# Characterising alligator weed (*Alternanthera philoxeroides*; Amaranthaceae) invasion at a northern New Zealand lake

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**Abstract:** Exotic plant invasions are a key threat to New Zealand biodiversity. Alligator weed (*Alternanthera philoxeroides*; Amaranthaceae) is an invasive, herbaceous weed native to South America. Little is known about its dynamics in natural ecosystems in its introduced range, despite known agricultural impacts. We quantified alligator weed infestation at Lake Rotokawau, Northland, and investigated alligator weed's relationship with other vegetation, both native and exotic, over a year (Nov. 2005 to Sep. 2006). We also examined the relationship between native vegetation and 'other' exotic vegetation at the site. Alligator weed, at its peak in spring, covered over 20% of the surveyed lake margin. Plant community composition of plots without alligator weed differed significantly from invaded plots even when alligator weed itself was removed from the analysis. Uninvaded plots were characterised by low beta-diversity and predominantly terrestrial plant species, with *Phormium tenax* contributing 41% of within-group similarity. In contrast, invaded plots had higher beta-diversity and were characterised by a variety of emergent sedges and herbs. Alligator weed cover was negatively related to cover of natives but not cover of 'other' exotics. Alligator weed cover was not related to species richness of natives or 'other' exotics. 'Other' exotic species were positively related to native cover and richness, likely due to shared responses to favourable environmental conditions.

**Keywords:** aquatic ecosystem; invasive species; novel ecosystem; plant community; species richness; vegetation cover

## Introduction

Invasive plants are widely recognised as one of the most important threats to native plant biodiversity (Kolar & Lodge 2001). Invasive species are those that proliferate, spread and persist in a new range to the detriment of the pre-existing native ecosystem (Mack et al. 2000; ISSG 2008). (Here we use 'exotic' to refer to non-native species, not all of which are invasive.) Invasive plants are considered contributing factors in the decline of 57% of New Zealand's two highest priority categories of threatened native plant species, with wetland species among those most vulnerable to weed encroachment (Dopson et al. 1999). Domination of a plant community by an invasive species alters, and often simplifies, the community. For example, invasion by the aquatic herb *Myriophyllum spicatum* (Haloragaceae) led to the loss of 13 of the 20 native species in a New York lake over 11 years, due to dense canopy formation and overshadowing of native species (Boylen et al. 1999), while both reed canary grass (*Phalaris arundinacea*; Poaceae) and the herb purple loosestrife (*Lythrum salicaria*; Lythraceae) were found to reduce plant community diversity in wetlands in the Pacific Northwest (Schooler et al. 2006).

Factors such as species diversity and available resources are recognised to influence invasion success. Elton (1958) suggested species diversity as a protective factor against invasion by exotic species, with more diverse ecosystems expected to have greater resource-use complementarity, leaving fewer unused resources available for invading species (van Ruijven et al. 2003). Some experimental work manipulating species richness has supported this theory (Naeem et al. 2000; van Ruijven et al. 2003). However, in some cases this may reflect sampling effects such as the increasing frequency of occurrence of a single, highly competitive species in more diverse plots (Wardle 2001). Studies correlating invader abundance with diversity in the field have often found exotic and native plant species richness to be positively correlated at broad spatial scales (Hager & Vinebrooke 2004; Houlahan & Findlay 2004; Fridley et al. 2007). This is likely to be because both native and exotic species respond similarly to the same environmental factors (e.g. nutrient levels) (Levine & D'Antonio 1999). For instance, Wiser et al. (1998) tracked invasion of New Zealand mountain beech (*Nothofagus solandri* var. *cliffortioides*; Nothofagaceae) forest by *Hieracium lepidulum* (Asteraceae) for 23 years, using permanent plots (400 m²). Invaded plots had higher species richness than uninvaded plots. At smaller spatial scales, effects of competition between individuals become more apparent. Thus at small scales, both negative and positive relationships have been observed between native and exotic species richness, reflecting variation in environmental characteristics such as productivity and homogeneity, which determine whether competitive exclusion or co-existence is favoured (Davies et al. 2007).

