). Carabid beetles are frequently used as indicators of environmental change and condition (Butterfield et al. 1995; Ferris & Humphrey 1999; Rainio & Niemelä 2003) and they are known to provide ecosystem services such as pest and weed control (e.g. Kulkarni et al. 2015). New Zealand carabids are generally nocturnal and flightless,

with 92% (391) of species being endemic to the country or certain regions of New Zealand (Laroche & Larivière 2001). Furthermore, a number of New Zealand carabids are threatened, including the critically endangered *Holcaspis brevicula* Butcher which is only known to occur in the former Eyrewell Forest on the Canterbury Plains ca. 20 km southeast from the area where the present study was carried out (Brockerhoff et al. 2005). The carabids of the foothills of the Southern Alps are not well studied, and there was uncertainty whether the range of *H. brevicula* extends beyond the Canterbury Plains into the adjacent foot hills.

The objective of this study was to compare the carabid beetle assemblages of natural Nothofagaceae forest (here *Nothofagus solandri* var. *solandri* (Hook. f.) Poole, also known as *Fuscospora solandri* (Hook.f.) Heenan & Smissen, or 'black beech'), regenerating *N. solandri* forest managed for timber, exotic pine plantation forest and exotic grazed pasture to examine the response of these beetles to different land use and land cover types. In addition, this study also acted as a survey for the critically endangered *Holcaspis brevicula* in an area of the Canterbury foothills that is the closest larger native forest about 20 km from where *H. brevicula* has been found in the past.

Methods

This study was conducted at Woodside Forest (lat. 43.26 S, long. 172.06 E; elevation 400–550 m) and adjacent parts of Oxford Forest Conservation Area (elevation ca. 550 m) in the Canterbury Foothills (Fig. 1). Mean annual rainfall in the area is ca. 1300 mm. Woodside Forest is a 121 ha privately owned property, managed primarily for timber production. Seventy percent of the property is in black beech (Novis et al. 2003), the natural native forest type of the area (Wardle, 1984). Much of this is managed for timber production under a government-approved Sustainable Forest Management Plan, with harvesting systems designed to mimic natural stand replacement (Novis et al. 2003). Another quarter of the property is in exotic conifer plantations of various species (Novis et al. 2003). Interspersed with the forest are clearings of grazed exotic pasture. The neighbouring Oxford Forest is an 11,000-ha natural forest managed by the Department of Conservation (DOC). The forest type is mainly black beech at low altitudes, grading to mountain beech (*N. solandri* var. *cliffortioides*, also known as *Fuscospora cliffortioides* (Hook.f.) Heenan & Smissen) above 600 m (Wardle 1984).

The Oxford Forest area was logged for timber from 1851, with the Woodside Forest property logged between 1895 and 1909. A number of fires in the latter half of the 19th century destroyed most of the forest, and timber production in the area ceased in 1915 (Novis et al. 2003). Areas of unmanaged natural beech on the Woodside Forest property, as well as adjacent parts of Oxford Forest, regenerated after a major fire in 1898. Other parts of the property were managed for sheep grazing from 1914. After the 1930s, grazing was reduced and more land reverted to beech. The present management

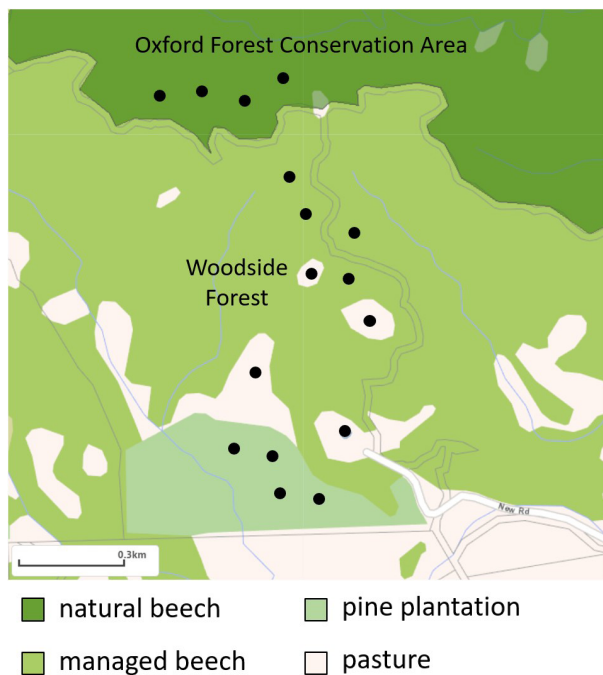


FIGURE 1: Map of the study area at Woodside Forest (latitude 43.26 S, longitude 172.06 E; elevation 400–550 m) and adjacent parts of Oxford Forest Conservation Area. The area is ca. 20 km northwest from the former Eyrewell Forest where *Holcaspis brevicula* was found in previous studies. Each dot represents the approximate location of one replicate group of five pitfall traps.

was initiated in 1973, when the area of regenerating beech was increased and managed for wood production, and exotic plantations were established (Novis et al. 2003).

