

Distribution and spread of environmental weeds along New Zealand roadsides

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Abstract: Most non-native weeds and other naturalised plants are in the early stages of invasion into New Zealand landscapes. For this invasion to be controlled, even partially, it is important to understand the dominant routes, mechanisms, and rates of weed spread across landscapes. With their linear corridors of disturbed habitats, roadsides are thought to play a large role in the spread of some weeds. We used both new surveys and existing data to assess which of the 328 environmental weeds listed by the Department of Conservation are most frequently found on roadsides, where, and whether distribution patterns are consistent with linear dispersal. We also analysed historical survey data for relationships between reserve weediness and proximity to roads. We surveyed 340 plots of 100-m-long stretches of roadside across four regions and found between 2 and 19 environmental weeds per plot; 128 species in total (Chao estimate 148). Especially abundant were agricultural species (weeds and cultivated), species that have been naturalised for well over 50 years, and species that disperse externally attached to vertebrates. While we purposefully sampled within 10 km of town limits, we found no strong effect of distance from town on roadside weed richness, including richness of just ornamentally sourced weeds. Instead, number of houses within 250 m and presence of an adjacent house or other residential structure were both important, as was presence of woody vegetation on and adjacent to roadsides. Reserves adjacent to roads had significantly higher weed richness than reserves further from roads, although the causal mechanisms are unclear. Our results suggest that while roadsides include suitable habitats for most environmental weeds, distributions are patchy and roads show little sign of acting as linear dispersal corridors, instead largely reflecting neighbouring land uses. As such, roadside weeds should best be managed as part of the wider landscape.

Keywords: invasive plant naturalisation; landscape ecology; propagule pressure; dispersal; transport; urban and rural roads

Introduction

The New Zealand flora now has a similar number of naturalised vascular plant species as native species (Buddenhagen et al. 1998; Williams & Cameron 2006; Howell 2008), and the rate of discovery of newly naturalised plant species is increasing (Gatehouse 2008; Howell 2008). About 19% of all naturalised species are currently listed as environmental weeds, being those naturalised plant species managed as weeds in conserved wildlands, by the New Zealand Department of Conservation (DOC) (Howell 2008) and/or one or more of the New Zealand regional councils (<http://www.biosecurityperformance.maf.govt.nz/>).

These alarming statistics can give the mistaken impression that New Zealand landscapes are awash with

a high diversity and abundance of weeds. Instead, most naturalised plants, including weeds, still occupy a tiny fraction of the suitable wildland habitats throughout New Zealand (e.g. Williams & Wiser 2004). It can be expected that the occupancy of weeds and other naturalised plants in New Zealand will continue to increase over the next centuries, and perhaps even for thousands of years as Europe's naturalised plants appear to have done (Pyšek & Jarošík 2005). Most environmental weeds originated as ornamental garden and amenity plants (Buddenhagen et al. 1998; Howell 2008) and therefore occur frequently near towns and houses (Timmins & Williams 1991; Sullivan et al. 2005; see also Botham et al. 2009). When we have surveyed plots in random wildland sites located many kilometres away from towns and cities, few, if any, environmental weed species are usually present (Sullivan et al. 2005, 2006).

If most environmental weeds are in the early stages of penetration into New Zealand landscapes, then we have the opportunity to prevent their further spread. The task would be greatly assisted if we understood which habitats facilitate environmental weed spread and by what means weeds are dispersed long distances. While these will vary among species, there are likely to be some habitats and dispersal vectors that commonly expedite the spread of environmental weed species. For example, creek beds facilitate the invasion of *Hieracium lepidulum* into montane *Nothofagus* forest in New Zealand's eastern Southern Alps (Miller 2006). Roadsides are thought to both facilitate weed establishment and act as corridors for weed dispersal agents such as vehicles, people, and stock (e.g. Wace 1977; Schmidt 1989; Milberg & Lamont 1995; Overton et al. 2002; Christen & Matlack 2006; Lippe & Kowarik 2007). Roadsides may therefore also be both convenient and informative places to do large-scale weed surveillance (e.g. Shuster et al. 2005).

