CrossMark

ORIGINAL PAPER

Invertebrate community turnover following control of an invasive weed

Corinne Watts[1] · Helen Ranson[2] · Stephen Thorpe[3] ·
Vanessa Cave[4] · Beverley Clarkson[1] · Danny Thornburrow[1] ·
Scott Bartlam[1] · Kerry Bodmin[5]

Abstract Non-native invasive plants are a significant threat to native biodiversity as they change community structure and ecosystem processes and it is becoming imperative that these invasive plants are controlled. We investigated the response of wetland invertebrates to glyphosate chemical control of an introduced tree, grey willow (*Salix cinerea*), in a before-after-control-impact (BACI) experiment within a New Zealand wetland. Our findings suggest that control of grey willow resulted in significant increases in the abundance of invertebrates within 2 years after herbicide application. Analysis of beetle communities revealed that the abundance and species richness of herbivorous and predacious beetles, the abundance of introduced species, and the species richness of native and introduced species were all significantly higher in the herbicide-treated plots than in the unsprayed plots. The composition of the beetle community separated into two clear groups—plots before spray/no spray and plots 1 and 2 years after herbicide application. We suggest that the beetle compositional changes were driven by complex changes in vegetation associated with the canopy collapse of grey willow trees and the initial influx of introduced plant species, predominantly weedy annuals and perennials, after willow control. Restoration via invasive plant control can promote the reestablishment of invertebrate communities typical of native wetlands, but their long-term sustainability is contingent on prevention of grey willow reinvasion and reestablishment of the native plant habitat.

Keywords Wetland · Community composition · *Salix cinerea* · Coleoptera · New Zealand

✉ Corinne Watts
wattsc@landcareresearch.co.nz

1 Landcare Research, Private Bag 3127, Hamilton 3216, New Zealand

2 Centre of Science and Primary Industries, Waikato Institute of Technology, Private Bag 3036, Hamilton, New Zealand

3 School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

4 AgResearch, Private Bag 3115, Hamilton 3240, New Zealand

5 National Institute of Water and Atmosphere, PO BOX 11-115, Hamilton 3251, New Zealand

Introduction

Invasive species are the second largest cause of native biodiversity loss, after habitat destruction, because they change community structure, biodiversity and ecosystem processes (Keane and Crawley 2002). While negative impacts of invasive plant species on native plant communities have been well demonstrated (Heads and de Lange 1999; Levine et al. 2003; Hulme and Bremner 2006), effects on invertebrate assemblages have received less attention. A few studies (Herrera and Dudley 2003; Gratton and Denno 2005), including one in New Zealand (Standish et al. 2001), have reported that introduced plant-dominated habitats have less abundance and diversity of invertebrates than native vegetation. In contrast, however, another study in New Zealand (Watts et al. 2012) showed that wetlands invaded by grey willow (*Salix cinerea*) had higher beetle abundance and species richness compared with native herbaceous vegetation reflecting increasing complexity of vegetation structure associated with grey willow invasion.

Over the past 150 years, 11 species and five hybrids of willows (*Salix* spp.) native to the Northern Hemisphere

were introduced into New Zealand for erosion control in riparian zones and to provide shelter and fodder for stock (Collier 1994; Wilkinson 1999). Three taxa, crack willow (*S. fragilis*), grey willow and pussy willow (*S. × reichardtii*), have rapidly spread and are now considered invasive plants in New Zealand (van Kraayennoord et al. 1995; Froude 2002). Their ability to reproduce vegetatively from broken branch or twig fragments, grow rapidly, tolerate a range of environmental conditions, including semi-shade and flooding, and, in the case of grey willow, produce prolific light wind-dispersed seed contributes to their invasiveness, and they now dominate many wetland and riparian ecosystems. Willows can successfully outcompete native wetland vegetation (Champion 1994), have adverse impacts on specialised native bird species and alter aquatic macroinvertebrate and fish communities (Collier 1994). Grey willow is possibly the most troublesome species, invading large areas of undisturbed wetlands, tolerating a variety of soils and forming dense thickets (Beard 2010). Over the past decade, grey willow is being controlled and eliminated from many wetlands. As far as we are aware, no published studies have investigated the responses of the terrestrial invertebrate community to willow control and the subsequent changes in habitat. This is surprising, considering the diversity of invertebrates within ecosystems and the important roles they have in ecosystem functioning such as herbivory, decomposition, pollination, and predation. In addition, wetland invertebrate communities are distinctive, comprising many specialist taxa sensitive to environmental change (Watts et al. 2008). These data would provide vital information on reference baselines and thresholds of plant-invertebrate dynamics in willow-infested wetlands.

This research investigates the response of wetland invertebrates to the chemical control of grey willow in a before-after-control-impact (BACI) experiment within a New Zealand wetland over 4 years. We focussed our study on beetles (Insecta: Coleoptera) because they have proved useful indicators of both environmental change and taxonomic diversity (Gerlach et al. 2013), have varying habitat preferences, are comparatively well known taxonomically, represent all trophic groups and are involved in many key ecological processes (Klimaszewski and Watts 1997). For example, sampling malaise-trapped beetles in New Zealand has provided a sensitive tool for monitoring habitat management and restoration (Hutcheson 1990; Hutcheson and Jones 1999; Hutcheson and Kimberley 1999). Based on previous studies, we predict a decrease in invertebrate abundance within the herbicide-treated plots resulting from less structurally complex vegetation, such as decreased canopy cover and height, in the first few years following willow control. Specifically, we hypothesised that (1) detritivorous beetles would be more prevalent after willow

control due to the increase in dead willow stems; (2) herbivorous beetles, associated with the palatable willow foliage, would decrease in the herbicide-treated plots after willow control; and (3) introduced beetles, particularly herbivores associated with the introduced willow cover, would decline in abundance in the herbicide-treated plots after willow control.

Methods

Study area and sampling design

The experiment was carried out in Whangamarino wetland, located approximately 45 km north of Hamilton, North Island, New Zealand. It is the second largest (7290 ha) wetland complex in the North Island and has been a Ramsar site since 1989. In 2007, grey willow swamp forest dominated approximately 20 % of Whangamarino wetland and its range was expanding (Duggan et al. 2013). In the southern portion of Whangamarino, an area of dense mature grey willow (>95 % canopy cover, 6–8 m in height and approximately 25 years old) was chosen for study. Other common plant species associated with the willow were the native sedges *Machaerina rubiginosa* and *Carex secta*, ferns *Gleichenia dicarpa* and *Dicksonia squarrosa*, shrub *Coprosma tenuicaulis*, herbaceous perennial *Typha orientalis*, and the introduced deciduous fern *Osmunda regalis* and herbaceous perennial *Lotus pedunculatus*.

The experimental area was divided east to west into two blocks (an unsprayed block and a herbicide-sprayed block) each 150 m wide and 100 m long, separated by a 50-m buffer. As there was a possible minor hydrological gradient north to south in the experimental area, the two blocks were replicated immediately south, separated by a 10-m buffer. The total area of the experiment was 7.1 ha. Each of the unsprayed (A and C) and the herbicide-sprayed (B and D) blocks contained three 10 × 10 m sampling plots (numbered 1–3), positioned using simple random sampling implemented through a purpose-built extension to ArcView 3.2 (ESRI 1999). This selected the south-west corner of each north–south-oriented 10 × 10 m plot, and all 12 sampling plots were permanently marked.