Four habitat types were compared in this study: ‘natural beech’ forest (at least 100 years old, in Woodside Forest and adjacent parts of Oxford Forest); ‘managed beech’ (approximately 30 yr old, naturally regenerating and managed for timber production); ‘pine’ plantation (ca. 30-year-old *Pinus radiata*, managed for timber production); and grazed ‘pasture’. Five pitfall traps were installed in each of four replicates of each habitat on 25–26 November 2004. Pitfall traps were made from 750 ml polypropylene cups, installed such that the opening (diameter 110 mm) was level with the surrounding surface. To increase trap efficiency, two white intersecting guide panels (1.2 m long × 0.1 m high) were installed over the pitfall traps such that there was no gap between the panels and the ground. A white plastic rain cover (150 × 150 mm), held down with large pebbles, was placed on top of the guide panels above the trap opening. Traps were filled with about 200 mL of trapping solution (70% water, 30% monoethylene glycol as preservative, with ca. 1 g salt and a large drop of soap added; salt acted as an additional preservative in case rain diluted the solution, and soap assisted with invertebrates sinking

into the liquid). Traps were cleared and reset monthly on 20–22 December 2004 and 25–26 January 2005, and the final collection was on 15–16 February 2005. All carabid specimens were transferred to 70% ethanol and later sorted to morphospecies for subsequent identification using various keys, named museum specimens, and specialist advice (see acknowledgements).

The effect of habitat type and sampling date on log+1 transformed mean carabids per 100 trap days per plot were tested using ANOVA. Tukey’s HSD test was used for pairwise comparisons. The effect of habitat type on the relative proportions of the two most abundant species, *Holcaspis intermittens* (Chaudoir) and *H. hudsoni* Britton, was analysed using a Generalised Linear Model (GLM) with a binomial error distribution, using backward stepwise selection. As this model was over-dispersed, significance testing was conducted using F-tests rather than χ^2 tests. These analyses were performed using R version 1.9.1 (R Development Core Team 2004).

Carabid species richness in each habitat was compared using sample-based rarefaction curves (EstimateS 7.0.0; Colwell 2004), re-scaled to show individuals on the x-axis (Gotelli & Colwell 2001)). This comparison was made by bisecting the rarefaction curves at the smallest total number of individuals caught in any habitat (i.e. at the end point of the natural beech curve). Species associated with each habitat were identified using the indicator species analysis of Dufrêne and Legendre (1997), carried out in PC-ORD 4.01 (McCune & Mefford 1999). This indicator species analysis method identifies indicator species that are characteristic of groups’ sites (such as habitat types), combining relative abundance data of species with their relative frequency of occurrence in the various groups of sites. Statistical significance of species indicator values is calculated based on a randomisation method (Dufrêne & Legendre 1997). Unconstrained principal coordinates analysis (PCoA) and constrained (or canonical) principal coordinates analysis (CAP) were performed using the CAP programme (Anderson 2003) to explore relationships among the carabid assemblages of the four habitat types. Chi-squared distances were used in the ordination to emphasise differences in composition (Quinn & Keough 2002; Anderson & Willis 2003). The unconstrained analysis was used to highlight overall patterns across the data cloud, whereas the constrained analysis imposed *a priori* habitat groupings, allowing location differences among groups to be seen more clearly because important ecological patterns can be masked in unconstrained PCoA, as explained in Anderson and Willis (2003). The null hypothesis of no difference in multivariate location among habitat types was tested by calculating the trace statistic of canonical discriminant analysis and obtaining a *P*-value (4999 permutations) (Anderson & Willis 2003). Gaussian bivariate ellipses (probability 0.95) were fitted to illustrate groupings by habitat).

Results

A total of 1192 carabids from 23 species were caught during this study. *Holcaspis brevicula* was not detected, but four other species of *Holcaspis* were found (Table 1).

TABLE 1: Species composition and abundance (carabids per 100 trap days), indicator values (see footnote) for the four habitat types, and total number of individuals and species caught in each habitat.