### Alligator weed

Alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb.; Amaranthaceae) is a herbaceous, stoloniferous perennial that grows either as a rooted emergent aquatic weed or in damp terrestrial sites. Native to South America, alligator weed's introduced range includes New Zealand, Australia, Asia, and more recently parts of Europe (Julien 1995; Julien et al. 1995;

Wagh et al. 1995; Stewart et al. 1996; Garbari & Pedulla 2001). In aquatic systems, alligator weed is characterised by very rapid growth beginning in spring, forming a dense mat of vegetation over the water's surface. In New Zealand, aquatic alligator weed is partially controlled by an introduced biological control agent, the alligator weed flea beetle (*Agasicles hygrophila*; Chrysomelidae). Herbivory by the flea beetle causes rapid dieback of large amounts of alligator weed in a short period of time during summer (Stewart et al. 2000; Bassett et al. 2010). In contrast, uncontrolled alligator weed continues strong growth throughout summer, with more gradual senescence in autumn/winter in response to cooler temperatures (Julien et al. 1992; Liu et al. 2004). In pasture ecosystems, alligator weed steadily increases in biomass and displaces other species (Julien & Bourne 1988), while alligator weed invasion may lead to yield losses of up to 45% for some horticultural crops (Shen et al. 2005). It is generally thought that this species decreases plant diversity and disrupts the ecology of invaded sites (Julien 1995; Timmins & Mackenzie 1995). However, these conclusions are based on research in pastoral ecosystems and casual observations in native systems. Few quantitative data have been collected on the ecology of alligator weed in natural ecosystems, although it has recently been found to alter nutrient cycling patterns and restructure invertebrate communities in a New Zealand lake system (Bassett et al. 2010, 2011). A range of native plant species have been recorded growing within floating alligator weed mats in China (Liu & Yu 2005), although another study from China found that diversity decreased with increasing dominance of alligator weed (Lin & Qiang 2006).

Our study aimed to investigate the role of alligator weed in a natural ecosystem in New Zealand. Ideally, plant communities would have been measured in a number of lakes with and without alligator weed invasion. However, many of New Zealand's wetlands are heavily degraded, and there is a strong imperative to control aggressive invaders such as alligator weed in those wetlands that retain some biodiversity value. Therefore this study was restricted to a description of a single invaded lake ecosystem. First, we quantified the extent of alligator weed infestation at the lake. We then tested the following hypotheses: (1) that community composition would vary with degree of alligator weed invasion (even when excluding alligator weed itself from analyses); (2) that alligator weed cover would be negatively related to cover and richness of native and 'other' exotic plant species; (3) that native and 'other' exotic plant species would be positively correlated with each other, reflecting similar responses to environmental variables.

## Methods

### Study site

The study was conducted at Lake Rotokawau (East), on the Karikari Peninsula, Northland, New Zealand (34.872 S, 173.319 E). The lake is 21.3 ha in area, shallow (< 1 m deep in summer) with an iron-pan base (Champion et al. 2005; Wells & Champion 2010). Most of the banks slope gently (<20°) although the northern edge slopes at almost 90° in places. The surrounding landscape is mostly human-modified, predominantly pastoral farming. This has likely contributed to the lake's hypertrophic nutrient status (Northland Regional Council 2005). The lake is surrounded by terrestrial scrub comprised of a mixture of native species such as mānuka (*Leptospermum scoparium*; Myrtaceae), bracken (*Pteridium esculentum*; Pteridaceae) and flax (*Phormium tenax;* Hemerocallidaceae), with some exotics, such as *Acacia longifolia* (Mimosoideae). Where the ground becomes seasonally inundated, this scrub gives way to a mosaic of native sedges, reeds and small aquatic herbs. In places, this region also includes a variety of exotic grasses and herbs, as could be expected given the dominance of exotic plants in the surrounding pastoral landscape, and the thin shape of the study site, with edge effects likely to increase invasion risk. Mean annual temperature is 15.1°C (summer mean 20°C, winter mean 11.8°C); and mean annual rainfall 1664 mm (Kerikeri Weather Station 2011).

### Sampling techniques

Plots (5 × 5 m) were examined at 50-m intervals around the entire circumference of the lake. This resulted in a total of 28 replicate 25-m$^2$ plots. Plots were centred on the elevational zone occupied by alligator weed (mean water depth ranging from $0.24 \pm 0.05$ m in late summer to $0.69 \pm 0.03$ m in winter). All emergent vascular plants within each quadrat were identified, and assigned a percentage cover score from 1 to 5, on a modified Braun-Blanquet scale, with cover categories as follows: 1 = present with > 0 and < 5% cover; 2 = 5–24%; 3 = 25–49%; 4 = 50–74%; 5 = 75–100%. Cover measurements were repeated at 3-monthly intervals from November 2005 to September 2006. The term 'other' exotics is used henceforth to refer to all other exotic plants, excluding alligator weed. Water depth was measured at all four corners of each quadrat at each sampling date. Means of the two shoreward corners of each plot were treated as 'top depth', while means of the two corners furthest from shore were used as a measure of 'bottom depth'.