However, the magnitude of the threat posed by roads to wildland areas is still not well understood (Forman & Alexander 1998; Forman 2000; Trombulak & Frissell 2000). Are roads and roadsides a route most weeds take when they move across rural landscapes? What proportion of weeds first establish in wildlands from adjacent roadside habitats or transported on vehicles (Lonsdale & Lane 1994)? Would surveillance for, and control of, roadside weeds near wildlands be a cost-effective way of inhibiting weed invasions? While we cannot yet answer these questions with any certainty, our study helps to lay a foundation for addressing these issues by building on previous work on the ecological impacts of roads in New Zealand (Wilson et al. 1992; Ullman et al. 1995; Spellerberg & Morrison 1998; Overton et al. 2002).

We collected roadside weed data from throughout New Zealand, using both existing data and our own surveys, to address the following questions. Our approach was a broad assessment of road and roadside contributions to weed spread. All would benefit from subsequent in-depth investigation.

- To what extent are environmental weeds found along roadsides, and in which roadside habitats?
- Which kinds of environmental weeds are found most often along roadsides?
- To what extent do environmental weeds show spatial patterns consistent with linear spread along roadsides?
- To what extent is the weediness of wildlands correlated with their proximity to roads?

Methods

Roadside weed survey

In 2005, we sampled roadsides radiating out from four small towns in each of four contrasting regions of New

Zealand (Table 1). We selected towns in each region that were surrounded by predominantly rural land and were at least 20 km from another town. We concentrated our sampling near towns because a higher abundance and diversity of environmental weeds occur in and near towns and cities (Timmins & Williams 1991; Sullivan et al. 2005).

We sampled a 10-km transect along one major road and one secondary road leading from each town, beginning at the town limit as marked by the first 100 kph road sign. One plot 100 m long and 20 m wide was located randomly within each 1-km segment of each transect, on a random side of the road. To maintain a consistent start point from towns, the first few sample points of some secondary roads were unavoidably on a primary road (Table 1). Where there was a fence running parallel to the road, the width of the zone between the edge of the pavement and the fence was recorded and species beyond the fence were recorded separately.

Within each plot we recorded mean slope and aspect, the percentage of bare ground, whether or not the roadside was mown, the presence of ditches, hedges and trees, and whether or not these were trimmed. Land use immediately beyond the plots was categorised as one or more of native forest/shrubland, mixed scrub, plantation, pastoral, cropping, horticulture, rest areas and laybys, parkland (e.g. cemeteries, sports grounds, school grounds), residential houses, other residential or industrial structures (e.g. factories) and 'other'.

We recorded all environmental weeds (restricted to those species listed on the DOC National Weeds Database February 2005; see Howell 2008). Unless specified otherwise, when we refer to weeds in the Methods and Results, we are referring to these environmental weeds. In all cases, we noted whether plants were planted, whether or not they were adult and/or juvenile, and we estimated their cover in each plot as rare < 5%; occasional 5–24%; common 25–50%; or abundant > 50% (for trees and shrubs, abundance was recorded as 1, 2–5, 6–20, or > 20 individuals).

In addition to this detailed sampling, we collected 'drive-by' data where we drove two 10-km stretches of road out from the town limit of selected towns, and recorded the presence/absence within each 1-km stretch of the transect of a set of readily apparent environmental weeds (e.g. those species with showy flowers when we sampled). This was done to further assess the strength of any gradient in environmental weed abundance, especially of ornamentally sourced species, at increasing distances away from towns. We collected this rapid assessment data from five towns in the Auckland Region (two transects out from Clevedon, Hunua, Papakura, Pokeno, and Waiuku) and four towns in the southern North Island (three transects out from Foxton, Levin, and Shannon, and one transect out from Otaki). Using this method, a total of 47 weed species were searched for in the Auckland Region in

Table 1. Towns and roads surveyed in 2005 for environmental weeds. Road types 1 and 2 are primary and secondary roads, respectively, described in Methods. Coordinates are the start of each 10-km transect, and use the New Zealand Map Grid (NZMG) projection. 'SH' refers to state highways.

