Ecological impacts of ground cover weeds in New Zealand lowland forests

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Abstract: Ecological impacts of three weed species of similar life form, *Asparagus scandens*, *Plectranthus ciliatus* and *Tradescantia fluminensis*, were investigated in six lowland forest remnants in New Zealand. All three species form dense, ground-covering mats of vegetation, and are tolerant of a broad range of light environments. Relationships between canopy openness, weed volume, native plant abundance and native species richness were investigated. Volume of all three weed species increased as canopy openness increased. *Tradescantia fluminensis* appeared to be most detrimental to native vegetation, with both native abundance and native species richness decreasing sharply as weed volume increased. *Plectranthus ciliatus* and *Asparagus scandens* were also associated with declines in native abundance and native species richness, but the correlations were less pronounced and were inconsistent across sites. Regression tree analyses on data from individual sites suggested a potential threshold of weed volume for *Tradescantia fluminensis*, beyond which both native abundance and native species richness declined abruptly. A threshold was also evident when data from all sites were analysed together. Where native species richness did decline in association with increasing weed volume, there did not appear to be any particular native species that were more likely to be excluded than others. All three ground cover weed species are associated with declines in native plant abundance and native species richness, particularly under high light conditions where the weeds are most abundant.

Keywords: biodiversity; invasive plant species; threshold effects; weed impacts; weed volume

Introduction

It is widely accepted that environmental weeds (sensu Falk-Petersen et al. 2006) can have detrimental impacts on native plant species, communities and ecosystems (Vilà et al. 2006). The number of experimental studies that attempt to quantify the impacts of environmental weeds (hereafter called weeds) has grown exponentially in the past decade (Lowry et al. 2013), although most have been limited to a single weed species at a single site (Skurski 2012). Many studies demonstrate a decrease in native abundance or species richness and/or a change in community composition in the presence of weeds (Sullivan et al. 2007; Hejda et al. 2009). However, others show that weeds do not necessarily have detrimental impacts (Mills et al. 2009; Meffin et al. 2010;), some report positive impacts (Rodriguez 2006), and many show that impacts are context-specific and vary according to the species and environmental conditions present (Vilà et al. 2006; Mason & French 2008). The detection of weed impacts may also vary according to the ecological measure that is examined (Pyšek et al. 2012) and the scale at which impacts are measured (Powell et al. 2013). Reviews have considered specific aspects of weed impacts on soil nutrient cycling (Liao et al. 2008) and plant reproductive mutualisms (Morales & Traveset 2009), specific weed groups such as graminoid and woody species (Mason et al. 2009), and specific types of ecosystems (Houlahan & Findlay 2004; Zedler & Kercher 2004). Such broad reviews generally conclude that impacts are variable. Thus, despite significant advances in this body of knowledge, generalisations about weed impacts remain largely elusive (Ricciardi et al. 2013).

Following a global assessment of weed impacts, Pyšek et al. (2012) concluded that life form is one species trait that offers the potential means of predicting impact. Indeed it seems intuitively likely that weeds of similar growth form could have similar direct impacts on native plant communities. For example, trees tend to cast shade, which may inhibit the establishment and growth of shade-intolerant species (e.g. Jäger et al. 2009), whereas low-growing, mat-forming herbs present a physical barrier that may prevent seedling recruitment of small-seeded species (e.g. Standish et al. 2001). A complicating factor is that weeds can be detrimental to native plant communities in ways that are unrelated to life form, for example trees and herbs can both have allelopathic effects. Weed impacts may also vary according to the native community invaded. The strongest impacts might occur when the weed represents a completely new life form, or where the weed is taller than the native community it has invaded (Pyšek et al. 2012). This context-dependency means weed impacts are likely to vary by species, which makes generalisation difficult. Nevertheless, it is arguably feasible to try to develop general principles about the impacts weeds are likely to be having *because* of their life form, regardless of whether additional impacts are also occurring for any given species and situation.

One life form that could be directly detrimental to native vegetation is the ground cover weed: the mat-forming herbaceous species that covers the soil surface and smothers other low-growing plants. There is mounting evidence that one of the primary mechanisms driving weed impacts is recruitment limitation through germination or seedling suppression (Skurski 2012), and this could well be the case for ground cover weeds. It has been well demonstrated that the ground cover weed species *Tradescantia fluminensis* inhibits native seedling regeneration both in New Zealand (Kelly & Skipworth 1984; Standish et al. 2001) and in Florida (McMillan 1999).

Ageratina riparia, Asparagus asparagoides, Delairea odorata and *Hedera helix* are additional ground cover weed species that have been shown to reduce native plant abundance and/or species richness in natural ecosystems (Alvarez & Cushman 2002; Barton et al. 2007; Biggerstaff & Beck 2007; Turner et al. 2008). Ground cover weeds that are shade-tolerant are often of particular concern, because they have the potential to invade undisturbed native forest. Invasion by such species can put forest ecosystems onto a trajectory of long-term decline and eventual collapse, because young native plants are not replacing old plants as they senesce (Esler 1978).

It is not yet widely known whether weed impacts tend to increase linearly as weed volume increases, or whether they occur only after the weed has reached some critical volume threshold. While the answer is likely to be context-dependent and thus difficult to generalise about, knowledge of such thresholds, if they exist, would help weed managers to prioritise control at sites where impacts – and thus biodiversity losses – are likely to be greatest (Suding & Hobbs 2009). There have only been a few studies examining these issues to date. Gooden et al. (2009) found that native species richness in a wet sclerophyll forest in Australia declined only after cover of the weed *Lantana camara* exceeded 75%. In a New Zealand study, Standish et al. (2001) found survival of native *Dysoxylum spectabile* seedlings decreased with increasing *Tradescantia* biomass, and concluded that they would only emerge where *Tradescantia* biomass was lower than 200 g m^{-2} (70–90% cover). Standish et al. (2001) also demonstrated that *Tradescantia* biomass increased logistically with light availability, which implies that impacts may be highest where the weed occurs in high light, such as on forest edges or in canopy gaps.