### Analyses

Alligator weed cover was greatest in spring. We thus used spring cover values as the basis for estimating total alligator weed cover, to describe the extent of overall invasion at the site. For this estimate, cover band scores were transformed to their minimum cover percentage, using 1% as the minimum for the <5% category. These minimum values thus provide a conservative estimate of total alligator weed coverage at its peak. Cover data were back-transformed to cover band mid-points for all seasons for all remaining analyses relating to our hypotheses.

*Hypothesis 1. That vegetation composition will vary with degree of alligator weed invasion*

ANOSIM (Analysis of Similarity) was used to investigate differences in community composition between plots without alligator weed and those with 'low' (cover score 1 or 2) or 'high' (cover score ≥ 3) cover of alligator weed, for each month separately. Data were square-root-transformed to down-weight the influence of dominant species, and a Bray–Curtis similarity coefficient was used to generate a dissimilarity matrix (Clarke & Warwick 2001). ANOSIM uses the dissimilarity matrix to generate an R-statistic that reflects the relative compositional differences between groups (absent, low, high alligator weed cover) vs within groups, and varies between −1 and 1, with 0 indicating completely random grouping, and 1 indicating total separation of groups. The dissimilarity matrix was also used to generate NMDS (non-metric multi-dimensional scaling) ordinations, which visually depict the relative dissimilarity

between plots. To identify species most responsible for differentiation between groups, we used SIMPER ('similarity percentage') analysis (Clarke & Warwick 2001). SIMPER quantifies the similarity within, and differences between, groups (i.e. beta-diversity), and the relative contribution of each species to these statistics. Similar trends were detected for all seasons, so results are presented here only for spring, in which differences were most pronounced.

*Hypothesis 2: That alligator weed cover would be negatively related to cover and richness of native and 'other' exotic plant species*
Native and exotic species cover were each compared between plots with or without alligator weed. This was done using binomial mixed models, including plot, season (i.e. time) and water depth (both top and bottom of plots) as random effects. We then excluded plots without alligator weed, and examined the relationship between alligator weed cover and native or 'other' exotic cover for only those plots where alligator weed was present. For this we used linear mixed models, again including plot, season and water depth (both top and bottom of plots) as random effects.

To examine the relationship between native species richness and alligator weed cover, we used a Poisson general linear mixed-effects model of native species richness as a function of alligator weed cover, including also 'other' exotic species richness, 'other' exotic cover, plot, season (i.e. time), and top and bottom water depths as random effects. Similarly, to examine the relationship between 'other' exotic species richness and alligator weed cover, we used a Poisson general linear mixed-effects model of 'other' exotic species richness as a function of alligator weed cover, including also native species richness, native cover, plot, season (i.e. time), and top and bottom water depths as random effects.

*Hypothesis 3: That native and 'other' exotic plant species would be positively correlated with each other*
To examine the relationship between cover of native and 'other' exotic plants, we used a linear model of native cover as a function of exotic cover, including plot, season and water level (top and bottom) as random effects in the model. The Poisson general linear mixed-effects model for 'other' exotic species richness, described above for Hypothesis 2, was also used to examine the relationship between 'other' exotic richness and native species richness.

Analyses were performed in R (v.2.13.1; R Development Core Team 2005) and PRIMER v6 (Clarke & Gorley 2006; http://www.primer-e.com/).

## Results

In summer, alligator weed was present in 27 of the 28 25-m$^2$ plots at Lake Rotokawau, while in all other seasons it was present in 24 of the plots, though not always the same 24 plots. At its peak (spring), alligator weed covered an average of 22.6 ± 4.0% of the 25-m$^2$ plots.