Town	Type	Coordinates	Description	Date
<i>Auckland Region</i>				
Helensville	1	E2640196; N6502687	SH16 towards Wellsford	15 Nov
Helensville	2	E2638055; N6504144	Mill Road/South Head Rd	15 Nov
Pukekohe	2	E2677728; N6441480	Puni Road/Waiuku Rd	16 Nov
Pukekohe	1	E2682662; N6434191	SH22 towards Pukekawa	16 Nov
Warkworth	1	E2659299; N6531166	SH1 towards Waiwera	14 Nov
Warkworth	2	E2658556; N6531354	Woodcocks Rd	14 Nov
Wellsford	1	E2645706; N6543523	SH16 towards Helensville	15 Nov
Wellsford	2	E2648278; N6544124	Whangaripo Valley Rd	14 Nov
<i>Waikato Region</i>				
Hamilton	2	E2712026; N6382333	Puketaha Rd	13 May
Hamilton	1	E2715803; N6374409	SH1 towards Cambridge	20 Apr
Matamata	2	E2755692; N6373162	Tower Rd	20 Apr
Matamata	1	E2754014; N6371353	SH27 Matamata to Tirau	20 Apr
Morrinsville	2	E2732258; N6392313	Morrinsville–Tahuna Rd	7 Apr
Morrinsville	1	E2731501; N6389985	SH26 towards Hamilton	7 Apr
Te Awamutu	1	E2716063; N6348154	SH3 Kihikihi–Otorohanga	25 Feb
Te Awamutu	2	E2713428; N6350768	Pokuru Rd	25 Feb
<i>Wellington Region</i>				
Bulls	1	E2713002; N6112698	SH3 north	3 Mar
Bulls	2	E2712370; N6111405	Parewanui Rd	3 Mar
Foxton	1	E2704234; N6080209	SH1 north	3 Feb
Foxton	2	E2705182; N6077814	Foxton–Shannon Rd	3 Feb
Levin	1	E2705038; N6061469	SH57 north	3 Sep
Levin	2	E2704565; N6064063	SH1 then Koputaro Rd	3 Sep
Otaki	1	E2692799; N6047910	SH1 north	3 Aug
Otaki	2	E2691085; N6046265	Otaki Gorge Rd	3 Aug
Palmerston Nth	1	E2737052; N6088312	SH57 near Aokautere south to Linton	3 Apr
Palmerston Nth	2	E2735205; N6089231	Pahiatua–Aokautere Rd	3 Apr
<i>Canterbury Region</i>				
Fairlie	1	E2336310; N5675749	SH8 Mount Cook Rd	22 Feb
Fairlie	2	E2336663; N5676799	SH79 then Clayton Rd	22 Feb
Geraldine	1	E2368922; N5676867	SH79 towards Fairlie	24 Feb
Geraldine	2	E2369661; N5679821	Woodbury Rd	24 Feb
Tekapo	1	E2308250; N5685848	SH8 towards Fairlie	21 Feb
Tekapo	2	E2307259; N5686334	SH8 then Godley Peaks Rd	23 Feb
Waimate	1	E2354527; N5604867	Hakataramea Highway towards Arno	24 Feb
Waimate	2	E2354663; N5607930	Hunter Rd	24 Feb

mid-November 2005, and 75 species in the Wellington Region in mid-December 2005. These drive-by data were analysed separately from the plot data. All our plot and roadside drive-by data are publicly available on the New Zealand Biodiversity Recording Network (<http://www.nzbrn.org.nz>).

All analyses were performed in R (R Development Core Team 2007). Mixed models used the function *glmmML* (GLM with random intercept by Maximum Likelihood) from the R package of the same name (Broström 2008), clustering by weed family and with a Poisson error distribution (there were no signs of overdispersion). Mantel tests with Pearson correlations and

species accumulation curves (Chao indices; Chao 1987) used the *vegan* package (Oksanen et al. 2008). We built generalised linear mixed models to predict weed species richness on roadsides from the following explanatory variables: road category (state highway or secondary road), distance from town limit, buildings within 250 m (as mapped on the NZMS 260 Topomap series), fence presence, standing/flowing water, presence of woody vegetation, cover of bare ground, dominant slope, presence of adjacent scrub/forest, adjacent agriculture/horticulture, adjacent forestry plantation, adjacent residential structures, evidence of stock grazing, evidence of mowing, and evidence of herbicide use. Mean roadside width was

included as a covariate and models were clustered by town. We separated those species known to only have ornamental use from the rest (Gatehouse 2008), based on the expectation that the former group would show a greater sensitivity to proximity to towns and housing and respond less strongly to adjacent agricultural land uses. Species classified by Gatehouse (2008) as only of ornamental use account for 58% of the environmental weeds listed by Howell (2008). Models were simplified in a stepwise manner to identify minimum adequate models. Reported *P*-values are those from the drop1 routine in R, assessing the contribution of each variable to the model when added last.