As a first attempt in addressing some of these questions, we investigated the effects of three highly invasive, shade-tolerant ground cover weed species on native plant recruitment in New Zealand lowland forests. These forests have been severely depleted and fragmented in the past, and are now one of the most damaged and threatened indigenous ecosystems in New Zealand (Ewers et al. 2006). Isolated forest fragments are often surrounded by farmland and can be vulnerable to weed invasion due to their typically large edge-to-interior ratios (Yates et al. 2004). Although few invasive weed species are capable of invading intact forest in New Zealand, shade-tolerant ground cover weeds are relatively common in these forest remnants. A better understanding of the impacts of these weeds will help weed managers prioritise control that will deliver the most benefits to native plant biodiversity. In this study, we test the following hypotheses: (1) weed volume is positively correlated with canopy openness; (2) native seedling abundance and/or native species richness is negatively correlated with weed volume; and (3) different ground cover weed species have similar impacts.

Methods

Weed species

Three ecologically similar environmental weeds were selected for this study. The species were chosen because (1) they are all capable of forming extensive, dense mats of vegetation in lowland New Zealand forests, (2) they all grow in a broad range of light environments from deep shade to full sun, and (3) we were able to locate two accessible lowland forest sites per species where the study weed was widespread but the rest of the vegetation was predominantly native.

Tradescantia fluminensis Vell. (Commelinaceae), hereafter called tradescantia, is a sprawling perennial herb native to South America that is naturalised or invasive in at least 26 countries around the world (Randall 2012). Tradescantia does not set seed in New Zealand, but can reproduce vegetatively from tiny stem fragments. The main dispersal vectors are humans (through weed dumping) and water (Butcher & Kelly 2011). First recorded in 1916 (Healy & Edgar 1980), tradescantia is now widely distributed throughout New Zealand, and is a common feature of lowland forest remnants (Esler 1978; Department of Conservation 2013). It is the most-studied of our three study species, and has been shown to reduce species richness and abundance of native forest seedlings (Kelly & Skipworth 1984; Standish et al. 2001) and epigaeic invertebrates (Standish 2004).

Plectranthus ciliatus E. Mey. (Lamiaceae), hereafter called plectranthus, is a straggling perennial herb from eastern South Africa. It is invasive in both New Zealand and Australia, and is a popular garden plant in many other countries. First recorded in New Zealand in 1975 (Webb et al. 1988), plectranthus is now patchily distributed around the North Island and top of the South Island (Department of Conservation 2013). Reproduction in New Zealand is thought to be largely vegetative, and dispersal of plant fragments is mainly by humans and water. It does set seed, but these are not obviously adapted for dispersal by birds, wind or water, so they may play only a minor role in its spread. We were unable to find any ecological studies on this species.

Asparagus scandens Thunb. (Asparagaceae), hereafter called climbing asparagus, is a scrambling or climbing perennial monocot native to South Africa and invasive in New Zealand and Australia. First recorded in New Zealand in 1959 (Healy & Edgar 1980), climbing asparagus is now common in the North Island and northern areas of the South Island (Timmins & Reid 2000). It reproduces both vegetatively and by seed in New Zealand, and is dispersed by birds and humans. Authors frequently state that climbing asparagus smothers understorey plants and reduces the regeneration of native species (e.g. Ward et al. 1999; Timmins & Reid 2000), but we were unable to locate any quantitative evidence.

Study sites

Six ecologically similar lowland forest sites extensively invaded by one of the ground-cover-weed study species were identified in the Bay of Plenty area of the North Island, New Zealand (Table 1). Two sites were found for each weed species, and were named accordingly: Tradescantia 1 and 2, Plectranthus 1 and 2, and Asparagus 1 and 2. Vegetation was predominantly native broadleaved-podocarp secondary forest, although a few exotic conifer trees were present at some sites.

Study design

At each study site, 32 plots of 2 × 2 m were established, at a minimum distance of 3 m apart, in areas with high weed cover (98–100%) (classed as 'high weed' plots). Our aim was to position 16 of the plots in high light, and 16 in low light. However, because the vegetation largely comprised intact, tall forest surrounded by roads or farmland, plots with truly high light (i.e. with open canopy overhead) were scarce. At most sites, the highest light environments we could find were along forest edges, with intact forest overhead. Accordingly, rather than having plots with strict high or low light, most ranged somewhere in between, in moderate light.

At each site, an additional eight pairs of 2 × 2 m plots were established on the edge of the weed invasion closest to

Table 1. Geographic and climatic characteristics of six study sites. Sites are denoted by weed name (Tradescantia, Plectranthus, Asparagus) and site number (1 or 2).

	Tradescantia 1	Tradescantia 2	Plectranthus 1	Plectranthus 2	Asparagus 1	Asparagus 2
Location	Fitzgerald Glade, SH5, near Tirau	Karangahake Gorge, SH2, near Paeroa	Hot Springs Road, Katikati	Sapphire Springs, Katikati	McLaren Falls, Tauranga	Wainui River, Katikati
Latitude, longitude	37°59' S, 175°53' E	37°25' S, 175°43' E	37°35' S, 175°51' E	37°35' S, 175°52' E	37°48' S, 176°02' E	37°39' S, 175°57' E
Size (ha)	70	30	2	30	20	125
Elevation (m a.s.l.)	270	55	120	90	110	80
Mean annual rainfall (mm)[1]	1290	1573	1279	1279	1917	1279
Mean daily min–max temp (°C)[1]	8.5–18.8	9.5–18.5	9.5–18.5	9.5–18.5	11.3–18.8	11.3–18.8
Soil types[2]	Ngakura	Komata hill	Otorohunga, Ngakura	Otorohunga, Ngakura	Otanewainuku, Opotiki	Otorohunga
Average (±SD) canopy height (m)	27 ± 1	12 ± 1	14 ± 1	14 ± 1	20 ± 1	17 ± 2
Surrounding matrix	Farmland, 1 km from Kaimai-Mamaku Forest Park	On the southern boundary of Coromandel Forest Park	Farmland, 0.1 km from Kaimai-Mamaku Forest Park	Farmland, 1 km from Kaimai-Mamaku Forest Park	Farmland, 5 km from Kaimai-Mamaku Forest Park	Farmland, 2 km from Kaimai-Mamaku Forest Park