Species	Origin**	Mean beetle abundance (IndVal)			
		Natural beech	Managed beech	Pine plantation	Pasture
<i>Amarotypus edwardsii</i>	N	0.32 (25*)			
<i>Anchomenus ?integratus</i>	N	0.64 (3)		0.67 (2)	
<i>Cicindela parryi</i>	N	0.64 (0)	0.41 (3)	0.42 (3)	3.44 (55*)
<i>Demetrida dieffenbachii</i>	N			0.67 (0)	1.25 (48*)
<i>Dicrochile whitei</i>	N		0.59 (2)	0.67 (2)	0.59 (2)
<i>Haplanister crypticus</i>	E		0.59 (2)	0.67 (2)	0.59 (2)
<i>Holcaspis angustula</i>	N	0.54 (20*)			
<i>Holcaspis elongella</i>	N	0.32 (6)	0.59 (1)	0.12 (2)	
<i>Holcaspis hudsoni</i>	N	2.36 (4)	3.67 (8)	22.42 (78*)	0.24 (0)
<i>Holcaspis intermittens</i>	N	7.55 (37)	9.59 (43*)	2.42 (8)	0.65 (1)
<i>Hypharpax australis</i>	E				0.12 (10)
<i>Mecodema fulgidum</i>	N	0.13 (1)	0.89 (16)	0.12 (1)	
<i>Mecodema ?rectolineatum</i>	N	0.32 (8)	0.30 (6)	0.12 (2)	
<i>Mecyclothorax rotundicollis</i>	N				6.11 (60*)
<i>Megadromus antarcticus</i>	N	0.64 (0)	1.66 (26)	1.38 (17)	1.68 (11)
<i>Megadromus n. sp. 1[#]</i>	N	0.32 (6)	0.72 (17)		
<i>Notagonum feredayi</i>	N			0.67 (3)	0.59 (2)
<i>Pentagonica vittipennis</i>	N	0.64 (2)	0.59 (2)	0.67 (2)	
<i>Scopodes fossulatus</i>	N		0.12 (1)	0.67 (0)	0.89 (33*)
<i>Selenochilus syntheticus</i>	N	0.64 (5)			
<i>Syllectus anomalus</i>	N				0.59 (5)
unknown sp.	?				0.59 (5)
<i>Zabronothus striatulus</i>	N			0.12 (10)	
Total individuals		200	297	458	237
Total species		13	12	15	13
Exotic species		0	0	0	1-2

* IndVal (indicator values) significant at $P < 0.01$

** Origin: N = native, E = exotic, ? = origin unknown

[#] an undescribed species known as "*Megadromus n. sp. 1*" that is relatively common in upland Nothofagaceae forest in this area (Peter Johns, pers. comm.). This is one of four species of *Megadromus* known from Nothofagaceae forests in the North Canterbury foothills between Mt. Oxford and Mt. Grey, the others being *M. antarcticus* (widespread in Canterbury), *M. rectangulus* (to the east from Mt Grey to Motunau Island, and the lowlands from Ashley, Rangiora, and Waipara north), and another undescribed species "*Megadromus n. sp. 2*" which occurs in Nothofagaceae forest between Ashley Gorge and Mt Grey (Peter Johns, pers. comm.).

Exotic species were present only in the pasture habitat, in very low numbers. Two individuals of the Australian species *Hypharpax australis* (Dejean) were caught in pasture, along with one individual of an unidentified species that is almost certainly exotic (Peter Johns pers. comm. 2005). Carabid relative abundance in pitfall traps was significantly affected by habitat type ($F = 3.368$, $df = 3$, $P = 0.022$), and carabids were most abundant in the pine plantation habitat. Tukey's pairwise comparisons indicated a significant difference in abundance between pine plantation and pasture, but no significant differences between these habitats and the natural or managed

beech habitats (Fig. 2). Sampling date had no significant effect on carabid relative abundance ($F = 2.843$, $df = 2$, $P = 0.225$), although more carabids appeared to be caught in January than in December or February.

Although the pine plantation had the highest number of species present of all habitats (Table 1), rarefied species richness was higher in natural beech and pasture than managed beech or pine (Fig. 3). However, 95% confidence intervals of all habitats overlapped, indicating a lack of significant differences in rarefied species richness between habitats.