Waikato roadside survey

We were kindly supplied with data from a more extensive Waikato roadside vegetation sampling project undertaken by J. M. Overton and colleagues, including one of us, MCS (Overton et al. 2002). They recorded all plants in a random sample of roadsides along state highways of the Waikato Region, approximately 1750 km in length, stratified by the New Zealand Land Cover Database (LCDB1). Unlike our survey, their sampling was not restricted to roadsides within 10 km of towns. Sampled were 276 sites, with plots laid out at different distances from the road edge at each site. Plots were of different sizes depending on the vegetation type, from 1 × 1 m in low vegetation to 20 × 20 m in tall forest (1434 plots in total). We do not use the paired plots they sampled 50 m beyond the road. We extracted the environmental weed records from these data. Poisson glmmML models were constructed to predict number of environmental weeds per site, clustered by land cover type to account for the stratification in random sampling. We combined variables to construct a set of explanatory variables closely analogous to those used in our plot data models (distance to the nearest town; presence of woody vegetation; the inverse of total vegetation cover – to be comparable with our cover of bare ground; dominant slope; presence of adjacent scrub/forest, adjacent agriculture/horticulture, adjacent forestry plantation, adjacent urban land use; evidence of mowing; evidence of herbicide use; plot width; elevation).

Historical and ecological traits predicting roadside weeds

We applied GLMs (generalised linear models) to historical and ecological data collated for all New Zealand naturalised plant species (Gatehouse 2008) to identify the traits that were disproportionately represented among those environmental weeds most often found on roadsides (see Results for traits). We used each weed's proportion occupancy of plots from our survey results and, independently, those from the Waikato roadside survey (Overton et al. 2002) as our measures of roadside occupancy. Comparing the traits of roadside weeds with weeds of other land uses was beyond the scope of our study.

The traits we used were date of first wild discovery in New Zealand (an estimate of the date of naturalisation), dispersal mode(s) (categorised as wind, water, explosive, vertebrate gut, external attachment to vertebrates, unspecified), human use (categorised as ornamental only; agriculture – crop and pasture species; utilitarian horticulture – used for shelter belts, hedges, land stabilisation, etc. in rural landscapes; forestry; and seed impurities), and life form (simplified to aquatic, terrestrial annuals, herbaceous perennials, woody vines, shrubs, and trees). See Gatehouse (2008) for details.

Roads and scenic reserve weediness

To assess the relationship between road proximity and weed invasion of native forest reserves, we inspected the scenic reserve survey data for the Bay of Plenty (Beadel & Shaw 1988; Clarkson & Regnier 1989), southern King Country (Fuller & Edwards 1989), Canterbury (Kelly 1972), and Otago and Southland (Allen et al. 1989). The most detailed analysis was made of the Canterbury dataset since one of us (JJS) had digitised it for the New Zealand Biodiversity Recording Network.

In the Canterbury data, we examined whether the presence of a road adjacent to a reserve affected the weed species richness in that reserve. Weed species richness was calculated from the 64 'troublesome' weed species consistently searched for by Kelly (1972), 58 of which are listed by Howell (2008) as environmental weeds. We controlled for variation due to the environmental variables collated by Kelly (1972) (reserve area, distance to nearest other reserve, average rainfall, minimum and maximum altitude, soil fertility, distance to the nearest town) as covariates in a Poisson GLM.

For the other survey regions, one of us (PAW) determined the presence or absence of the category 'exotic scrub/shrubs' or 'exotic forest/trees', and whether these were environmental weeds, for each reserve in relation to the presence or absence of roads bordering each reserve. Reserves that were purely open land, coastal herbfields, or islands were excluded. Included in these descriptions were lianas and robust, semi-woody vines and perennial herbs such as Russell lupin (*Lupinus polyphyllus*). Also noted were species mentioned elsewhere in the reserve descriptions, but not those merely ticked as present in the standard species lists. The existence of roads adjacent to the legal boundary of the reserves was determined from the maps attached to each reserve report. Unformed roads and tracks were excluded. Whether the two exotic classes were more frequently present when roads were adjacent was tested with chi-square tests.