[1]Meterological data are taken from the NIWA CliFlo database (http://cliflo.niwa.co.nz), and are based on 30-year period of data from nearest weather station.
[2]S-map Online: http://smap.landcareresearch.co.nz

one of eight, randomly selected, high-weed plots in low light described above. This was usually within 5 m of the associated high-weed plot, but in a few cases was up to 10 m away. The first plot of each pair was established so that the weed covered 50% of the plot (classed as 'medium weed' plots). The second plot of each pair was established immediately adjacent to the medium-weed plots, where the weed covered less than 1% (usually 0%) of the plot (classified as 'low weed' plots). This gave us a total of 48 plots per study site: 16 high-weed in high light, 16 high-weed in low light, 8 medium-weed in low light, and 8 low-weed in low light. Medium- and low-weed plots could not be established in high light because the weed was invariably highly abundant when it was present in high light. Consequently, we were unable to separate the effects of high weed volume from the effects of high light on native abundance and native species richness. These categories of weed cover class were nominal only, and were not used in any of the statistical analyses (weed volume was, see below).

Vegetation measures

Vegetation was assessed between June and September 2011 according to the Landcare Research Recce method (Hurst & Allen 2007). The basis of this method is to visually assess vegetation cover within the following height classes: <0.1 m, 0.1–0.3 m, 0.3–1 m, 1–2 m, 2–5 m, 5–12 m. Because the focus of our study was the impact of ground cover weeds on seedling regeneration, analyses are restricted to the lowest three height classes (i.e. up to 1 m tall). We do, however, report on the abundance of the most common native woody species in all height classes. This was to examine whether any particular species were present as big plants but not small plants, thereby indicating a potential lack of seedling recruitment. Species that had live leaves in any given height class were given a cover class score as follows: <1% cover = 1, 1–5% cover = 2, 6–25% cover = 3, 26–50% cover = 4, 51–75% cover = 5, 76–100% cover = 6. Native abundance scores for individual species in each plot were calculated by summing cover-class scores. For example, if a species had been scored 3 in the height class 0.1–0.3 m and 2 in the height class <0.1 m, it received

an overall score of 5. Overall native abundance per plot was calculated by summing the individual species' abundance scores. Native species richness per plot was calculated by counting the number of native species present.

Weed height was measured in each plot. In most cases, weed height was largely uniform across the plot, particularly for tradescantia and plectranthus. However, where this was not the case, we measured top and bottom heights, and averaged those values. Weed volume in each plot was calculated by multiplying the height of the weed by the area covered by the weed: 100% (4 m²) for high-weed plots, 50% (2 m²) for medium-weed plots, and 1% (0.04 m²) for low-weed plots. This gave a measure of cubic metres of weed per 4-m² plot. Using 1% cover as the multiplier for the low-weed plots allowed us to account for the odd weed tendril encroaching into a plot. In plots where the weed was completely absent, this calculation resulted in a weed volume of zero.

Percent canopy openness above plots was used as an indicator of light availability. To quantify this we used the HemiView Forest Canopy Analysis System v8 (Delta-T Devices, Cambridge, UK). Photographs of the forest canopy were taken from approximately 1 m above the middle of each plot using a Canon EOS 50D digital SLR camera and 4.5 mm Sigma EX DC hemispherical (fisheye) lens. Photographs were then digitally analysed using the HemiView image processing software.

Statistics

All analyses were done using the statistical software R 2.9.2 (R Development Core Team 2011). Given the observational nature of the data, and non-random selection of the study sites, we investigated relationships between key variables and potential explanatory variables at each site separately, using linear models, supported by graphical exploration. Models were examined for goodness of fit using diagnostic plots.

To examine the relationship between weed volume and canopy openness, we analysed data from the 32 high-weed plots at each site using a linear model with weed volume as response variable and percent canopy openness as predictor.

We used only high-weed plots for these analyses because they were the only plots located in a range of light conditions. While the weed in these plots had similar cover, there was variability in weed height, and thus volume (see Vegetation measures above). Although the canopy was largely intact at sites, there were one or two plots per site with a very high value of canopy openness. To test the effect these potential outliers might have on our results, we also ran analyses with those plots removed (the 'Plectranthus 2' site had one potential outlier plot removed, and all other sites had two potential outlier plots removed).

To examine the relationship between native abundance and weed volume, and between native species richness and weed volume, we analysed data from all 48 plots at each site. We used linear models with native abundance or number of native species as response variables, and weed volume as predictor.

The data suggested that there may be a threshold of weed volume where native abundance or native species richness declined abruptly. To explore this and create a hypothesis for possible future studies, we used regression trees, which explain variation in the response variable (native abundance or native species richness) by defining a split in the data based on the predictor variable specified (weed volume) (Zuur et al. 2007). Regression trees are a useful means of identifying non-linear patterns in complex ecological data (e.g. De'ath & Fabricius 2000; Towns et al. 2003). Because regression trees are most successfully applied to large datasets, we combined data from all sites. However, we also applied regression tree analysis to the six sites individually, to investigate whether similar relationships were evident at this level. We evaluated the trees using 10-fold cross validation (CV) to optimise the size of the final tree and to assess whether any observed relationship held after cross validation (Zuur et al. 2007).