Other exotic plants recorded include terrestrial species at the upper edges of 25-m$^2$ plots, such as gorse (*Ulex europeaus*; Fabaceae) and woolly nightshade (*Solanum mauritianum*; Solanaceae)*,* as well as grasses and herbs of aquatic margins, such as *Paspalum* spp. (Poaceae) and *Lotus pedunculatus* (Fabaceae). Native species ranged from emergent aquatics, including numerous sedge and rush species (e.g. *Machaerina juncea* (previously *Baumea*), *M. teretifolia*, *Eleocharis acuta*, *E. sphacelata* (Cyperaceae); *Typha orientalis* (Typhaceae)), to small aquatic herbs (e.g. *Myriophyllum propinquum* (Haloragaceae) and *Glossostigma elatinoides* (Phrymaceae)) and the larger herb *Persicaria decipiens* (Polygonaceae), woody terrestrial species (e.g. *Coprosma propinqua* (Rubiaceae)*, Leucopogon fasciculatus* (Ericaceae), *Leptospermum scoparium* (Myrtaceae)) and those with an affinity for moist terrestrial margins (e.g. *Phormium tenax* (Hemerocallidaceae)*,* and the ferns *Histiopteris incisa* (Dennstaedtiaceae), *Adiantum cunninghamii* and *A. hispidulum* (Pteridaceae)). No threatened native plants were recorded at the site, although the regionally uncommon *Empodisma minus* (Restionaceae) was present.

**Hypothesis 1. That vegetation composition will vary with degree of alligator weed invasion**
Plots without alligator weed in spring were clearly separated from those with alligator weed by ANOSIM and NMDS (Table 1, Fig. 1a). This effect was still apparent, though weakened, even when alligator weed was removed from the analysis, indicating that plots with alligator weed differed significantly from uninvaded sites in terms of other plant species composition, rather than just being defined by dominant alligator weed (Table 1, Fig. 1b). Interestingly, the centroids are similar for low and high invasion, so statistical differences must reflect differences in dispersion around those centroids.

**Table 1.** Relative similarity of plant community composition in plots at Lake Rotokawau (northern New Zealand), in austral spring 2006, with varying degrees of alligator weed invasion. R-statistics closer to 1.00 indicate a high degree of dissimilarity between sites with the two cover levels compared in a given row: where alligator weed was included, overall R-statistic = 0.65, $P$ = 0.001; where alligator weed was excluded, overall R-statistic = 0.28, $P < 0.01$. Pair-wise statistics are presented in the table. 'Low' alligator weed cover = alligator weed present but covering < 25% of plot; 'high' alligator weed cover, > 25% of plot.

| Alligator weed cover levels being compared | Alligator weed included in analysis | | Alligator weed excluded from analysis | |
|---|---|---|---|---|
| | R-statistic | P-value | R-statistic | P-value |
| Absent vs low | 0.70 | < 0.01 | 0.45 | < 0.05 |
| Absent vs high | 0.98 | 0.001 | 0.58 | < 0.01 |
| Low vs high | 0.42 | 0.001 | 0.06 | 0.22 |
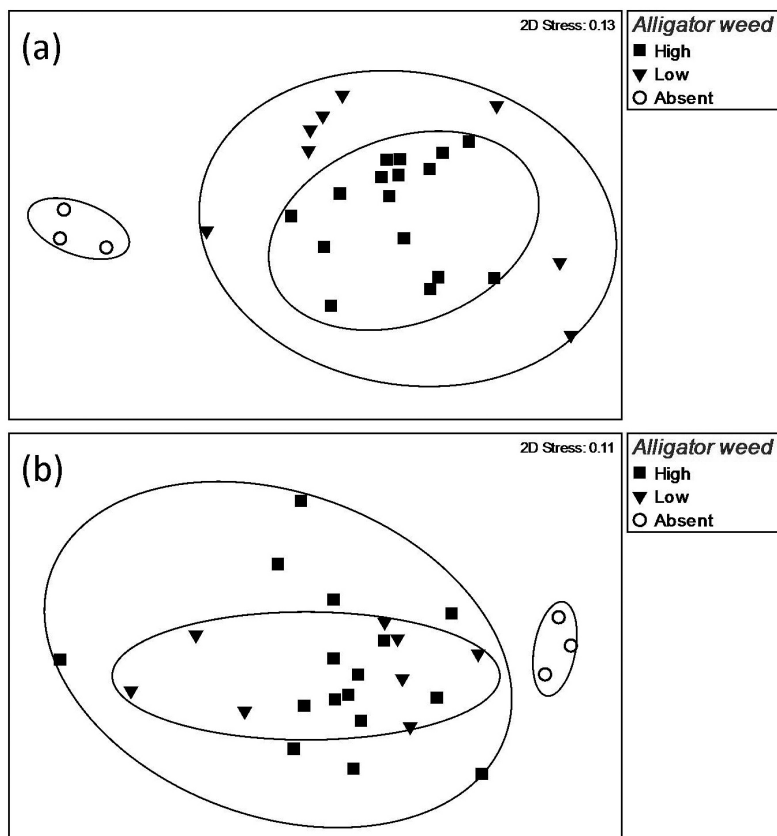
**Figure 1.** Relative similarity of 25-m$^2$ plots at Lake Rotokawau (northern New Zealand) by plant community composition in austral spring 2006, as depicted by NMDS: (a) with alligator weed (*Alternanthera philoxeroides*) cover included in analysis, and (b) with alligator weed cover excluded from analysis. Plots further apart are more dissimilar in composition than those closer together. See Table 1 for significance values from corresponding ANOSIM analyses.