Results

How weedy are New Zealand roadsides?

In our surveys, we found 128 (39%) environmental weeds growing on roadsides throughout the four regions

(see Timmins et al. 2006). Using the Chao index (Chao 1987; Colwell & Coddington 1994) to extrapolate our plot sampling for all regions (Fig. 1), we estimate that there were about 148 (SE 8.1) roadside environmental weed species in these areas, under half of DOC's list. In each region, less than a third of all listed environmental weeds are estimated to be on roadsides surrounding the periphery of towns (Fig. 1). The frequency distribution of roadside occupancy among environmental weeds approximated an inverse binomial distribution for each region, with only 33 species occurring in more than 10% of our 100-m-long roadside plot in one or more regions.

The average species richness of environmental weeds per plot was 6.5 (SEM 0.26) in south Canterbury, 8 (0.33) in Wellington, 6.6 (0.28) in Waikato, and 8.2 (0.34) in Auckland. Species richness per plot ranged from two to 19 ($n = 340$).

We found 50 environmental weeds in our Waikato sampling, 33 of which overlapped with Overton et al. (2002). Overton et al. (2002) found 62 environmental weeds, including 29 species not found in our survey, consistent with the estimate of total environmental weed species richness on these Waikato roadsides in Fig. 1.

Factors explaining roadside weed distribution and abundance

Few environmental variables were consistently important across regions for predicting the species richness of

environmental weeds in our roadside plots (Tables 2, 3). The species richness of weeds of ornamental use was higher on roadsides with nearby residential structures and with woody vegetation (Table 3). The species richness of other weeds was greatest on roadsides with woody vegetation and adjacent scrub or native forest (Table 2).

To our surprise, there were no strong effects of distance from towns on the number of environmental weeds found along roadsides in our plot data, even those species of solely ornamental use (Table 2, 3). There was also no significant effect of distance from towns in our drive-by data, even among those environmental weeds that have been used solely as ornamentals (Fig. 2). However, in the Overton et al. (2002) Waikato data, which were not restricted to within 10 km of towns, the richness of weeds of only ornamental use did gradually decline with distance from the nearest town (Table 2, Fig. 3).

The effects of adjacent residential structures and the number of houses with 250 m of a roadside plot were more useful for predicting the species richness of roadside environmental weeds than proximity to the nearest town. We built simple Poisson glmmML models predicting the species richness of weeds of ornamental origin using just one 'residential' variable as a predictor (distance from town, mapped buildings within 250 m, or the visible presence of adjacent residential houses and other structures), and including road category and clustering by town. Weed richness was significantly greater

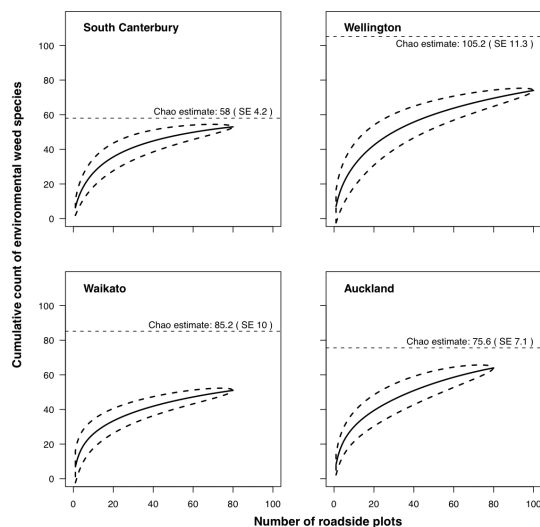


Figure 1. Accumulation curves for environmental weed species for each region we sampled, including the Chao estimate (Chao 1987) of total species richness of roadside environmental weeds. The curves include 95% confidence intervals and represent 100 random permutations of our roadside plots (Oksanen et al. 2008). Note that we searched for 328 environmental weed species listed in the DOC National Weeds Database.