Results

Weed volume reached high levels at all six sites, even at low levels of canopy openness, and was positively correlated with percent canopy openness at all six sites (Fig. 1, Table 2). However, when the one or two potential outlier values of canopy openness at each site were excluded from analyses, the correlation was only significant at the two plectranthus sites and one of the tradescantia sites (Table 2). As mentioned above, we were unable to quantify the relationship of weed volume along the full continuum of light levels from low to high because of the nature of the vegetation at our study sites.

A total of 40 woody native species (trees and shrubs) were recorded, along with approximately 50 species of native ferns, grasses, herbs and vines. Woody species were the most abundant life form, and comprised the majority of forest subcanopy and canopy cover. All of the commonly recorded woody species occurred in the lower two height classes (Table 3). Most species were also present in the higher height classes, although some appeared to be far less abundant in the middle height classes (e.g. *Knightia excelsus*, *Myrsine australis*) (Table 3). Additionally, the most commonly recorded woody species present in low- or medium-weed plots were also present in high-weed plots (Table 4). Other exotic species present were mainly shade-intolerant species, and occurred at low abundance
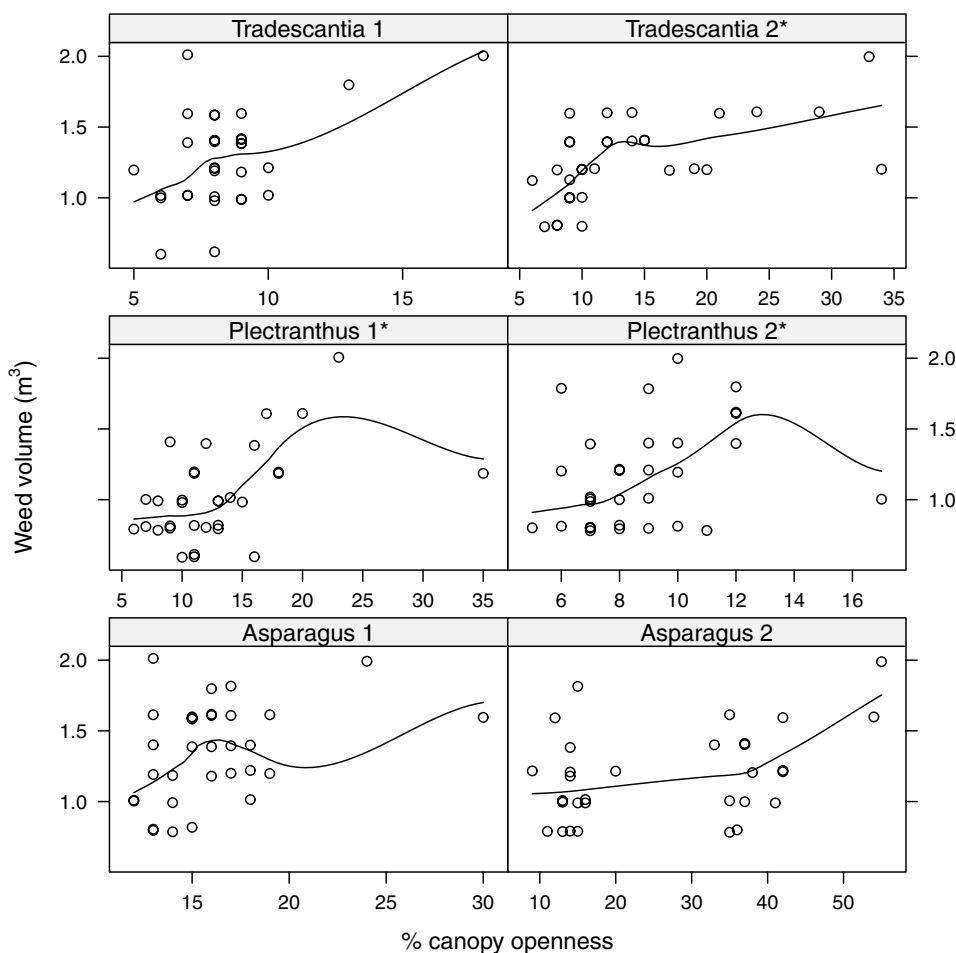

Figure 1. Relationship between weed volume (m^3) and canopy openness in high-weed plots (plots with 100% cover of weed), with 'smoother' lines. Sites are denoted by weed name (Tradescantia, Plectranthus, Asparagus) and site number (1 or 2). *$P < 0.05$ after one (at Plectranthus 2) or two (at all other sites) potential outlier values of canopy openness have been excluded from analyses. Data points are jittered for clarity.

Table 2. Results from linear model analyses. Bolded *P*-values are those that are statistically significant ($P < 0.05$). Sites are denoted by weed abbreviation (Trad = tradescantia, Plec = plectranthus, Asp = asparagus) and site number (1 or 2).

Relationship tested	Site	Slope	Std error	*t*	*P*-value
Weed volume (m³) vs % canopy openness[1]	Trad 1	0.04	0.05	0.78	0.44
	Trad 2	0.03	0.01	2.77	**<0.01**
	Plec 1	0.04	0.02	2.54	**0.01**
	Plec 2	0.08	0.03	2.85	**<0.01**
	Asp 1	0.04	0.03	1.58	0.12
	Asp 2	0.01	0.01	0.95	0.34
Native abundance vs weed volume (m³)[2]	Trad 1	−13.91	1.88	−7.41	**<0.001**
	Trad 2	−13.61	1.92	−7.10	**<0.001**
	Plec 1	−9.12	2.16	−4.21	**<0.001**
	Plec 2	−5.23	1.97	−2.65	**<0.01**
	Asp 1	−1.77	1.81	−0.98	0.33
	Asp 2	−4.13	2.04	−2.02	**0.04**
Native species richness vs weed volume (m³)[2]	Trad 1	−3.82	0.70	−5.43	**<0.001**
	Trad 2	−4.68	0.72	−6.52	**<0.001**
	Plec 1	−3.00	0.81	−3.70	**<0.001**
	Plec 2	−1.16	0.74	−1.58	0.12
	Asp 1	−1.32	0.67	−1.94	**0.05**
	Asp 2	−1.48	0.76	−1.94	**0.05**

[1]Analyses done on data from high-weed plots, in either high light or low light, with the top one or two values of canopy openness removed from each site (see Methods).
[2]Analyses done on data from high-, medium-, and low-weed plots, all in low light.