Indicator species analysis found two species, *Holcaspis angustula* Chaudoir and *Amarotypus edwardsii* Bates, to be significant indicators of the natural beech habitat (Table 1, $P < 0.05$). *Holcaspis intermittens* was a significant indicator of managed beech, although a high indicator value (37) was also found for this species in natural beech. *Holcaspis hudsoni* was a significant indicator of the pine plantation habitat. Four species, *Mecyclothorax rotundicollis* (White), *Cicindela parryi* (White), *Demetrida dieffenbachii* (White) and *Scopodes fossulatus* (Blanchard), were significant indicators of pasture. *Holcaspis intermittens* and *H. hudsoni*, were the dominant species in traps in the three forest habitats. The relative proportions of these two species differed across the habitats, with *H. intermittens* dominant in natural beech and managed beech, and *H. hudsoni* dominant in pine ($F = 108.47$, $df = 3$, $P < 0.001$).

The unconstrained PCoA (Fig. 4a) separated the carabid community of the pasture habitat from that of the three forest habitats, along both Axis 1 (explaining 38.1% of the variation) and Axis 2 (explaining 8.7% of the variation). Constraining the PCoA using the CAP procedure, according to the *a priori* habitat groupings, clarified the differences in carabid community composition (Fig. 4b, trace = 1.612, $P = 0.0002$). CAP Axis 1 explained the most variation, separating pasture from the forested habitat types (canonical correlation $\delta = 0.912$). The forest habitats were separated along Axis 2 (canonical correlation $\delta = 0.737$). All three forested habitats overlapped in multivariate space, with managed beech carabid communities sharing characteristics with those of both natural beech and pine.

Discussion

Differences and affinities between assemblages

The perhaps most striking finding of this study is the strong separation between the carabid assemblages found in the three forest habitat types and those in the pasture grassland area. This was seen in the limited overlap between these habitat types in the principal coordinates analyses and in the large proportion of species that occurred only in one or the other habitat. Ten species were found only in the forest habitat and four species only in pasture grassland. Among the nine species that occurred in both forest and pasture, six species showed strong preferences for either forest or pasture in terms of their relative abundance between habitat types. Therefore, most species were either forest specialists or open-habitat species, whereas only three species of low to moderate abundance appeared to be habitat generalists. The strongest separation between assemblages was between the largely undisturbed natural beech forest and the pasture grassland, both of which had several unique species (that did not occur in any other habitat types) and showed significant indicator values for these respective habitats. The assemblage in managed (and previously disturbed and regenerating) beech forest had several affinities with the pine forest assemblage which was apparent in both the principal coordinates analyses and the presence

and abundance data (in Table 1), suggesting that these are forest specialists that are tolerant of disturbance or more capable of recolonisation following disturbance. There was somewhat less overlap between the natural beech forest and pine forest assemblages than between the two beech forest assemblages.

Comparison with other studies

The separation of assemblages in forest and grassland contrasts with the findings of a similar study on carabid assemblages on the Canterbury Plains nearby (i.e. ca. 20 km to the east of the present study). In that study, carabid assemblages in small native forest remnants, pine plantation forest, pasture grassland and gorse shrubland differed little in terms of species composition, and these assemblages largely overlapped in principal coordinates analyses (Berndt et al. 2008). This difference is probably explained by the different land use history between these areas. Woodside Forest and the adjacent Oxford Forest Conservation Area cover a natural forest area of more than 11,000 ha with comparatively less disturbance, and consequently, this area has retained an assemblage of forest specialists. By contrast, the Canterbury Plains have experienced severe natural forest loss and disturbance, and today natural forest remnants represent less than 1% of the land area there (Ecroyd & Brouckerhoff 2005), so that mostly forest generalists and habitat generalists persist whereas forest specialists are rare (Berndt et al. 2008).

A study in the North Island documented distinguishable assemblages of carabids and other beetles (mainly Scarabaeidae and Scolytinae) between native forest, plantation forest, clear-felled plantation forest and pastoral grassland (Pawson et al. 2008). The species composition of beetles in mature plantation forest was most similar to that of native forest. Apart from habitat type, the proportion of native vegetation (primarily forest) within the surrounding 500 m was the strongest predictor of variation in beetle species composition (Pawson et al. 2008). Our contrasting findings between the Oxford Forest and the Canterbury Plains assemblages are consistent with this observation about the importance of natural forest vegetation in the surrounding area. A comparison of herbivorous caterpillars and parasitoids in native Nothofagaceae forest and adjacent pine plantations in the northern South Island reported differences in insect species composition between forest types that appeared to be driven mostly by species variation in lower trophic-level taxa (Peralta et al. 2018). This supports the notion that the understorey plants of plantation forests, and not only the canopy tree species, play an important role in the composition of insect assemblages.