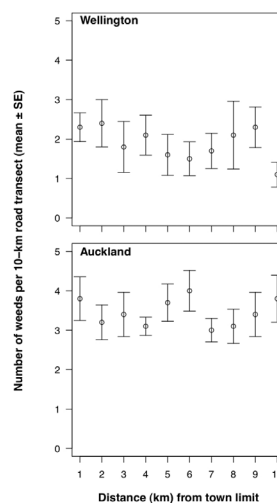


Figure 2. The surprisingly weak relationship between distance away from towns and mean number of environmental weeds of solely garden ornamental use growing on roadsides. Neither relationship is significant. In Wellington, 31 readily apparent species of solely ornamental origin were searched for along 10 roads out from four towns. In Auckland, 25 such species were searched for along 10 roads out from five towns.

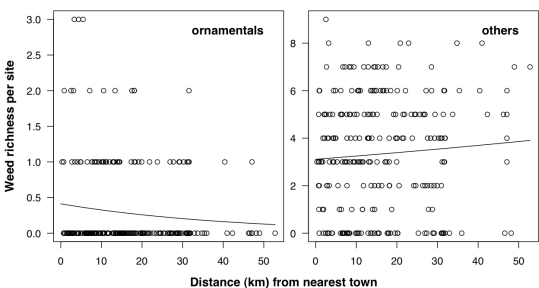


Figure 3. Richness of environmental weeds of ornamental use only declines with increasing distance from the nearest town, unlike the richness of other environmental weeds. These trends are from the Waikato data of Overton et al. (2002). Plotted is the weed richness per roadside site and the fitted model from glmmMLs of distance to town clustered by land cover (to accommodate the stratified random sampling). Only the ornamental model was significant (ornamentals: d.f. = 1, LRT = 4.45, $P < 0.05$, others: d.f. = 1, LRT = 2.13, $P = 0.14$). This distance effect for ornamentals was strengthened ($P < 0.01$) after habitat and adjacent land variables were included (Table 3).

Table 2. Results of minimum adequate GLMs predicting roadside plot species richness of environmental weed species with human uses other than ornamental, using environmental variables from inside and adjacent to the plots, analysed independently for each region sampled. The sign (+/–) indicates direction of the effect, and the superscript its statistical significance when added last to the model ($***P < 0.001$, $**P < 0.01$, $*P < 0.05$, no asterisk means a variable retained in minimum adequate model, $P < 0.15$). Excluded from the table are variables not present in any minimum adequate model (distance to town, mapped buildings within 250 m, primary/secondary road, adjacent plantation, adjacent agriculture/horticulture, adjacent urban, evidence of herbicide use, plot slope). The Waikato data from Overton et al. (2002) were analysed instead with a Poisson glmmML model to account for stratified sampling, and with comparable explanatory variables, measured differently, except for the absence of grazing and fence presence/absence and addition of elevation.

Variable	Auckland	Waikato	Waikato (Overton)	Wellington	Canterbury
Adjacent scrub/forest				+	+**
Adjacent urban			—*		
Bare ground	—		—***		
Fence			NA	—	
Grazed					—*
Herbicide use			—		
Mown	—*				
Slope			—**		
Standing/flowing water			NA		+
Woody vegetation	+			+**	

Table 3. Results of minimum adequate GLMs predicting roadside plot species richness of those DOC weed species with ornamental use only, using environmental variables from inside and adjacent to the plots, analysed independently for each region sampled. See Table 2 for details.

Variable	Auckland	Waikato	Waikato (Overton)	Wellington	Canterbury
Adjacent agriculture	—		—***		
Adjacent plantation			—*		
Adjacent scrub/forest			—*		
Adjacent urban			—***	+***	+**
Bare ground	—			+	
Distance to town			—**		
Dominant slope	+				
Fence	+	—**			
Herbicide use			+*		
Mown	—		+*		
Woody vegetation	+*	+***		+**	

in plots adjacent to residential structures in the Auckland (d.f. = 1, LRT (Likelihood-Ratio Test statistic) = 3.9, $P < 0.05$), Wellington (d.f. = 1, LRT = 15.7, $P < 0.001$), and Canterbury (d.f. = 1, LRT = 10.1, $P < 0.01$) regions, and significantly increased with the number of nearby houses in the Wellington Region (d.f. = 1, LRT = 13.6, $P < 0.001$). In no case was there a significant effect of distance to town. The richness of weeds not solely of ornamental use was not significantly predicted by any of these variables. Surprisingly, distance to town did not significantly predict the presence of adjacent residential structures in roadside plots and was only weakly correlated with the number of mapped buildings within 250 m (Pearson's product-moment correlation, d.f. = 338, $r = -0.1$, $t = -2.31$, $P < 0.05$).