Table 3. Abundance of common native woody species by vegetation height class. Species reported are those that occur in a minimum of 10 plots per site, at two or more sites. *n* = number of plots (out of a possible 48 at each site) in which the species was recorded. Numbers represent the total cover-class score recorded for each native species in each height class. Sites are denoted by weed abbreviation (Trad = tradescantia, Plec = plectranthus, Asp = asparagus) and site number (1 or 2).

Species	Site	*n*	Vegetation height class (m)					
			5–12	2–5	1–2	0.3–1	0.1–0.3	<0.1
Alectryon excelsus	Trad 1	25	15	0	1	8	14	4
	Trad 2	29	69	13	1	10	9	4
	Plec 1	17	0	0	5	8	14	7
Dysoxylum spectabile	Plec 1	21	10	5	9	23	20	14
	Plec 2	36	63	58	42	42	22	10
Geniostoma ligustrifolium	Trad 1	10	5	14	16	11	5	3
	Plec 1	31	5	51	44	25	17	11
	Plec 2	34	8	73	42	36	14	7
	Asp 1	19	0	9	11	26	24	14
	Asp 2	32	0	3	0	12	35	26
Hedycarya arborea	Trad 1	26	19	16	17	14	12	11
	Trad 2	28	19	44	42	23	6	10
	Plec 1	19	0	0	5	19	18	13
	Plec 2	37	11	67	38	31	16	14
	Asp 1	11	0	0	0	2	8	7
	Asp 2	21	0	11	24	20	14	8
Knightia excelsa	Trad 1	19	17	0	0	0	7	8
	Plec 1	27	9	0	2	7	25	23
	Plec 2	30	11	0	0	5	25	25
	Asp 1	30	72	23	7	1	9	11
	Asp 2	45	67	16	2	2	25	28
Melicytus ramiflorus	Trad 1	27	49	22	18	15	9	4
	Trad 2	44	161	117	32	14	7	1
	Plec 1	42	82	89	35	45	29	20
	Plec 2	38	63	87	26	23	14	10
	Asp 1	23	41	40	9	12	11	5
	Asp 2	34	11	16	1	22	31	20
Myrsine australis	Plec 1	13	4	3	0	10	11	9
	Plec 2	19	20	22	6	9	10	4
	Asp 1	17	9	19	1	5	11	13
	Asp 2	17	2	6	0	2	13	13
Piper excelsum	Trad 1	47	31	123	85	55	30	17
	Trad 2	42	13	111	80	50	15	15
	Plec 1	42	20	104	70	53	16	30
	Plec 2	43	0	84	78	60	24	23
	Asp 2	16	0	6	5	10	10	13

Table 4. Average abundance of the most common woody native species in the lower three vegetation height classes (<0.1 m, 0.1–0.3 m, 0.3–1 m) for each weed species studied. The numbers in brackets below weed-cover-class headings represent the average (± standard deviation) weed volume (m^3) per plot across both sites for each weed species (low light plots only). Native species reported are those recorded in more than five plots at each of the two sites for that weed species. Each number represents the average cover-class score for that native species in each weed cover class over both sites.

	Weed cover class		
Tradescantia	Low	Medium	High
	(0.002 ± 0.003)	(0.49 ± 0.10)	(1.10 ± 0.25)
Alectryon excelsus	0.9	0.8	0.4
Geniostoma ligustrifolium	0.6	0.3	0.2
Hedycarya arborea	2.2	1.5	0.3
Litsea calicaris	0.7	0.9	0.1
Melicytus ramiflorus	0.9	0.8	0.4
Piper excelsum	3.1	3.2	1.3
Plectranthus	Low	Medium	High
	(0.001 ± 0.002)	(0.41 ± 0.12)	(0.91 ± 0.19)
Dysoxylum spectabile	1.8	2.4	1.0
Geniostoma ligustrifolium	1.7	1.1	1.0
Hedycarya arborea	1.1	1.9	1.0
Knightia excelsa	1.5	1.6	0.9
Melicytus ramiflorus	1.6	2.0	1.3
Myrsine australis	0.6	0.6	0.5
Piper excelsum	2.9	3.2	1.7
Asparagus	Low	Medium	High
	(0.006 ± 0.003)	(0.62 ± 0.17)	(1.24 ± 0.34)
Geniostoma ligustrifolium	2.1	3.2	0.8
Hedycarya arborea	0.9	1.4	0.3
Knightia excelsa	0.8	1.7	0.6
Melicytus ramiflorus	0.9	1.6	0.9
Myrsine australis	0.4	0.8	0.6

in plots with high light on the edge of the forest. These species were likely having only minor impacts on the native vegetation compared with the ground-cover-weed study species so are not reported here.

Data from all six sites gave estimates of a negative relationship of native abundance with weed volume in a linear model (Fig. 2, Table 2). Tradescantia and plectranthus had strong evidence of a negative relationship with native abundance, with all four sites having P-values < 0.01 (Table 2). Evidence for climbing asparagus was less clear, with one site having a P-value of 0.04 and the other not having a significant correlation (Table 2).