In contrast, once alligator weed was excluded, no differences were detected between plots with high or low cover of alligator weed (Table 1, Fig. 1b). SIMPER analysis indicated that plots without alligator weed in spring were dominated by native flax *Phormium tenax* (Hemerocallidaceae; responsible for 41% of within-group similarity and 14% of difference between sites with alligator weed absent vs high cover) and bracken fern (*Pteridium esculentum*, Pteridaceae; 17% of within-group similarity and 8% of difference between sites with alligator weed absent vs high cover), and the exotic *Ageratina adenophora* (Asteraceae; 41% of within-group similarity and 15% of difference between sites with alligator weed absent vs high cover). These plots from which alligator weed was absent also had very high within-group similarity (74%). The low sample size for this group may have contributed to their high within-group similarity. In contrast, within-group similarity was much lower for plots with low or high alligator weed cover (20% and 23% respectively). Plots with high alligator weed cover in spring were characterised by abundant exotic *Paspalum distichum* and *P. urvillei* (Poaceae; combined responsible for 42% of within-group similarity), several native sedge species (Cyperaceae; combined responsible for 25%), and native herbs *Persicaria decipiens* (Polygonaceae; 11%) and *Glossostigma elatinoides* (Phrymaceae; 10%).

Plots without alligator weed in spring were also characterised by deeper water stopping abruptly at high vertical banks (reflected in the more terrestrial nature of plants at the upper margin of these plots), contrasting with the very low slope of banks, and resulting shallow water, characterising the more heavily invaded parts of the lake margin. However, it should be noted that differences in water level and bank slope were only apparent observationally, based on the spring dataset used for the NMDS. In contrast, a linear model for the entire data set (rather than the single month presented above for multivariate analyses) did not show any relationship between alligator weed cover and water depth (top depth $P = 0.93$, bottom depth $P = 0.49$) when controlling for plot, season and cover of native and 'other' exotic plants. Native cover was similarly unrelated to water depths in a binomial (alligator weed present/absent) mixed effects model ($P = 0.06$ for bottom depth and $P = 0.49$ for top depth). In contrast to alligator weed and native cover, cover of 'other' exotics was significantly related to water depth in a binomial (alligator weed present/absent) mixed-effects model (top depth $P = 0.01$, bottom depth $P = 0.02$). The relationship was negative for bottom depth, and positive for top depth, indicating that the 'other' exotics at the site favoured intermediate water depths within the elevational zone sampled (although a different suite of more terrestrial exotics would be well represented if higher elevational zones were also sampled; I. Bassett pers. obs.).

**Hypothesis 2: That alligator weed cover would be negatively related to cover and richness of native and 'other' exotic plant species**

Native cover did not differ between plots with alligator weed and plots without alligator weed, using the binomial model introduced above ($P = 0.37$). However, where alligator weed was present, native cover had a negative, linear relationship with alligator weed cover ($P < 0.001$; Fig. 2a). A binomial model indicated a marginally significant relationship between 'other' exotic cover and the presence/absence of alligator weed ($P = 0.054$). However, for plots in which alligator weed was present, there was no relationship between alligator weed cover and cover of 'other' exotic plants ($P = 0.87$; Fig. 2b). Poisson

generalised linear models showed no significant evidence that species richness of either native or exotic plants was related to alligator weed cover ($P = 0.82$ and $0.79$ respectively).

**Hypothesis 3: That native and 'other' exotic plant species would be positively correlated with each other**

'Other' exotic cover had a marginally significant positive relationship with native cover ($P = 0.065$). A Poisson generalised linear model found exotic species richness was also positively related to native species richness ($P = 0.04$).