Native vs. exotic species

Another noteworthy result of our study is the rarity of exotic species at Oxford and Woodside Forests. Only three individuals from two exotic carabid species were found in our samples. Neither species occurred in the natural Nothofagaceae forest while one occurred only in the pasture area. By contrast, five exotic beetle species occurred on the Canterbury Plains and several of these

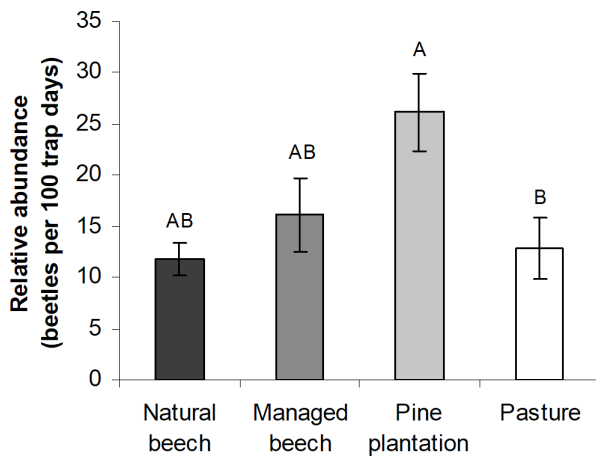


FIGURE 2: Mean relative abundance (\pm S.E.) of carabid beetles in each habitat type. Bars sharing a letter do not differ significantly ($\alpha = 0.05$).

were abundant, especially in the open habitats of pasture and recently harvested and replanted plantation forest (Berndt et al. 2008). The most common exotic species in that area was *Hypharpax australis* which was also found in the grassland in the present study, albeit in very low numbers. This indicates that these particular exotic

carabids are open-habitat specialists that colonise open habitats and cleared forest areas but either do not enter or do not survive in closed forest. This finding is consistent with other studies. For example, Harris and Burns (2000) and Pawson et al. (2008) documented a substantially greater number and abundance of exotic beetle species in grassland than in natural forest remnants in the North Island. Collectively, these studies and our results suggest that New Zealand’s natural forest is remarkably resistant to invasion by exotic beetles. This may be due to the high level of endemism in New Zealand’s biota and to the relatively limited disturbance experienced by New Zealand’s natural forests (Brockerhoff et al. 2010). Furthermore, older plantation forests (i.e. with trees older than ca. 20 years) share many characteristics with natural forests. They have similar species composition (i.e. beetle assemblages) and a small proportion of exotic beetles compared with pasture grassland vegetation. However, in other countries natural forests are by no means resistant to invasion by non-native beetles. This is particularly true in North America where more than 100 non-native beetle species have been recorded feeding on forest trees, including numerous important forest pests (Aukema et al. 2010), and many other non-native insects are also found in forests (e.g. Liebhold et al. 2016).