Data from all six sites also gave estimates of a negative relationship of native species richness with weed volume in a linear model (Fig. 3, Table 2). Tradescantia again had the strongest evidence of a negative relationship with native species richness, with both sites having P-values < 0.001. Both climbing asparagus sites and one plectranthus site had significant estimates (Fig. 3, Table 2).

There was strong support for a potential threshold effect for the two tradescantia sites, estimated at 0.85 and 0.90 m^3 per 4-m^2 plot (CV error rate 0.36 ± 0.06 standard error and 0.48 ± 0.13 for native abundance, 0.57 ± 0.11 and 0.50 ± 0.11 for native species richness) (Table 5). These results indicate strong predictive power for this model, when compared with an expected CV error rate of 1.00 for no relationship. There was some support for an overall threshold of 0.75 m^3 per 4-m^2 plot when all sites were combined (CVs 0.84 ± 0.09 and 0.87 ± 0.08) (Table 5). However, there was no clear support for a threshold for plectranthus or climbing asparagus when sites were analysed separately (Table 5). All tree models gave point estimates of a threshold in the range of 0.75–1.10 m^3 per 4-m^2 plot.

Discussion

Impacts of ground cover weeds

A common concern of natural area managers is the potential for weeds to be detrimental to native biodiversity in some way. In the majority of situations, the nature, severity, and long-term implications of weed impacts are unknown. A growing body of evidence indicates that native abundance and native species richness are frequently diminished in the presence of weeds, but other studies show neutral, and even positive, impacts of weeds on native biodiversity (Ortega & Pearson 2005; Hejda et al. 2009; Vilà et al. 2011). This variability of results, along with poor comparability of scale and methods among studies, means that the ability to generalise about weed impacts remains limited (D'Antonio & Kark 2002). Natural area managers are forced to make 'best guesses' about which weeds are likely to be having the worst effects. Our results do not prove that the weeds are *causing* declines in native plant abundance and species richness, because we cannot be sure that there are not other, unmeasured factors driving the plant distributions within plots. However, we have shown that three
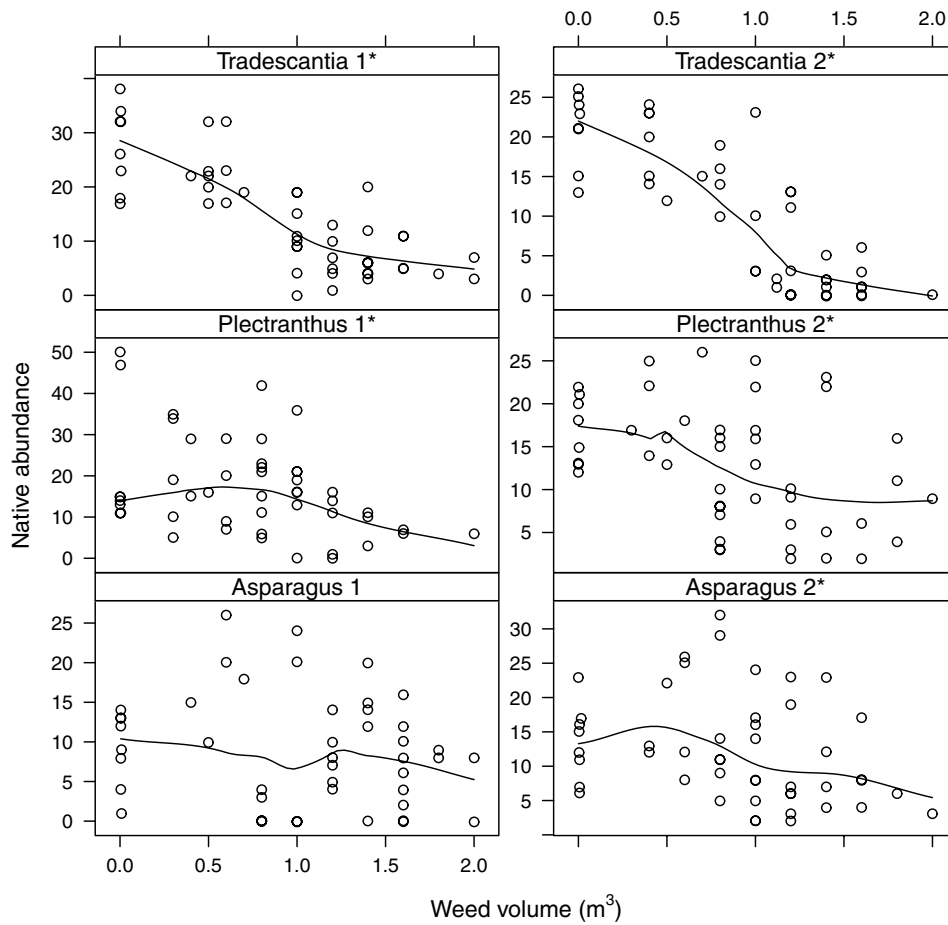
Figure 2. Relationship between native abundance and weed volume (m^3) in all plots (*$P < 0.05$), with 'smoother' lines. Sites are denoted by weed name (Tradescantia, Plectranthus, Asparagus) and site number (1 or 2). Data points are jittered for clarity.
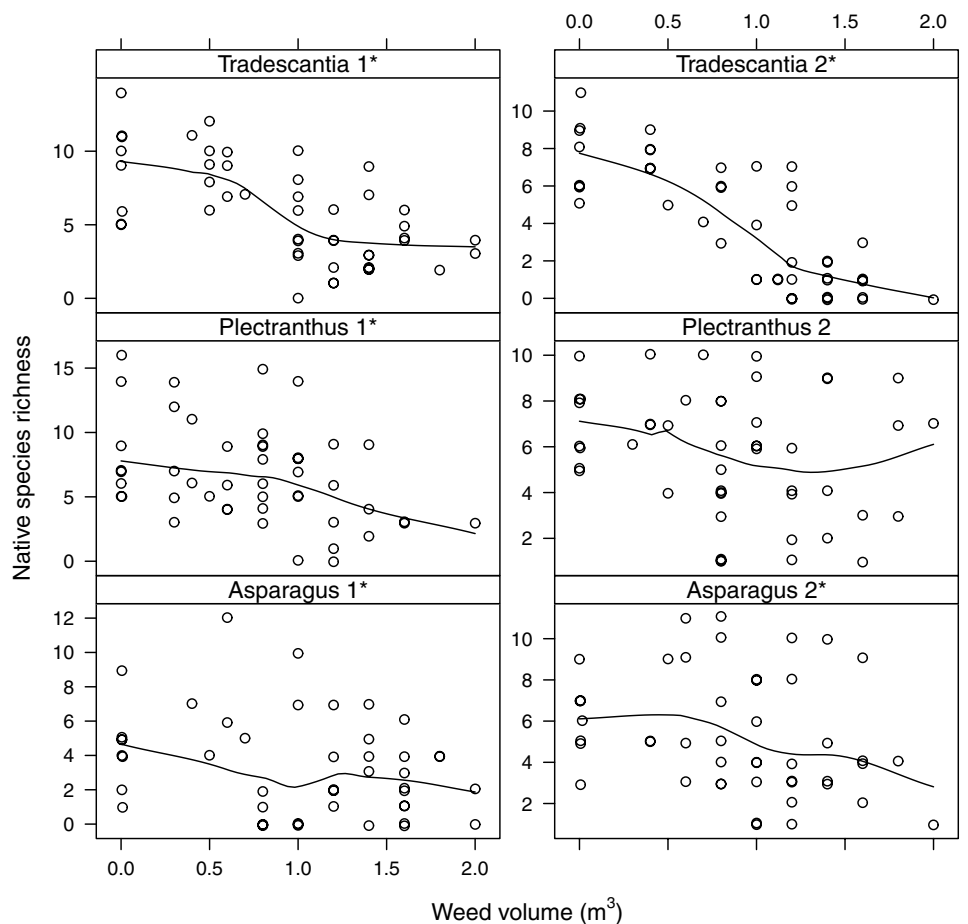