## Discussion

High alligator weed cover was found to be associated with low native cover. In contrast to native cover, cover of other exotic plant species was not negatively related to alligator weed cover. Given that this study does not track alligator weed invasion over time, and we did not experimentally manipulate alligator

weed cover, it is not possible to attribute low native cover to an effect of alligator weed invasion. Indeed it may be that sites with low alligator weed cover reflect the invasion resilience of the native flora. If this is the case, it appears that native vegetation at the site is better than other exotic vegetation at competitively excluding alligator weed. Conversely, it may be that native vegetation is more vulnerable to competitive exclusion by alligator weed than are other exotic species at the site. If this latter case is true, this may potentially facilitate a shift to further exotic dominance of the plant community over time.

As predicted in Hypothesis 3, native plants were positively related to 'other' exotic plants in terms of both cover and species richness. This indicates that natives and 'other' exotics are likely responding similarly to environmental variables at the site, as has been found in numerous other studies (Wiser et al. 1998; Levine & D'Antonio 1999; Hager & Vinebrooke 2004; Houlahan & Findlay 2004; Fridley et al. 2007). When contrasted with the negative relationship between native cover and alligator weed cover, this is further suggestive of a particularly strong competitive interaction between native vegetation and alligator weed at the site, though as noted above our dataset does not enable us to conclude that it is the alligator weed that is excluding the native species rather than the reverse.

Plots without alligator weed were clearly distinct from invaded plots, both as measured by ANOSIM and by relatively low beta-diversity (as indicated by high within-group similarity). *Phormium tenax* was the strongest native contributor to this within-group similarity, and it may be that this species is a particularly effective competitor against alligator weed. It would be interesting to test this hypothesis with manipulated competition experiments, and to determine how life-stage of *Phormium tenax* affected competitive ability.

As previously noted, Elton (1958) proposed species richness as a key factor in invasion resilience. Although our results supported our prediction of a negative relationship between alligator weed and native cover, neither native nor exotic species richness varied with alligator weed cover. As an observational study, conducted post-invasion, this research correlates alligator weed invasion with current diversity, which may not be the same as diversity at the time of original invasion (Levine & D'Antonio 1999). The lack of correlation between alligator weed cover and native species richness may reflect an already impacted native flora, which has been reduced sufficiently throughout the lake for these effects to be no longer evident. Alternatively, it may indicate that species richness is not an important factor influencing alligator weed invasion in this system. Replicated research comparing uninvaded ecosystems and those ranging from lightly/newly invaded to heavily/historically invaded would help to clarify the extent of alligator weed's impacts on plant communities and the degree of resilience afforded by native vegetation. However, logistical problems involved in obtaining suitable sites for this work can be prohibitive, as experienced in this study. This is due both to the degraded state of many northern New Zealand waterways (the part of New Zealand where alligator weed invasion is currently most advanced) and to the strong desire of managers to actively control alligator weed in more valuable sites, making it difficult to secure appropriate experimental sites for an adequate length of time. Alternatively, greenhouse and/or field-based studies manipulating competition could further elucidate competitive interactions between alligator weed and different combinations of native taxa.
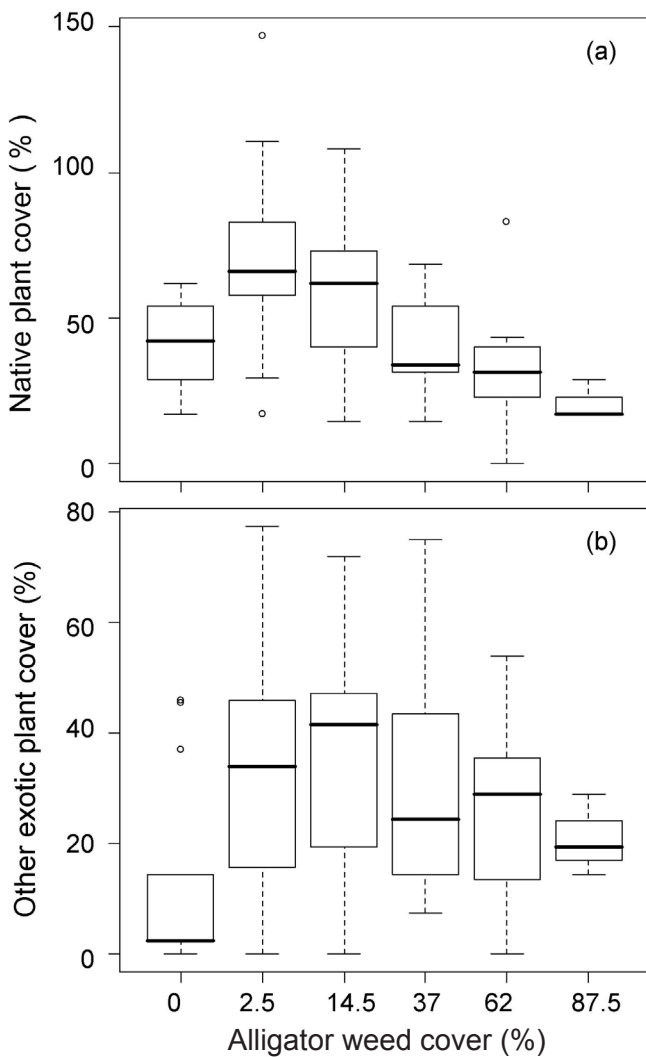