Invertebrates and the associated environmental variables (see details below) were sampled 1 year before the herbicide application during the austral summer (January–March 2011). Samples were collected from all plots during the month immediately before and after herbicide was applied to blocks B and D on 8 February 2012. One and two years 'after spray', samples were then collected during summer 2013 and 2014, respectively.

Glyphosate (*N*-phosphonomethyl-glycine), a broad-spectrum, non-selective water-soluble systemic herbicide,

which inhibits amino acid synthesis in plants (Franz 1985; Kolpin et al. 2006), was used for the herbicide-treated blocks (B and D). The herbicide and surfactant Supersil™ (polyether modified polysiloxane) was applied at a volume rate of 9 L ha^{-1} using a high-volume sprayer from a helicopter during calm, dry conditions. This appears to be the most effective and widely used concentration and application method to control large-scale dense infestations of *Salix* species in New Zealand, with minimal non-target impacts (Bodmin and Champion 2010).

Invertebrate sampling and identification

Invertebrates were sampled using a modified malaise trap (Watts et al. 2012) placed in the centre of each 10 × 10 m sampling plot. Each trap required a relatively flat, dry, open area of approximately 1 m^2. If this was not found in the centre position, the nearest suitable area within the plot was selected. The collecting jar of the malaise trap, orientated north, contained 100 ml monopropylene glycol. One malaise trap per plot (a total of 12 traps) was set from 14 January to 14 March 2011 (pre-spray; 59 days duration), 10 January to 7 March 2012 (at spray; 57 days), 15 January to 13 March 2013 (1 year after spray; 57 days) and 10 January to 16 March 2014 (2 years after spray; 55 days). The traps were emptied twice at 30-day intervals and captured invertebrates preserved in 70 % ethanol. Subsequently, samples were sorted and counted using a binocular microscope for the following taxa: Diptera, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera and Araneae.

Beetles selected for further taxonomic identification were sorted on the basis of external morphology to recognised taxonomic units (hereafter, referred to as species) and, where possible, given generic and species-level identifications by S Thorpe. Each species was classified as predator, herbivore (including xylophages) or detritivore (including fungivores, saprophages and scavengers) according to Klimaszewski and Watts (1997) or other published accounts of a species or genus. Klimaszewski and Watts (1997), Kuschel (1990) and knowledge from S Thorpe were used to classify whether a beetle species was native, introduced or of unknown status.

Vegetation and habitat sampling

To determine the effects of changes in the vegetation and habitat following herbicide treatment on the invertebrate community, 15 environmental and habitat variables were measured at each plot. These measurements were taken within the malaise-trapping session each year or within 2 weeks of its completion. From each of the 10 × 10 m plots, the total percentage cover for each plant species was

calculated as the sum of the estimated per cent covers for live foliage in the five vegetation tiers: <0.3, 0.3–1, 1–2, 2–5, >5 m. From these data, the following variables were derived: per cent total vegetation cover (%TVC), per cent total grey willow cover (%WC), per cent non-willow-introduced vegetation cover (%IC), per cent native vegetation cover (%NC), total number of plant species (TSP), total number of introduced plant species (ISP) and total number of native plant species (NSP). Canopy density (CD) was measured at 1.5 m above the ground using a convex spherical canopy densiometer at the four corners of the 10 × 10 m plot and averaged.

Within each of the 10 × 10 m plots, nine 1 × 1 m subplots were established to obtain data on grey willow and environmental variables associated with wetland water: one 1 × 1 m subplot was placed in each of the four corners, one at the mid-point along each of the four boundaries and one in the centre. Willow stems, ≥2.5 cm in diameter and taller than 1.8 m, within or closest to each 1 m^2 subplot ($n \leq 9$) were tagged with a permanent marker. The height (AWH) and number (ANW) of the tagged grey willow stems were averaged over the nine subplots. The water table (cm) in the nine 1-m^2 subplots was measured using a metric tape measure at the lowest part of each subplot and all nine values averaged (WD). If the water table was below the soil surface, then a small hole was dug at the lowest point in the subplot to measure the water table depth. Positive values indicated that the water table was above the surface and negative values were below. For the purpose of analysis, the lowest recorded water depth value was used as the baseline value and all other values were converted to relative values. Water pH (WPH) and conductivity (WC) were measured with a TPS WP-81 fieldmeter in the standing water or water that filled a peat extraction hole in subplot 1 (south-west corner of the 10 × 10 m plot).

A number of studies have found habitat variables associated with the leaf litter and coarse woody debris (dead wood) to be important in the recovery of insect communities during wetland restoration (Gratton and Denno 2005; Watts et al. 2008, 2012; Grégoire Taillefer and Wheeler 2012). Two leaf-litter variables were measured at the mid-point of each malaise-trapping session: (1) litter depth (mm) was measured to the bottom of the F-horizon (non-saturated, partly decomposed organic litter layer) at four random points within 5 m of the malaise traps and averaged, and (2) a litter biomass (LB) sample was collected within a circular metal ring (area = 0.025 m^2) immediately after the litter depth was recorded. The litter was oven-dried for 24 h at 60 °C and weighed (g). The amount of standing dead wood (DW) in each 10 × 10 m plot was estimated using a three-point scale, with 'one' being no trunks dead and 'three' being all/nearly all trunks dead.

Data analysis

Numerical changes in the invertebrate community after willow control were examined using the total abundance data collected in each malaise trap for the 2-month sampling period each year over the 4-year study. Changes in total abundance (i.e. the number of individuals collected in malaise traps), geometric mean abundance and species richness (i.e. the number of unique species collected in malaise traps) were investigated.

Invertebrate abundance

The invertebrate Order abundance data consist of the number of invertebrates collected in malaise traps of Order k, at plot j, in each year t of the four-year study. To assess the impact of herbicide on the abundance of invertebrates, the geometric mean of the Order abundances was calculated for each plot in every year. The geometric mean, rather than the arithmetic mean, was analysed so the very abundant Order, Diptera, did not dominate the abundance measure. The geometric mean data were analysed by repeated measures using REML, with a first-order antedependence model on the correlation within plots over time. The fixed model included a factor for year, a treatment factor describing whether or not the plot was treated with herbicide in February 2012, and the interaction between year and treatment. In order to stabilise the variance, the geometric means were ln-transformed before analysis.

To explore the effect of herbicide on the individual Orders, the total abundance of each Order was separately analysed using repeated measures as above.

Beetle community data

As beetles were identified to species level, this enabled the impact of the herbicide treatment on their abundance and species richness to be assessed in greater detail.

For each plot, and for each year, geometric mean species abundance and species richness were calculated. These were analysed using repeated measures with a first-order antedependence. Additional uniform correlation within plots was included in the analysis of the geometric mean. Inspection of the residual plots indicated that neither the geometric mean nor species richness data required transforming a priori.

To examine whether the trophic composition of the beetle population changed in response to grey willow control, for each trophic group the total number of beetles caught and the number of unique beetle species caught, at

each plot per year, were analysed separately using split plot in time ANOVAs. More complex correlation structures than the uniform correlation over time generated by the split plot in time model were not needed to describe the datasets. The abundance data were ln-transformed prior to analysis to stabilise the variance. The composition of native versus introduced beetle species was similarly analysed. All of the above analyses were conducted using GenStat 16 (VSN International 2013).