Figure 3. Relationship between native species richness and weed volume (m^3) in all plots (*$P < 0.05$), with 'smoother' lines. Sites are denoted by weed name (Tradescantia, Plectranthus, Asparagus) and site number (1 or 2). Data points are jittered for clarity.

Table 5. Summary of estimated weed volume thresholds on native abundance and native species richness, based on the first split of each regression tree. The explanatory variable is weed volume (m^3 per 4-m^2 plot), and response variables are native abundance (see Methods for score calculation) and native species richness (number of native species). Sites are denoted by weed abbreviation (Trad = tradescantia, Plec = plectranthus, Asp = asparagus) and site number (1 or 2).

| Site | Estimated threshold of weed volume (m^3)[1] | Native abundance | | Native species richness | |
		Cross-validated relative error rate	Standard error	Cross-validated relative error rate	Standard error
Trad 1	0.85	0.36	0.06	0.57	0.11
Trad 2	0.90	0.48	0.13	0.50	0.11
Plec 1	1.10	0.97	0.22	1.03	0.22
Plec 2	0.75	0.89	0.17	0.97	0.15
Asp 1	0.75	1.09	0.24	1.06	0.28
Asp 2	0.90	0.97	0.17	1.08	0.17
All sites	0.75	0.84	0.09	0.87	0.08

[1]The estimated threshold at each site was the same for both response variables.

species of ground cover weed are associated with declines in both the abundance and species richness of native vegetation in lowland forest remnants in New Zealand. Other studies have shown that tradescantia strongly inhibits regeneration of native species in New Zealand (Kelly & Skipworth 1984; Standish et al. 2001), but this is the first indication that taxonomically unrelated, but ecologically and morphologically similar, weed species appear to have similar effects.

It is unclear why tradescantia is more strongly associated with declines in native abundance and species richness than plectranthus or climbing asparagus. The simplest explanation may be that it is a superior competitor for resources; however, this has not been quantified to date. Additionally, unlike the other two species, tradescantia forms a dense mat of horizontal interleaved stems at the soil surface (KGM pers. obs.), which likely presents a formidable physical barrier to seedling establishment. Standish et al. (2001) showed that an increase in tradescantia biomass (g m^{-2}) was associated with a rapid decrease in light availability at ground level, and this may be an additional mechanism driving declines in native abundance and native species richness. It is uncertain whether light availability at ground level is particularly low beneath tradescantia. Our attempts to measure this were hindered by the tendency of both tradescantia and plectranthus stems to lean over at the slightest disturbance, resulting in a gap in the weed 'canopy'. However, our field observations indicated that light levels at the soil surface appeared to be higher beneath climbing asparagus than they were beneath tradescantia and plectranthus. This could be one reason why climbing asparagus is less strongly associated with declines in native abundance.

Another New Zealand study demonstrated that tradescantia increases litter decomposition and alters nutrient availability in lowland forests, but the authors could not speculate on the impact of those changes (Standish et al. 2004). In our study, some native species appear to be less abundant in the middle height classes compared with the upper and lower height classes, suggesting that something may be limiting recruitment at the juvenile stage for these species. This could be an impact of the weed, or some other external factor such as herbivory of young plants, or a past disturbance event that caused plants of a certain age or size to be drastically reduced. Future research associated with this project will include an assessment of recruitment of native species from seed in the presence of these three weeds, and will examine potential

impacts of herbivorous mammals on seedling recruitment.