**Figure 2.** Variation (minimum, maximum, interquartile range, median) in (a) native and (b) 'other' exotic vegetation cover with varying alligator weed (*Alternanthera philoxeroides*) cover, from Lake Rotokawau, northern New Zealand. Dataset includes four replicate (seasonal) sampling dates from November 2005 to September 2006.

Although we cannot attribute causation in the present study, the pattern of a more negative association between weed cover and the cover rather than species richness of natives is similar to that observed by Knight and Reich (2005) for the invasive shrub *Rhamnus cathartica* (Rhamnaceae) in Minnesotan oak woodlands. This is consistent with the hypothesis that native species may be able to maintain a presence, as represented by species richness, under heavy infestations of alligator weed or other exotics, probably due to more favourable environmental conditions in heavily invaded areas; this would partially offset the negative effects of weed invasion.

Overall, our study highlights the invaded and degraded nature of this lake, with 21 exotic plant species recorded at the site, substantial algal blooms observed during the experiment, and alligator weed at its peak alone covering more than 20% of the site. However, relative to other lakes in the region, Lake Rotokawau's biodiversity values have recently been ranked as moderate (Wells & Champion 2010). The number of Northland lakes infested with alligator weed has increased rapidly over the last 10 years (Wells & Champion 2010). The dominance of alligator weed documented here for Lake Rotokawau provides a salutary reminder of the importance of spread prevention by early eradication of invasive aquatic weeds such as alligator weed.

## Acknowledgements

## References

Bassett IE, Beggs JR, Paynter Q 2010. Decomposition dynamics of invasive alligator weed compared with native sedges in a Northland lake. New Zealand Journal of Ecology 34: 324–331.

Bassett I, Paynter, Q, Beggs JR 2011. Invasive *Alternanthera philoxeroides* (alligator weed) associated with increased fungivore dominance in Coleoptera on decomposing leaf litter. Biological Invasions 13: 1377–1385.

Boylen CW, Eichler LW, Madsen JD 1999. Loss of native aquatic plant species in a community dominated by Eurasian watermilfoil. Hydrobiologia 415: 207–211.

Champion PD, Wells RDS, Matheson F, de Winton MD 2005. Northland lakes assessment 2004/05. NIWA Client Report HAM2005-113. Whangarei, Northland Regional Council. 265 p.

Clarke KR, Gorley RN 2006. PRIMER v6: User manual/tutorial. Plymouth, PRIMER-E.

Clarke KR, Warwick RM 2001. Change in marine communities: An approach to statistical analysis and interpretation. 2nd edn. Plymouth, PRIMER-E.

Davies KF, Harrison S, Safford HD, Viers JH 2007. Productivity alters the scale dependence of the diversity–invasibility relationship. Ecology 88: 1940–1947.

Dopson SR, de Lange PJ, Ogle CC, Rance BD, Courtney SP, Molloy J 1999. The conservation requirements of New Zealand's nationally threatened vascular plants. Threatened Species Occasional Publication 13. Wellington, Department of Conservation. 194 p.

Elton CS 1958. The ecology of invasions by animals and plants. London, Methuen. 181 p.

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology 88: 3–17.

Garbari F, Pedulla ML 2001. *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae), a new species for the exotic flora of Italy. Webbia 56: 139–143.

Hager HA, Vinebrooke RD 2004. Positive relationships between invasive purple loosestrife (*Lythrum salicaria*) and plant species diversity and abundance in Minnesota wetlands. Canadian Journal of Botany 82: 763–773.

Houlahan JE, Findlay CS 2004. Effect of invasive plant species on temperate wetland plant diversity. Conservation Biology 18: 1132–1138.