To further assess the effect of herbicide application on the beetle community, classification cluster analysis and ordination techniques were performed in the PATN multivariate analysis package (Belbin 1995). The programmes FUSE (agglomerative hierarchical fusion) and SSH (semi-strong hybrid multidimensional scaling) were selected. In addition, a flexible unweighted pair-group technique using UPHMA clustering method and the Bray-Curtis association measure were selected. The resulting two-dimensional ordination with a stress value of 0.171 appeared to summarise the data sufficiently (Belbin 1995). To examine beetle species' responses to the environmental variables, we implemented the programme PCC (principal component correlation) within PATN combining the environmental data and plot ordination results. The variables were then plotted as vectors on the two-dimensional ordination to indicate the direction and significance (length of vector) of each variable.

Results

Overall effect on grey willow

The grey willow control operation resulted in significant kill of the dense willow canopy in the sprayed plots, with low non-target plant mortality. Virtually, all willow individuals were killed outright and remained as dead standing spars for the first year after spray, which had started to collapse 2 years after treatment. Willow re-invasion into the sprayed plots was by seedling establishment.

Changes in invertebrate abundance following grey willow control

The analysis of the geometric mean abundance of invertebrates and individual Order abundances provided strong evidence of an interaction between year and treatment (ln(geometric mean): $F_{3,11.4} = 41.9$, $P < 0.001$; Order abundances: Table 1), indicating that, in terms of abundance, the unsprayed plots and herbicide-sprayed plots responded differently to one another over time. Post hoc tests provided evidence that there were significantly more

Table 1 The *F* statistic, numerator degrees of freedom (ndf), denominator degrees of freedom (ddf) and *P* value for the test of significance of interaction between year and treatment in the analysis of total abundance of each Order

Order	*F* statistic	*ndf*	*ddf*	*P* value
ln(total abundance of Diptera)	9.8	3	11.3	**0.002**
ln(total abundance of Hemiptera)	5.6	3	10.5	**0.015**
ln(total abundance of Coleoptera)	35.9	3	11.7	**<0.001**
ln(total abundance of Lepidoptera)	20.8	3	11.6	**<0.001**
ln(total abundance of Hymenoptera)	23.0	3	10.8	**<0.001**
ln(total abundance of Araneae)	19.7	3	11.6	**<0.001**

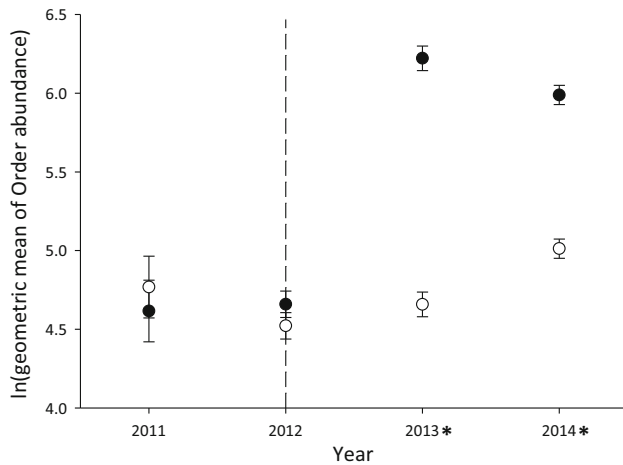Significant results (*P* value ≤0.05) are highlighted in bold

Fig. 1 Geometric mean of the invertebrate Order abundances (mean ± SEM, on ln scale) from malaise trapping at Whangamarino. *Open circles* unsprayed plots (*n* = 6), *closed circles* herbicide-treated plots (*n* = 6). *Years* with *asterisk* indicate significant differences at the 5 % level between the unsprayed plots and the herbicide-treated plots within that year. Time of herbicide application in February 2012 is shown with a *dashed vertical line*

invertebrates caught in traps 1 year after treatment in the herbicide-sprayed plots than in the unsprayed plots (Figs. 1, 2). The abundance data of the beetle taxa showed similar trends in all the Orders sampled except the Hemiptera and Hymenoptera (Fig. 2). Two years after spray, the mean abundance (ln scale) of all the Orders except Hemiptera was also significantly higher in the herbicide-sprayed treatment (Fig. 2). Hemiptera abundance increased in unsprayed treatment 2 years after treatment (Fig. 2b) with the invasion of the introduced giant willow aphid (*Tuberolachnus salignus*) at the study site. In addition, the abundance of Hymenoptera (mainly introduced *Vespula* species) also increased in the unsprayed treatment in 2014, but abundances were still significantly less than in the herbicide treatment (Fig. 2e). In 2011, Lepidoptera abundance was significantly higher in the unsprayed treatment (Fig. 2d). The samples were dominated by large number of *Protithona fugitivana* (Tortricidae), which were uncommon in subsequent years.

Changes in beetle community following grey willow control

Species richness and abundance

In total, 11,034 beetles comprising 101 species, were collected. The most common beetle caught was *Cyphon* species (Scirtidae) with 6485 specimens.

Significantly more beetles and beetle species were caught in the 2 years post-spray in the herbicide-treated plots than in the unsprayed plots (Table 2; Fig. 3).

Trophic composition

Of the beetle species caught, 46 species were detritivores, 34 species were herbivores and 21 species were predators. The mean abundance and species richness of predacious and herbivorous beetles were significantly higher in the 2 years post-spray in the herbicide-treated plots than in the unsprayed plots (Table 3; Fig. 4). There was no evidence of an effect of herbicide on detritivores.

Native and introduced beetles

Of the 101 beetle species caught, 69 were native species, 29 were introduced species and the status of 3 species was unknown. Native beetle species accounted for 82 % of the total abundance of beetles collected. Two of the unknowns were specimens classed as Corticariinae (321 individuals) and Coccinellidae (543 individuals) and were a mixture of introduced and native species. Both are complex groups that need to be revised taxonomically before their native or introduced status can be determined.