Many studies have found that weeds are associated with a reduction in native species richness (e.g. Hejda et al. 2009; Vilà et al. 2011), suggesting that native species can differ in their resistance to invasion. In the current study, all three ground cover weeds were associated with a reduction in native species richness. However, our results showed that all native species present in the forest canopy were also present in the lowest height classes (Table 3), indicating that all species are regenerating – to some extent – despite the presence of these ground cover weeds. Furthermore, all common woody species present in low-weed or medium-weed plots were also present in high-weed plots (Table 4). These results suggest that all native species recorded have a similar likelihood of establishing in the presence of ground cover weeds. Interestingly, Standish et al. (2001) showed that some native species were likely to be less tolerant of dense tradescantia than others, with the woody species *Piper excelsum* particularly susceptible. However, *Piper excelsum* was one of the most commonly occurring species in our plots. It is unclear why we got such disparate results, but our future research will examine this question further.

In a study from the USA, Yurkonis and Meiners (2004) found that increasing cover of the invasive vine *Lonicera japonica* was associated with a decline in native species richness, but not with an increase in native extinction rates. They concluded that declines in native species richness associated with *L. japonica* invasion resulted from the effects on local colonisation rates only, and not through the competitive displacement of established species (Yurkonis & Meiners 2004). Effects of the weeds in our study systems may be similar; fewer seedlings (regardless of species) are able to recruit into plots with high weed volume.

Threshold of weed volume

It has been shown that, for some weeds, major impacts only occur after a certain threshold of weed volume is exceeded. This information can be useful to managers seeking to prioritise weed control at sites where impacts on native biodiversity are likely to be greatest. Our results indicate that there may be an 'impact' threshold of weed volume for our three study species. Using regression trees to analyse the relationships between weed volume and native abundance and native species

richness for all three weed species combined, we revealed a potential weed volume threshold of 0.75 m^3 of weed per 4-m^2 plot. When the weed species were analysed separately, tradescantia exhibited a potential threshold (0.85–0.90 m^3 of weed per 4-m^2 plot), but plectranthus and climbing asparagus did not. Accordingly, the threshold concept may be most useful in guiding the management of tradescantia in particular. In another New Zealand study, Standish et al. (2001) estimated that regeneration of even the most shade tolerant native species was prevented where biomass of tradescantia exceeded 200 g m^2, or 70–90% cover. Our estimated threshold of 0.85–0.90 m^3 of weed per 4-m^2 plot for tradescantia corresponds to an average stem height of 21–23 cm. This is highly compatible with the results reported by Standish et al. (2001), despite their slightly different measure of stem height. Their results show that tradescantia stem height in almost all quadrats under the 200 g m^2 threshold was less than 21 cm, whereas tradescantia stem height in almost all quadrats over the 200 g m^2 threshold was greater than 24 cm (Standish et al. 2001, fig. 4a).

Few other studies have examined weed thresholds, although Gooden et al. (2009) found that native species richness in an Australian forest declined only after *Lantana camara* cover exceeded 75%. Alvarez and Cushman (2002) suggested that a minimum level of invasion was required before detrimental impacts of *Delairea odorata* occurred, although they were unable to quantify that threshold. Additional research would be valuable in further assessing the validity and utility of these thresholds, and whether they might apply to other environmental weeds.

If there is a threshold of weed volume beyond which the most severe impacts occur, then knowledge of the environmental conditions under which weed volume is highest is useful to weed managers. Several studies have shown that tradescantia biomass is significantly and positively correlated with light intensity (this study; Kelly & Skipworth 1984; Standish et al. 2001), and we have shown that this is also the case for plectranthus. It was not clear from our data whether volume of climbing asparagus is positively correlated with canopy openness in the same way. Our results also show that tradescantia and plectranthus are most strongly associated with declines in native plant abundance and species richness where they are highly abundant. Similarly, Standish et al. (2001) demonstrated that tradescantia has the highest impacts on native seedlings in high light environments where it is most abundant. Standish et al. (2001) also suggested that, where tradescantia cover is less than 70%, native woody species may eventually shade it out. Because the only plots we were able to locate in high light all had very high weed volume, we were unable to fully determine the shape of the relationship between light, weed volume, and native abundance or native species richness. Nevertheless, it seems reasonable to assume that tradescantia and plectranthus could be most detrimental to native abundance and native species richness in high light environments, because that is where they are most abundant.

Management implications

Ground cover weeds are associated with a reduction in both native abundance and native species richness in New Zealand lowland forests, particularly where weed volume is high. In the long term, this could compromise the health of these forests, particularly since many are highly fragmented and under threat from other invasive species such as possums (*Trichosurus vulpecula*) (Burns et al. 2011). However, it is only in high light environments, such as the forest edge or in canopy gaps, that these weeds attain the highest volumes. This suggests that the forest interior, where the canopy remains intact, is less susceptible to the most severe impacts of these weeds. Accordingly, managers of lowland forests in New Zealand could prioritise management of these species in high light environments, where the weed is likely to be most damaging to the native flora. Additionally, management to prevent or repair damage to the forest canopy (e.g. controlling possums, replanting canopy gaps) may also reduce opportunities for invasion by these weed species. Future research of these three weed species will examine how different control methods affect subsequent native and exotic plant recruitment, and how native plant recruitment from seed is affected by weed volume and the presence of seed predators and herbivores.

Summary

All three ground-cover-weed species studied were associated with declines in native abundance and native species richness in our lowland-forest study sites. In general, weed volume increases as canopy openness increases, and native abundance and species richness decrease as weed volume increases. Accordingly, the most severe impacts may be where these ground cover weeds occur in high light environments, perhaps when a critical threshold of weed volume is exceeded. This potential threshold appears most likely for tradescantia. Despite these negative associations, many native plant species do regenerate in the presence of ground cover weeds, particularly in the shady interior of the forest.

Acknowledgements

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