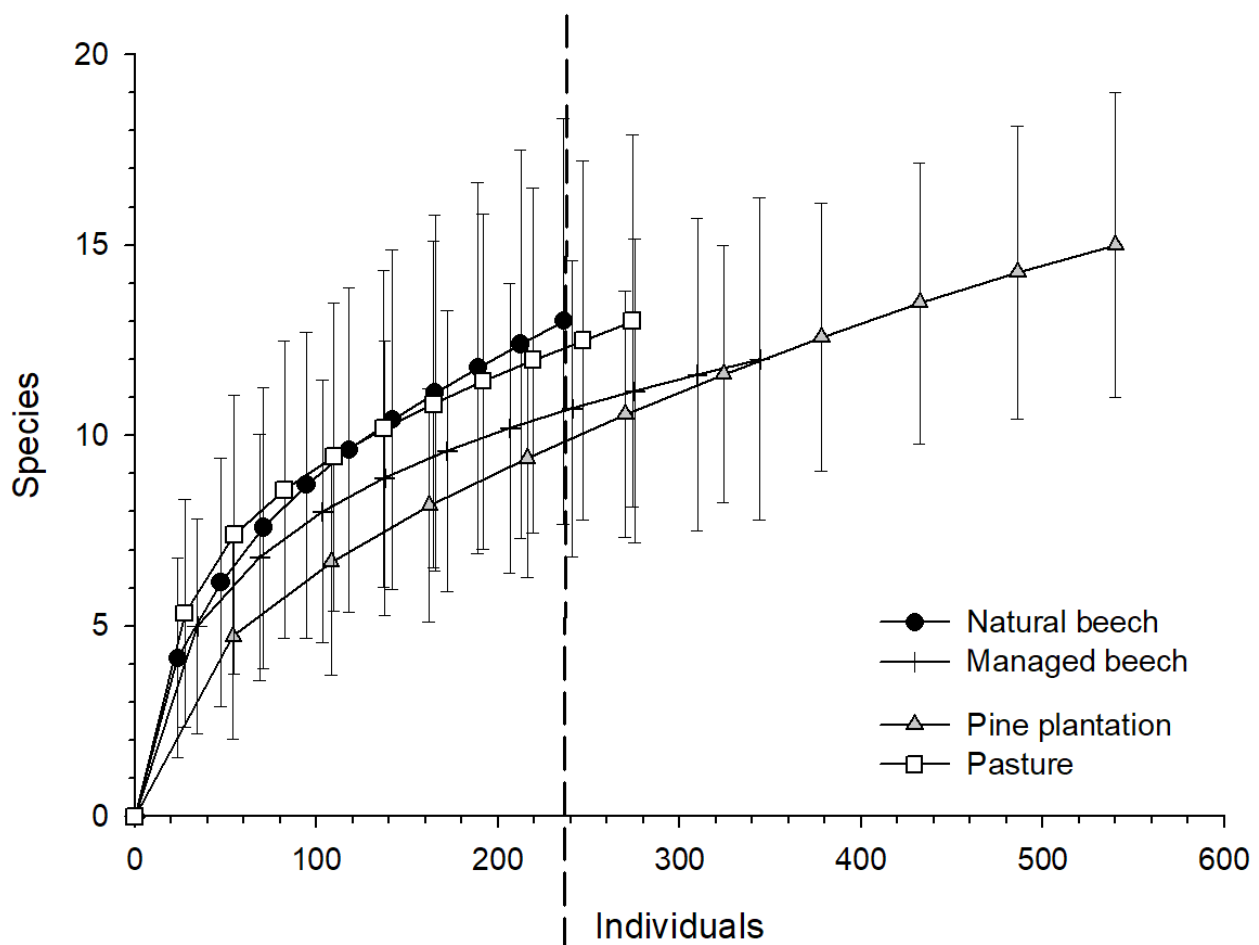


FIGURE 3: Sample-based rarefaction curves (\pm 95% CI) of carabid species richness in each habitat type, rescaled to show individuals on the x-axis. Species richness is compared at the end point of the natural beech curve, indicated by the dashed line.