The mean abundance of introduced and unknown beetles was higher in the herbicide treatment than the unsprayed treatments in the 2 years following treatment (Table 4; Fig. 5a). For native beetles, mean abundance changed over time in both the unsprayed treatment and herbicide treatment ($F_{3,30} = 5.6$, $P = 0.003$), and furthermore, their abundance was significantly higher (across all years) in the herbicide-treated plots ($F_{1,10} = 5.8$,
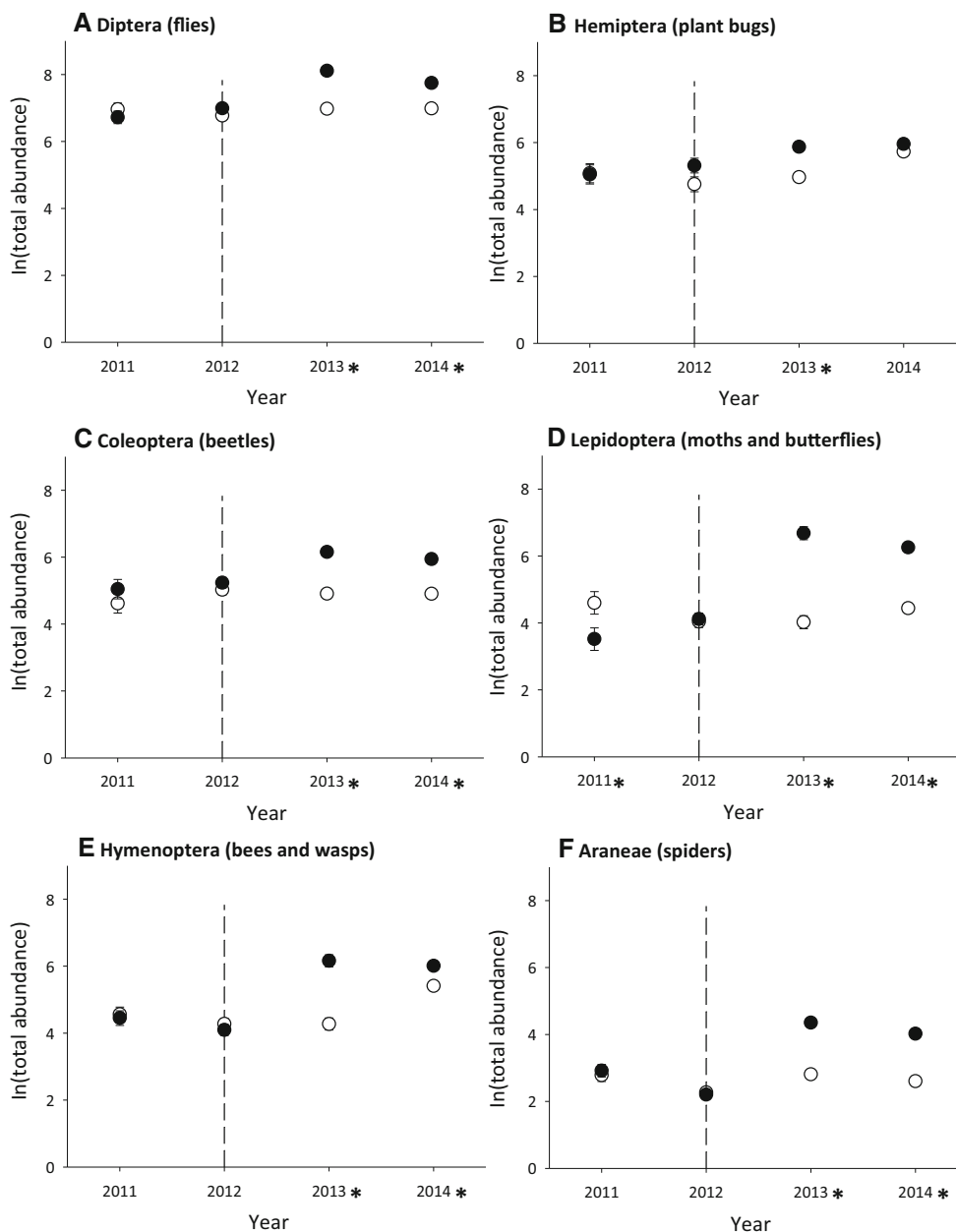
Fig. 2 Total abundance (mean ± SEM, on ln scale) of **a** Diptera, **b** Hemiptera, **c** Coleoptera, **d** Lepidoptera, **e** Hymenoptera and **f** Araneae caught in malaise traps at Whangamarino. *Symbols* and *asterisks* are as in Fig. 1. Note that the SEMs are too small to observe on graphs with the same *y*-axis scale

Table 2 The *F* statistic, numerator degrees of freedom (ndf), denominator degrees of freedom (ddf) and *P* value for the test of significance of interaction between year and treatment in the analysis of beetle abundance and species richness

Variable	*F* statistic	*ndf*	*ddf*	*P* value
Geometric mean beetle abundance	89.5	3	9.5	**<0.001**
Beetle species richness	9.4	3	11.2	**0.032**

Significant results (*P* value ≤0.05) are highlighted in bold

$P = 0.037$). However, the interaction between treatment and year was not significant ($F_{3,30} = 2.5$, $P = 0.080$; Fig. 5a).

Significantly more native and introduced species were caught in the herbicide treatment than in the unsprayed treatment in the 2 years following spray (Table 4; Fig. 5b). No herbicide effect was detected for the unknowns. However, their richness was lower in 2011 across all sites (Fig. 5b).
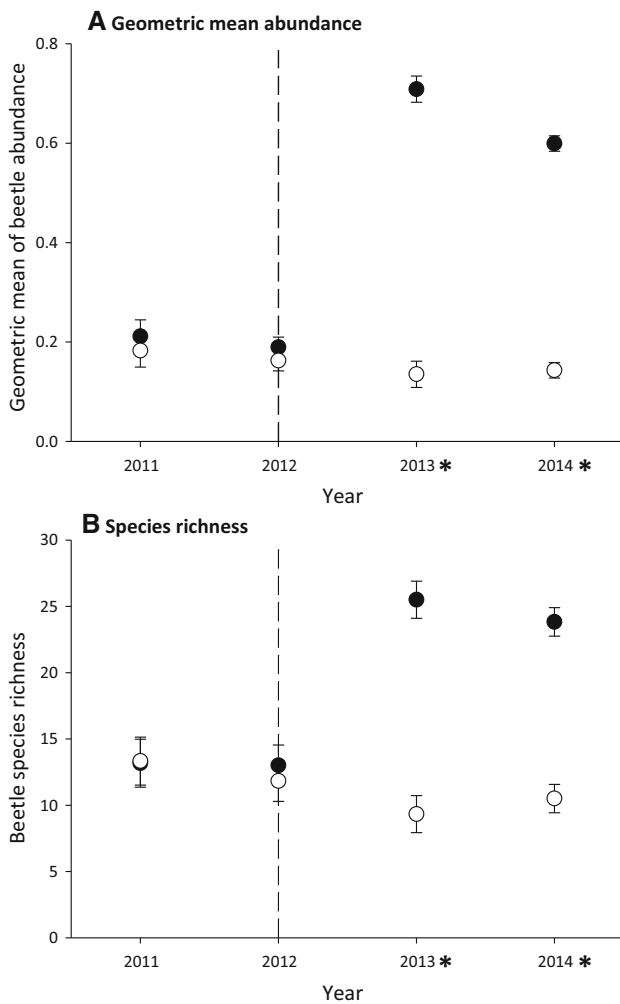
Fig. 3 **a** Geometric mean of beetle abundance (mean ± SEM) and **b** beetle species richness (mean ± SEM) caught in malaise traps at Whangamarino. *Symbols* and *asterisks* are as in Fig. 1
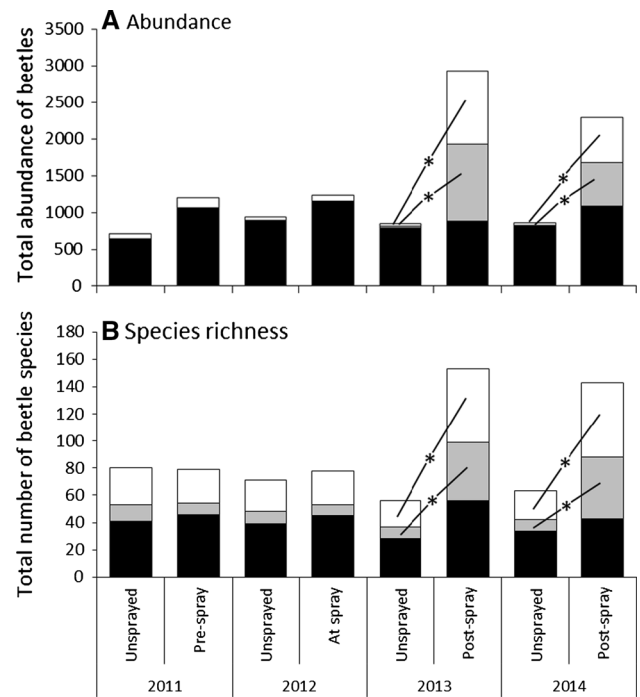