Invasive Species Specialist Group (ISSG) 2008. About invasive species. http://www.issg.org/about_is.htm (accessed 17 August 2010).

Julien MH 1995. *Alternanthera philoxeroides* (Mart.) Griseb. In: Groves RH, Shepherd RCH, Richardson RG eds The biology of Australian weeds. Vol. 1. Melbourne, Australia. RG and FJ Richardson. Pp. 1–12.

Julien MH, Bourne AS 1988. Alligator weed is spreading in Australia. Plant Protection Quarterly 3: 91–96.

Julien MH, Bourne AS, Low VHK 1992. Growth of the weed *Alternanthera philoxeroides* (Martius) Grisebach (alligator weed) in aquatic and terrestrial habitats in Australia. Plant Protection Quarterly 7: 102–108.

Julien MH, Skarratt B, Maywald GF 1995. Potential geographical distribution of alligator weed and its biological control by *Agasicles hygrophila*. Journal of Aquatic Plant Management 33: 55–60.

Kerikeri Weather Station 2011. Kerikeri Weather Station. Retrieved 9 June 2011 from http://www.kerikeriweather.co.nz/.

Knight KS, Reich PB 2005. Opposite relationships between invasibility and native species richness at patch versus landscape scales. Oikos 109: 81–88.

Kolar CS, Lodge DM 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16: 199–204.

Levine JM, D'Antonio CM 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15–26.

Lin J-C, Qiang S 2006. Influence of *Alternanthera philoxeroides* on the species composition and diversity of weed community in spring in Nanjing. Chinese Journal of Plant Ecology 30: 585–592.

Liu C, Yu D 2005. Occurrence of native aquatic plants within floating mats of *Alternanthera philoxeroides*. Journal of Freshwater Ecology 20: 407–408.

Liu C, Wu G, Yu D, Wang D, Xia S 2004. Seasonal changes in height, biomass and biomass allocation of two exotic aquatic plants in a shallow eutrophic lake. Journal of Freshwater Ecology 19: 41–45.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710.

Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T, Gale

S 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91: 97–108.

Northland Regional Council 2005. Annual monitoring report 2004-2005. Whangarei, Northland Regional Council.

R Development Core Team 2005. R: a language and environment for statistical computing. Version 2.13.1. Vienna, Austria, R Foundation for Statistical Computing. http://www.r-project.org.

Schooler SS, McEvoy PB, Coombs EM 2006. Negative per capita effects of purple loosestrife and reed canary grass on plant diversity of wetland communities. Diversity and Distributions 12: 351–363.

Shen J, Shen M, Wang X, Lu Y 2005. Effect of environmental factors on shoot emergence and vegetative growth of alligatorweed (*Alternanthera philoxeroides*). Weed Science 53: 471–478.

Stewart CA, Emberson RM, Syrett P 1996. Temperature effects on the alligator weed flea beetle, *Agasicles hygrophila* (Coleoptera: Chrysomelidae): implications for biological control in New Zealand. In: Moran VC, Hoffman JH eds Proceedings of the IX International Symposium on Biological Control of Weeds. University of Cape Town, South Africa. Pp. 393–398.

Stewart CA, Chapman RB, Frampton CMA 2000. Growth of alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae)) and population development of *Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae) in northern New Zealand. Plant Protection Quarterly 15: 95–101.

Timmins SM, Mackenzie IW 1995. Weeds in New Zealand Protected Natural Areas Database. Department of Conservation Technical Series 8. Wellington, Department of Conservation. 287 p.

van Ruijven J, De Deyn GB, Berendse F 2003. Diversity reduces invasibility in experimental plant communities: the role of plant species. Ecology Letters 6: 910–918.

Wagh GK, Ghate HV, Ghate VS 1995. First record of the alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb. from Pune, Maharashtra. Journal of the Bombay Natural History Society 92: 141–143.

Wardle DA 2001. Experimental demonstration that plant diversity reduces invisibility: evidence of a biological mechanism or a consequence of sampling effect? Oikos 95: 161–170.

Wells R, Champion P 2010. Northland lakes ecological status 2010. NIWA Client Report HAM2010-058. 9 p. Retrieved from the Northland Regional Council website (www.nrc.govt.nz), 10 April 2012.

Wiser SK, Allen RB, Clinton PW, Platt KH 1998. Community structure and forest invasion by an exotic herb over 23 years. Ecology 79: 2071–2081.