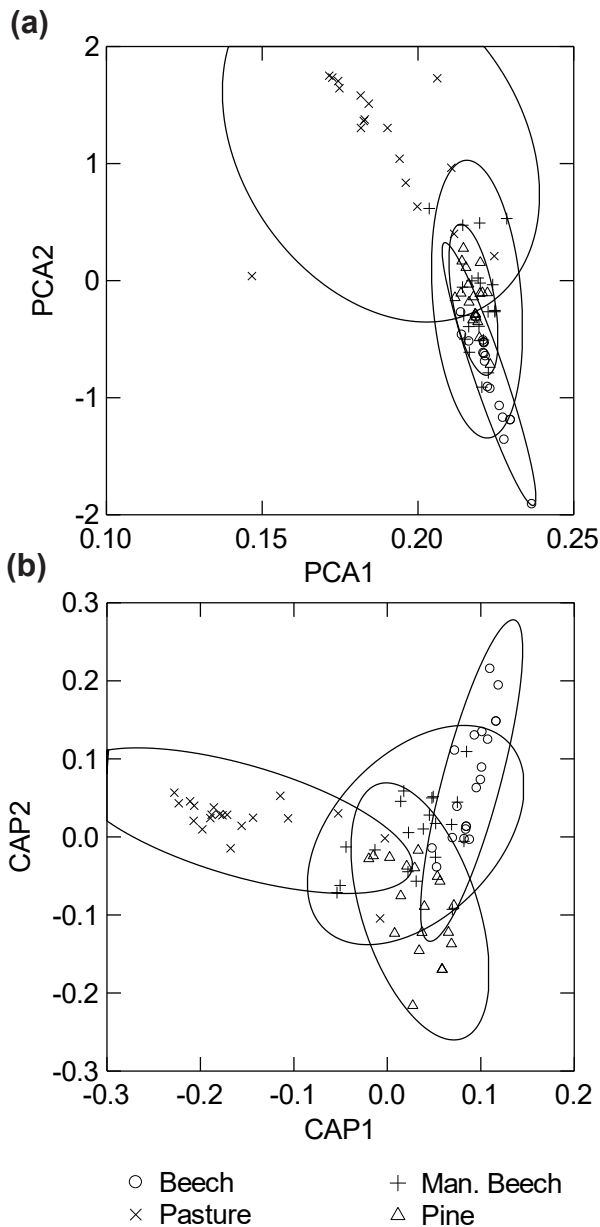


FIGURE 4: (a) Unconstrained principal coordinates analysis of pitfall trapped carabid beetles in four habitat types. Two (out of 20) pasture traps were outliers and not included on the graph (Axis 1 scores of -1.4 and -15.1). (b) Constrained principal coordinates analysis of pitfall trapped carabid beetles in four habitat types. Gaussian bivariate ellipses (probability 0.95) are shown on both graphs.

Characteristics of species in the different habitats

Three species (*Amarotypus edwardsii*, *Holcaspis angustula* and *Selenochilus syntheticus*) were unique to the natural beech forest, the original forest type of the area. These species appear to be forest specialists as they were not found in our earlier survey of small forest remnants or plantation forests or other vegetation on the

Canterbury Plains nearby (Berndt et al. 2008). *Holcaspis angustula* has also been found in a native forest reserve on Banks Peninsula where it was typical of dense, moist native forest areas (Bowie et al. 2018). It was the least abundant of four species of *Holcaspis* in that study, and it appears to have declined since an earlier survey 30 years ago (Bowie et al. 2018). According to Larochelle and Larivière (2001), *H. angustula* may also occur in plantation forest, tussock grassland and pasture. However, based on our findings and those of Bowie et al. (2018), *H. angustula* shows clear preferences for dense forest. *Amarotypus edwardsii* is a flightless forest species; it lives on tree trunks in wet forests and shrubland, feeding on invertebrates among mosses and lichens (Johns 1980; Larochelle & Larivière 2001), although it must also be active on the ground at times to have been caught in the pitfall traps in this study. However, in the central North Island, *A. edwardsii* was commonly found in pine plantations, and although it has been recorded in pasture grassland, this was restricted to traps placed no more than 25 m from a forest edge (Pawson et al. 2008). Therefore it cannot be considered an old forest specialist. *Selenochilus syntheticus* is a flightless species of dry lowland Nothofagaceae forests (Larochelle & Larivière 2001), but otherwise little is known about this species.

Two other species of *Holcaspis* (*H. intermittens* and *H. hudsoni*) were the most abundant species in the forest habitats. These two species differed in dominance in each habitat, with a greater proportion of *H. intermittens* caught in beech and managed beech, and a greater proportion of *H. hudsoni* caught in pine. *Holcaspis intermittens* is a dry forest and shrubland species (Larochelle & Larivière 2001), but it is thought to have a preference for more densely vegetated sites with higher humidity (Johns 1986). *Holcaspis hudsoni* has a broader habitat range than *H. intermittens*, being recorded from dry forests, shrublands and pine plantations, as well as tussock grasslands and pasture (Larochelle & Larivière, 2001). In this study, most beech forest plots had significant understorey vegetation, whereas the pine plantation had more limited undergrowth. This may have been due to greater canopy closure in the pine plantation than in the beech forest (Bockerhoff et al. 2003), or to differences in soil moisture. Beech forests on moist soils in the Canterbury Foothills where the study was located support a dense undergrowth of the fern species *Blechnum discolor* and *Polystichum vestitum*, whereas on drier slopes and ridges the shrubs *Cyathodes fasciculata* and *C. juniperina* are often prominent in the understorey (Wardle 1984).

The pasture carabid assemblage was characterised by dominance of small species, and exotic species present in low numbers. *Mecyclothorax rotundicollis*, a pasture habitat indicator species in our study, is a widespread, flighted species with a small body size (<10 mm). It tolerates or perhaps even prefers modified vegetation such as pasture and crop fields (Johns 1986; Larochelle & Larivière 2001). Habitats with greater disturbance, such as the grazed pasture in this study, tend to support carabid assemblages of a smaller average body size, as

was found in a study of carabids in grassland in England (Blake et al. 1994). *Cicindela parryi*, a tiger beetle, is typically found in open habitat, although usually in forest gaps, rather than in larger pasture areas (Larochelle & Larivière 2001). Flighted species have the ability to disperse quickly which is an advantage if they rely on potentially ephemeral newly created open habitats such as forest gaps created by windthrow.