Fig. 4 Trophic composition of **a** abundance and **b** species richness of beetles caught in malaise traps at Whangamarino. *Black bars* detritivores, *grey bars* predators, *white bars* herbivores. A *line* with asterisk between trophic groups indicates significant differences at the 5 % level between the mean of the unsprayed plots and the mean of the herbicide-sprayed plots within that year. Herbicide application occurred in February 2012, so herbicide-treated plots in 2011 were 'pre-spray', and those in 2012 were 'at spray'

Table 3 The *F* statistic, numerator degrees of freedom (ndf), denominator degrees of freedom (ddf) and *P* value for the test of significance of interaction between year and treatment in the analysis of trophic composition

Variable	*F* statistic	*ndf*	*ddf*	*P* value
ln(total abundance of detritivores)	0.5	3	30	0.680
ln(total abundance of herbivores)	22.5	3	30	**<0.001**
ln(total abundance of predators)	75.7	3	30	**<0.001**
Species richness—detritivore	2.0	3	30	0.135
Species richness—herbivore	10.9	3	30	**<0.001**
Species richness—predator	36.0	3	30	**<0.001**

Significant results (*P* value ≤ 0.05) are highlighted in bold

Beetle community composition and correlated environmental variables

Beetle community composition at Whangamarino changed 1 year after grey willow control in the herbicide-treated plots (B and D; Fig. 6). Four groups with differing beetle species composition were identified by the classification (FUSE) analysis and were overlaid on the ordination (Fig. 6). Beetles collected from plot B1 in the 2 years before herbicide treatment (group I) had comparable beetle assemblages and were dominated by large abundances of *Cyphon* species (Scirtidae). All the remaining pre-treatment and unsprayed plots formed a distinct group with similar beetle compositions (group II). The beetles collected from plots B and D, 1 and 2 years after herbicide treatment, formed two groups of similar assemblages (Fig. 6). All herbicide-treated plots (B and D) 2 years after treatment had a similar composition (group III) and were distinct from all the B and D plots 1 year after treatment (group IV; Fig. 6).

Table 4 The F statistic, numerator degrees of freedom (ndf), denominator degrees of freedom (ddf) and P value for the test of significance of interaction between year and treatment in the analysis of native and introduced beetles

Variable	F statistic	ndf	ddf	P value
ln(total abundance of native beetles)	2.5	3	30	0.080
ln(total abundance of introduced beetles)	16.5	3	30	**<0.001**
ln(total abundance of unknown beetles)	22.4	3	30	**<0.001**
Species richness—native	17.0	3	30	**<0.001**
Species richness—introduced	9.0	3	30	**<0.001**
Species richness—unknown	0.9	3	30	0.446

Significant results (P value ≤ 0.05) are highlighted in bold
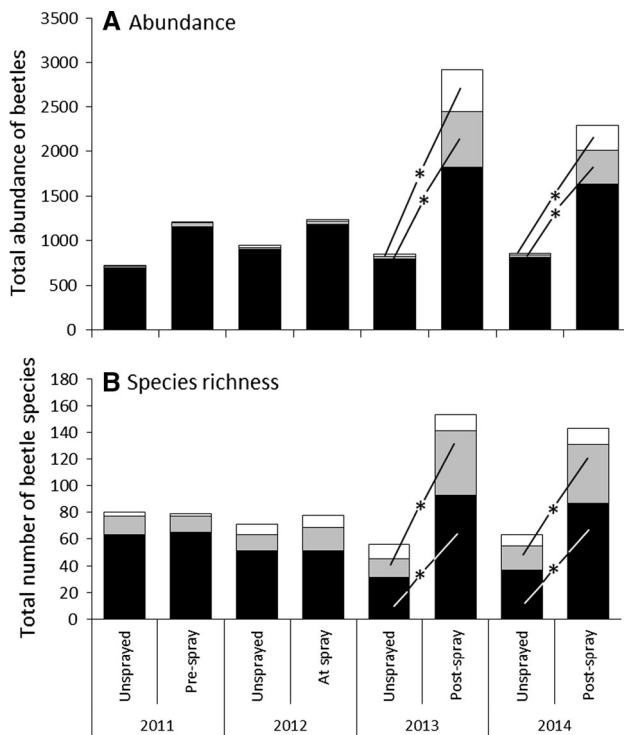

Fig. 5 Native, introduced and unknown status of **a** abundance and **b** species richness of beetles caught in malaise traps at Whangamarino. *Black bars* native beetles, *grey bars* introduced beetles, *white bars* unknown status. A *line* with *asterisk* between groups indicates significant differences at the 5 % level between the mean of the unsprayed plots and the mean of the herbicide-sprayed plots within that year. Herbicide application occurred in February 2012, so herbicide-treated plots in 2011 were 'pre-spray', and those in 2012 were 'at spray'

The ordination analysis showed significant variation in beetle species composition during the 2 years after grey willow control was associated with changes in the vegetation including canopy density, total grey willow cover, average grey willow canopy height and average number of grey willow stems (Table 5; Fig. 6). In addition, the increase in introduced plant species richness and therefore total plant species richness detected in the herbicide-treated plots (B and D) 1 year following herbicide treatment were also found to be significant variables (Table 5; Fig. 6).

Many of these environmental variables were correlated with each other (Fig. 6).

Of the 69 beetle species collected, the abundances of 34 taxa were significantly correlated with plots in relation to changes in the vegetation structure following grey willow control. This was most clearly observed for *Zorion* sp. 1 (Cerambycidae), *Scymnodes loewi* (Coccinellidae) and *Dasytes* sp. 1 (Melyridae), which were more abundant 1 year following spray in the herbicide-treated plots, which were characterised by loss of grey willow canopy and the presence of abundant weedy introduced annuals and perennials (Fig. 6). Conversely, *Microcryptorhynchus* sp. 1 (Curculionidae) and *Bicava* sp. 1 (Latridiidae) were associated with B and D plots before spray and with the unsprayed plots. *Adalia bipunctata* (Coccinellidae) appears to be associated with the native sedges that had become dominant under the dead willow trees in the B and D plots 2 years post-treatment.

Discussion

Contrary to our predictions, our results provided strong evidence that grey willow control resulted in significant increases in the abundance of invertebrates collected in malaise traps 1 year after herbicide application. More specifically, the abundance and species richness of predacious and herbivorous beetles, the abundance of introduced species, and the species richness of native and introduced species were all significantly higher in the herbicide-treated plots than in the unsprayed plots. No willow-dependent beetle taxa were found during the present study confirming observations by Harman (2004) that mostly generalist insect taxa have been recorded feeding on grey willow in New Zealand. The composition of the beetle community separated into two clear groups—plots before treatments and plots after herbicide application. This appears to be driven by complex changes in vegetation, including both canopy collapse and the invasion of new plant species, predominantly weedy introduced annuals and perennials, 1 year after herbicide application.

Table 5 Environmental variables explaining significant variation in beetle species composition

Environmental variables	Code	Correlation coefficient
Canopy density	CD	0.809
Total grey willow cover	%WC	0.765
Average grey willow canopy height	AWH	0.746
Average number of grey willow stems	ANW	0.715
Introduced plant species richness	ISP	0.701
Total plant species richness	TSP	0.698

Correlation coefficients were calculated between environmental variables and SSH ordination axis scores using PCC analyses in PATN. Correlation coefficients presented are significant at $P < 0.01$

One and two years after herbicide spray, there were consistent increases in the total abundance of invertebrates and mean abundance of the six Orders analysed compared with the unsprayed plots. The only exception was the abundance of Hemiptera, which increased in unsprayed plots in 2014 with the invasion of the introduced giant willow aphid (*T. salignus*) at the study site. These sap-feeding aphids are very large (>5 mm body length), can reach high densities on their host plants (*Salix* and *Populus* spp.) and excrete vast amounts of sugar-rich honeydew (Collins et al. 2001). They were first recorded in Auckland in late December 2013 and since then have rapidly spread throughout New Zealand (Sopow et al. 2014). In addition, the abundances of Hymenoptera (mainly introduced *Vespula* spp.) also increased in the unsprayed plots in 2014. This increase was likely to be correlated with the invasion of the introduced giant willow aphid as *Vespula* wasps were observed feeding on the copious amounts of honeydew produced by the giant willow aphid. *Vespula* species are a conspicuous component of other ecosystems where honeydew provides an energy source for birds and insects (Beggs 2001; Murphy and Kelly 2003).

We have evidence that environmental factors associated with the death of grey willow trees, such as less dense canopy and less grey willow cover and height, influenced beetle species composition within the herbicide treatment due to simplification of habitat structure. Other studies have shown strong correlations between invertebrate assemblages and habitat structure, particularly vegetation (Davis et al. 2002; Grimbacher and Catterall 2007; Watts et al. 2012). Canopy density and height have been shown to influence invertebrate communities and other functionally important environmental attributes (Nakamura and Yamada 2005; Watts et al. 2008).

The increased abundance and species richness of beetles in the herbicide treatment appeared to be partly explained by the increase in plant diversity as indicated by the ordination. The open habitat under the dead willow trees allowed 24 new introduced plant species to invade and establish. Other studies have found greater abundances and species richness of insects in areas with higher plant diversity (Crisp et al. 1998; Haddad et al. 2001; Watts and Gibbs 2002). Higher plant species richness can provide greater structural complexity, more habitat variation and a greater diversity of alternate resources (Haddad et al. 2001). When considered at a functional trait level, our results were consistent with other long-term studies that have found herbivore and predator arthropod species richness was strongly and positively related to plant species richness (Haddad et al. 2009). Furthermore, the increase in introduced beetles in the herbicide-treated plots may be a result of an increase (24 species) in introduced plant species 1 year after control. Other studies have also found a positive relationship between the proportions of introduced and native beetles and the proportions of introduced and native plant species present at a site (Kuschel 1990; Watts et al. 2012). The marginal decline in the diversity and abundance of introduced beetles in the herbicide-treated plots 2 years after control parallels a minor reduction in the richness of introduced plant species recorded as native wetland sedges became common.

Watts et al. (2012) found that introduced beetles dominated willow-invaded wetlands. In contrast, we found that native beetles prevailed in the grey willow swamp forest at Whangamarino, a result we attribute to three reasons. First, the understorey (approximately <2 m) beneath the grey willow supported a diverse native wetland plant community, including *M. rubiginosa*, *C. secta* and *C. tenuicaulis*. Second, the area surrounding the willow-infested habitat was large (>1200 ha), dominated by native species-rich wetland vegetation. This habitat would act as a source for native invertebrates to colonise the willow-invaded habitat. Third, the grey willow sampled may not have been there long enough (25 years) to influence changes in the invertebrate assemblages to becoming a community dominated by introduced taxa (Watts et al. 2012). We also found an increase in the native beetle species richness post-treatment. One year post-spray, we found nine new native beetle species present in the herbicide treatments. Similar to the long-term resident native beetle taxa found during the study, all of these new species were generalists.

One year after herbicide application, there was an influx of introduced plants, in terms of both species richness and % vegetation cover. However, this was short term and
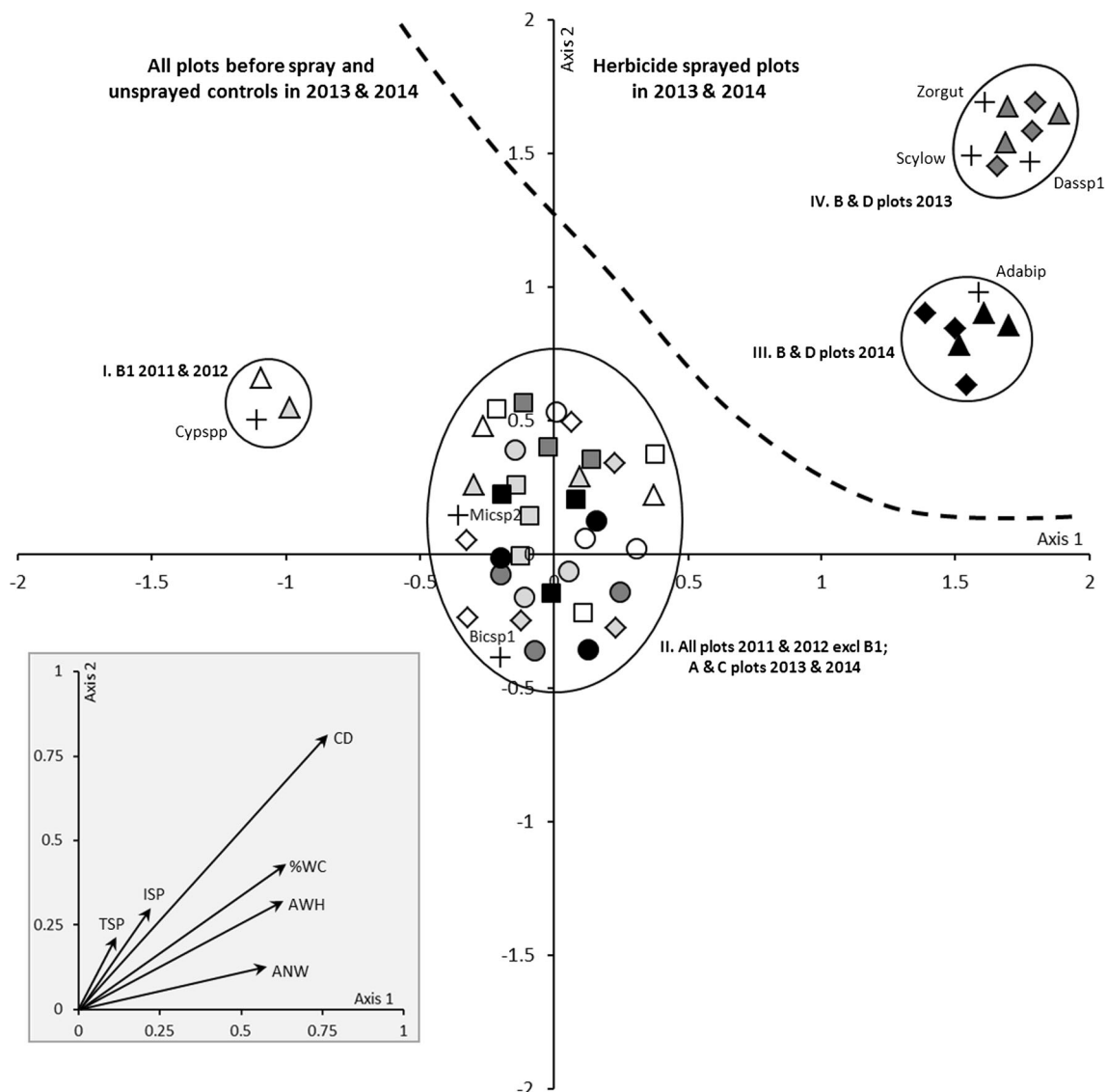
Fig. 6 Distribution of beetle species (+) caught in malaise traps (*symbols*) defined by the two-dimensional SSH ordination analyses. Four groupings with similar beetle species composition identified by the FUSE clustering analysis have been superimposed as ellipses around plots: (group I) plots B1 in 2011 and 2012; (group II) all plots sampled in 2011 and 2012, excluding B1 and plots A and C in 2013 and 2014; (group III) all B and D plots in 2014; and (group IV) all B and D plots in 2013. *Squares* A plots (unsprayed), *triangles* B plots (herbicide-treated), *circles* C plots (unsprayed); and *diamonds* D plots (herbicide-treated). *White symbols* samples collected in 2011, *light grey symbols* samples collected in 2012, *dark grey symbols* samples collected in 2013 and *black symbols* samples collected in 2014. *Inset* significant (*P* value <0.01) environmental variables defined by the two-dimensional SSH ordination analyses. The length of the environmental arrow indicates the degree of corrections, and the angle between the arrows shows the degree of intercorrelation in their effects on beetle community composition. See Table 5 for environmental variable codes