Absence of Holcaspis brevicula

One of the objectives of this study was to determine whether the range of the critically endangered *Holcaspis brevicula* extends beyond the Canterbury Plains into the adjacent foot hills of the Southern Alps. Our survey in the closest larger and unfragmented natural forest and adjacent areas revealed the presence of four other species of *Holcaspis*, but no *H. brevicula*. It is unlikely that we overlooked *H. brevicula* among any of the other *Holcaspis* specimens because none of them are closely related to *H. brevicula* which is the only species of the *algida* complex that occurs in this area (Butcher 1984). Therefore, it is likely that its only occurrence is indeed in the area of the former Eyrewell Forest (Bockerhoff et al. 2005), although it cannot be ruled out entirely that a population remains elsewhere. As Eyrewell Forest has been converted to a dairy farm in the last few years (Hancock 2019), it is unlikely to have survived there.

Effects of land management and forest regeneration

The four adjacent habitat types sampled for this project differed considerably in terms of their vegetation history and the current vegetation. The natural beech forest experienced relatively little disturbance although it is not clear to what extent this area was affected by the forest fire in the 1800s. The area of managed beech forest was affected by logging and fire between 1860 and 1910) and then grazed until the 1930s after which there was gradual re-establishment and regeneration of the beech forest (Novis et al. 2003; Allen et al. 2012). The period since then allowed ample opportunity for recolonisation by carabids from the adjacent forests and restoration of a relatively 'natural' forest carabid assemblage, although the species composition differed somewhat from the natural beech forest. The close-to-nature management of this managed beech forest, which aims to mimic the scale and intensity of natural disturbance events in the forest (Novis et al. 2003; Allen et al. 2012), does not appear to have any detrimental effects on the local ground beetle community. The pine forest area was planted in the 1970s on land that was previously pasture, so this area experienced disturbance more recently. In addition, the canopy tree, *Pinus radiata*, is not native to New Zealand; however, there was an understorey of mainly native plants of which many were shared with the adjacent native beech forest. Despite these differences, the species composition of the pine forest area was almost identical to that of the managed beech forest, although there were differences in the relative abundance of several species. By contrast, the open pasture grassland area, which differed substantially from the three forest types in terms of vegetation

structure and plant species composition, also revealed a distinct beetle assemblage, even though the pasture area is very small and surrounded by beech forest.

It is likely that habitat connectivity plays an important role in maintaining native biodiversity in managed forests (e.g. Norton 1998), and the different forest habitats at Woodside are interconnected, with pasture present more as clearings than matrix habitat. The relatively small patches of the managed beech, pine forest and pasture habitat types created more edge or boundary habitat where assemblages partly overlap (Koivula et al. 2004) with forest species and open-habitat species potentially 'spilling over' into adjacent habitats. However, the size and quality of habitats may be more important than edge effects and connectivity (e.g. Hodgson et al. 2011), and the relatively large natural beech forest directly adjacent to the managed habitats probably plays a key role in the resemblance of these assemblages and the almost complete absence of non-native ground beetle species.

Native invertebrates can be abundant in exotic habitats (Watts & Gibbs 2002; Harris et al. 2004; Derraik et al. 2005; Berndt et al. 2008; Pawson et al. 2008), in some cases with similar species assemblages to equivalent native habitats. However, exotic habitats cannot and should not replace native ones, and the conversion and degradation of natural vegetation is a major cause of the worldwide loss and decline of biodiversity (Newbold et al. 2015). Furthermore, where possible, it would be preferable in terms of biodiversity conservation to restore natural vegetation and plant native trees. Nevertheless, as New Zealand is dominated by production land uses with crop plants of exotic origin, it is important to acknowledge the potential contribution of these land uses to the conservation of native biodiversity and to consider how these can be managed to maximise conservation opportunities.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

LAB and EGB jointly conceived and planned the study and carried out much of the field work. LAB identified most of the carabids and did most of the data analysis. LAB and EGB jointly wrote the manuscript.

Acknowledgements

We would like to thank John and Rosalie Wardle for access to Woodside Forest and the Department of Conservation for access to Mt. Oxford Forest (National Permit Number CA-13813-FAU). We greatly appreciate the assistance of Peter Johns, André Larochelle and Rowan Emberson with carabid identification, Janette Beaton, Chris Berry and Alan Leckie in the field and laboratory, and Steve Pawson for advice on statistical analyses. Funding for this study was provided by the Foundation for Research, Science and Technology (C04X0304).

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