declined 2 years after spray. The majority (19) of the 24 introduced plants recorded after the spray were weedy annuals and perennials, such as Australian fireweed (*Senecio bipinnatisectus*), Brazilian fireweed (*Erechtites valerianifolia*) and Scotch thistle (*Cirsium vulgare*). An increase in the diversity of palatable, flowering introduced plant species in the herbicide treatment after willow control creates an additional food source that may have caused the unexpected increase in the abundance and species richness of opportunistic herbivorous beetles. For example, *Dasytes*

sp. 1 (Melyridae) was not collected in pre-treatment, but hundreds were caught in the herbicide treatment later. The adults of soft-winged flower beetles feed predominantly on the pollen of flowering annuals or perennials (Klimaszewski and Watt 1997). In addition, two native species of tumbling flower beetles (*Mordella promiscua* and *Zeamordella monacha*; Mordellidae) were frequently observed in the field feeding on the pollen in the flowers of Australian fireweed, Brazilian fireweed and ragwort (*Senecio vulgaris*). These beetle species also considerably increased

in the herbicide-treated plots 1 and 2 years after spray. Previous work has demonstrated that the abundance of herbivores was significantly lower in weed-invaded habitats compared with native vegetation, but this was highly dependent on the palatability of the invasive plant species (Gerber et al. 2008).

Significant increases in the diversity of herbivorous insects, as observed in the beetles in the present study, may also support a greater diversity of higher trophic groups such as insect predators (Knops et al. 1999). Before herbicide treatment, 10 predacious beetle species with less than 8 specimens each were caught. Following herbicide treatment, 11 new species with up to 386 specimens per taxa were collected. The most species-rich family was the Coccinellidae (ladybirds), with 10 species. The introduced two-spotted ladybird (*Adalia binpuctata*) increased from an average of 2 beetles per trap before spray to 31 per trap after herbicide treatment. The increase in predacious beetle taxa and in the abundance of spiders at the herbicide-treated plots is likely to be caused by an increase in their food source as indicated by an increase in the herbivorous beetles, and probably other herbivorous insects (e.g. aphids, Hemiptera) in general. In other studies, consumer groups (e.g. herbivores and their natural enemies) associated with weed vegetation were positively linked to the diversity and abundance of their resource (Hawes et al. 2003; Poyry et al. 2006).

Unexpectedly, we found no evidence that the abundance and diversity of detritivorous beetles differed with habitat change after grey willow control. Watts et al. (2012) found that the beetle fauna in willow-dominated wetlands was characterised by detritivores resulting from increased amounts of coarse woody debris compared with native sedgelands. In contrast, other studies have found that detritivores were underrepresented in weed-invaded habitats as a result of poor litter quality; trends, however, were species dependent (Gerber et al. 2008). There is mixed evidence that decomposition rates are influenced by the species richness of decomposer communities (Gessner et al. 2010). However, a recent study strongly indicated that the diversity of decomposer body size was consistently positively correlated with decomposition rates across biomes (Handa et al. 2014). While we did not directly measure decomposition rates in the field, it is likely that these have not changed substantially with willow control as the detritivorous beetle communities did not differ over the four-year study. In the present study, the dead willow trunks were still standing, possibly continuing to provide habitat and shade for detritivorous taxa. When the dead willow stems fall and create coarse woody debris on the ground surface, we would expect detritivorous taxa to increase in the herbicide-treated plots.

Our study suggests that beetles could potentially be used as bioindicators as they reflected similar patterns of change

in abundance observed in the total invertebrate abundance and some Orders (e.g. Lepidoptera, Diptera and Araneae). In addition, these changes were observed over a relatively short period of time. Beetles have been considered to be representative of insects in general (Hutcheson 1990) largely due to their functional and taxonomic diversity (New 2010). Further work is required to identify specimens of the other Orders sampled from Whangamarino to species level. This would determine whether these Orders showed the same taxonomic and functional changes that were observed in the beetles and allow conclusions to be drawn regarding the suitability of beetles as bioindicators.

To date, changes in the invertebrate communities have reflected changes in the vegetation following grey willow control. However, the wetland vegetation is in a state of transition, and it is unknown how the invertebrate community will respond in the longer term (>5–10 years) to the removal of grey willows. The ordination analysis indicated that the beetle communities within the herbicide treatment 2 years after spray were distinct. At this time, a number of young grey willow seedlings (< 2 m) had established in the plots. If these willows grow and spread, it is likely that the insect communities, particularly beetles, would return to communities similar to those sampled before spray or that had no spray. If grey willows are prevented from establishing in the plots and native sedges dominate, then it is likely that the trajectory of the invertebrate community will become more typical of assemblages found within native wetland ecosystems. Watts et al. (2012) found that the composition and functional traits of the beetle community in restored native wetlands 9 years after willow removal were similar to non-invaded native wetlands. However, long-term assessments (>10–20 years) are required to monitor the trajectories of the recovery of the invertebrate community after grey willow control.

In contrast to our original predictions, we observed an increase in the abundance of invertebrates, introduced and herbivorous beetles, and no change in the detritivorous beetles in the 2 years following grey willow control. The fluctuations were driven by complex changes in the vegetation associated with the canopy collapse of grey willow trees and the initial influx of introduced plant species, predominantly weedy annuals and perennials, after willow control. While the native plant species richness and % cover declined in the first year after willow control, it appears that this was recovering to pre-spray levels 2 years after treatment. Our study supports increasing evidence that restoration via invasive plant control can promote the reestablishment of invertebrate communities typical of native wetlands (Watts et al. 2012), at least in the short term. However, the long-term viability of invertebrate communities at Whangamarino should focus on restoration of native ecosystem resilience, involving combinations of

willow control, minimising re-invasion, and re-establishing native species (e.g. *Dacrycarpus dacrydioides*) capable of outcompeting willow.

References

Beard C (2010) Wetlands and lowland floodplains. In: Collier KJ, Hamilton DP, Want WN, Howard-Williams C (eds) The waters of the Waikato. Ecology of New Zealand's longest river. Environment Waikato and the Centre for Biodiversity and Ecology Research (The University of Waikato), Hamilton, pp 265–279

Beggs J (2001) The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. Biol Conserv 99:17–28

Belbin L (1995) PATN: pattern analysis package. CSIRO Division of Wildlife and Ecology, Canberra

Bodmin KA, Champion PD (2010) Review of Whangamarino Wetland vegetation response to the willow control programme (1999–2008). NIWA client Report HAM 2010-010. National Institute of Water and Atmospheric Research Ltd, Hamilton, New Zealand, 73 p

Champion P (1994) Extent of willow invasion—the threats. In: West CJ (ed) Wild willows in New Zealand. Proceedings of a willow control workshop hosted by Waikato Conservancy, Hamilton. Department of Conservation, New Zealand, pp 43–49

Collier KJ (1994) Effects of willows in waterways and wetlands—an aquatic habitat perspective. In: West CJ (ed) Wild willows in New Zealand. Proceedings of a willow control workshop hosted by Waikato Conservancy, Hamilton. Department of Conservation, New Zealand, pp 33–41

Collins CM, Fellowes MDE, Sage RB, Leather SR (2001) Host selection and performance of the giant willow aphid, *Tuberolachnus salignus* Gmelin—implications for pest management. Agric For Entomol 3:183–189

Crisp PN, Dickinson KJM, Gibbs GW (1998) Does native invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation. Biol Conserv 83:209–220

Davis ALV, Van Aarde RJ, Scholtz CH, Delport JH (2002) Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. Glob Ecol Biogeogr 11:191–209

Duggan K, Roberts L, Beech M, Robertson H, Brady M, Lake M, Jones K, Hutchinson K, Patterson S (2013) Arawai Kakariki wetland restoration. Research and Development Group, Department of Conservation, Wellington

ESRI (1999) ArcView 3.2. Environmental Systems Research Institute. ArcView GIS: Release 3.2 [software]. Environmental Systems Research Institute, 1992–1999, Redlands, California

Franz JE (1985) Discovery, development and chemistry of glyphosate. In: Grossbard E, Atkinson D (eds) The herbicide glyphosate. Butterworth, London, pp 3–15

Froude VA (2002) Biological control options for invasive weeds of New Zealand protected areas. Prepared for Department of Conservation, New Zealand, 68 p

Gerber E, Krebs C, Murrell C, Moretti M, Rocklin R, Schaffner U (2008) Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. Biol Conserv 141:646–654

Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. J Insect Conserv 17:831–850

Gessner MO, Swan CM, Dang CK, McKie BG, Bardgett RD, Wall DH, Hattenschwiler S (2010) Diversity meets decomposition. Trends Ecol Evol 25:372–380

Gratton C, Denno RF (2005) Restoration of arthropod assemblages in a Spartina salt marsh following removal of the invasive plant *Phragmites australis*. Restor Ecol 13:358–372

Grégoire Taillefer A, Wheeler T (2012) Community assembly of Diptera following restoration of mined boreal bogs: taxonomic and functional diversity. J Insect Conserv 16:165–176

Grimbacher PS, Catterall CP (2007) How much do site age, habitat structure and spatial isolation influence the restoration of rainforest beetle species assemblages? Biol Conserv 135:107–118

Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. Am Nat 158:17–35

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. Ecol Lett 12:1029–1039

Handa IT, Aerts R, Berendse F, Berg MP, Bruder A, Butenschoen O, Chauvet E, Gessner MO, Jabiol J, Makkonen M, McKie BG, Malmqvist B, Peeters E, Scheu S, Schmid B, van Ruijven J, Vos VCA, Hattenschwiler S (2014) Consequences of biodiversity loss for litter decomposition across biomes. Nature 509:218–221

Harman HM (2004) Feasibility of biological control of grey willow, *Salix cinerea*. DOC Science Internal Series 183. Department of Conservation, Wellington, New Zealand, 29 p

Hawes C, Haughton AJ, Osborne JL, Roy DB, Clark SJ, Perry JN, Rothery P, Bohan DA, Brooks DR, Champion GT, Dewar AM, Heard MS, Woiwod IP, Daniels RE, Young MW, Parish AM, Scott RJ, Firbank LG, Squire GR (2003) Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide–tolerant crops. Philos Trans R Soc Lond B Biol Sci 358:1899–1913

Heads MJ, de Lange PJ (1999) *Parsonia praeruptis* (Apocynaceae): a new threatened, ultramafic endemic from North Cape, New Zealand. N Z J Bot 37:1–6

Herrera AM, Dudley TL (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. Biol Invasions 5:167–177

Hulme PE, Bremner ET (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. J Appl Ecol 43:43–50

Hutcheson J (1990) Characterization of terrestrial insect communities using quantified, Malaise-trapped Coleoptera. Ecol Entomol 15:143–151

Hutcheson J, Jones D (1999) Spatial variability of insect communities in a homogenous system: measuring biodiversity using Malaise trapped beetles in a *Pinus radiata* plantation in New Zealand. For Ecol Manag 118:93–105

Hutcheson JA, Kimberley MO (1999) A pragmatic approach to characterising insect communities in New Zealand: Malaise trapped beetles. N Z J Ecol 23:69–79

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Klimaszewski J, Watts JC (1997) Coleoptera: family-group review and keys to identification. Fauna of New Zealand Number 37. Manaaki Whenua Press. Canterbury, New Zealand

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286–293

Kolpin DW, Thurman EM, Lee EA, Meyer MT, Furlong ET, Glassmeyer ST (2006) Urban contributions of glyphosate and its degradate AMPA to streams in the United States. Sci Total Environ 354:191–197

Kuschel G (1990) Beetles in a suburban environment: a New Zealand case study. DSIR Plant Protection report no. 3, Department of Scientific and Industrial Research, 118 p

Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc B Biol Sci 270:775–781

Murphy DJ, Kelly D (2003) Seasonal variation in the honeydew, invertebrate, fruit and nectar resource for bellbirds in a New Zealand mountain beech forest. N Z J Ecol 27:11–23

Nakamura F, Yamada H (2005) Effects of pasture development on the ecological functions of riparian forests in Hokkaido in northern Japan. Ecol Eng 24:539–550

New TR (2010) Butterfly conservation in Australia: the importance of community participation. J Insect Conserv 14:305–311

Poyry J, Luoto M, Paukkunen J, Pykala J, Raatikainen K, Kuussaari M (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. Oikos 115:401–412

Sopow S, Gresham B, Gunawardana D, Flynn A (2014) *Tuberolachnus salignus*, a new aphid on the block. Forest Health News 246. Newsletter of the Scion Forest Protection team, Rotorua, New Zealand

Standish RJ, Robertson AW, Williams PA (2001) The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. J Appl Ecol 38:1253–1263

van Kraayennoord CWS, Slui B, Knowles FB (1995) Introduced forest trees in New Zealand, 15. The willows. Forest Research Institute Bulletin No. 124, New Zealand, 32 p

VSN International (2013) GenStat for windows, 16th edn. VSN International, Hemel Hempstead

Watts CH, Gibbs GW (2002) Revegetation and its effect on the ground-dwelling beetle fauna of Matiu-Somes Island, New Zealand. Restor Ecol 10:96–106

Watts CH, Clarkson BR, Didham RK (2008) Rapid beetle community convergence following experimental habitat restoration in a mined peat bog. Biol Conserv 141:568–579

Watts C, Rohan M, Thornburrow D (2012) Beetle community responses to grey willow (*Salix cinerea*) invasion within three New Zealand wetlands. N Z J Zool 39:209–227

Wilkinson AG (1999) Poplars and willows for soil erosion control in New Zealand. Biomass Bioenergy 16:263–274