Historical and ecological traits predicting roadside weeds

The environmental weeds common on roadsides were all species typical of rural New Zealand landscapes, typically grasses and herbaceous pastoral weeds with the woody exceptions of Scotch broom (*Cytisus scoparius*), blackberry (*Rubus fruticosus* agg.), and gorse (*Ulex europaeus*). For example, the five species present in the most plots per region were, for Canterbury, *Agrostis capillaris* (77 plots), *Dactylis glomerata* (58 plots), Scotch broom (44 plots) *Cirsium arvense* (33 plots), and *Hieracium pilosella* (26 plots); for Wellington, *Dactylis glomerata* (90 plots), *Schedonorus phoenix* (89

plots), *Agrostis capillaris* (62 plots) *Cirsium arvense* (43 plots), and *Holcus lanatus* (41 plots); for Waikato, *Dactylis glomerata* (66 plots), *Lolium perenne* (55 plots), blackberry (54 plots) *Schedonorus phoenix* (47 plots), and *Holcus lanatus* (39 plots); and for Auckland, *Dactylis glomerata* (65 plots), *Schedonorus phoenix* (58 plots), *Holcus lanatus* (50 plots) *Cyperus eragrostis* (45 plots), and blackberry (39 plots).

In a Poisson glmmML clustered by family, the following factors significantly explained which environmental weed species were present on roadsides: recency of naturalisation (negative, d.f. = 1, LRT = 9.5, $P < 0.01$), life form (trees and vines disproportionately likely to be on roadsides, d.f. = 5, LRT = 23.6, $P < 0.001$), use in agriculture (positive, d.f. = 1, LRT = 5.9, $P < 0.05$), vertebrate gut seed dispersal (positive, d.f. = 1, LRT = 17.7, $P < 0.001$), and explosive seed dispersal (positive, d.f. = 1, LRT = 12.9, $P < 0.001$). With respect to date of naturalisation, the 34 weed tree species we found on roadsides naturalised 24 years earlier on average than the remaining 29 trees listed by DOC that we did not find, even though the latter group still naturalised 67 years ago on average (Fig. 4). The data from Overton et al. (2002) showed similar patterns (the same significant variables acting in the same directions), with the exceptions of adding wind dispersal (positive, df = 1, LRT = 4.7, $P < 0.05$) and removing the agricultural crop use and seed dispersal by attachment to vertebrates.

The absence of many recently naturalised species

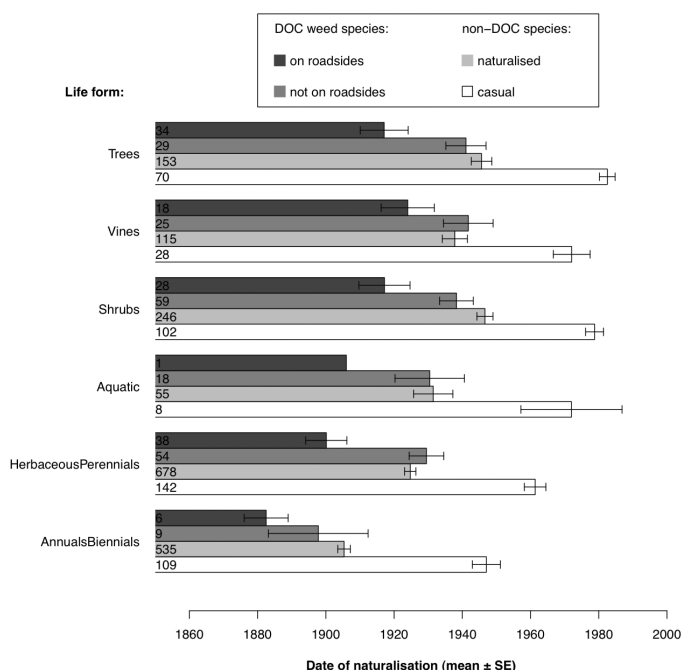


Figure 4. Mean year of naturalisation for environmental weeds we recorded along roadsides and those we did not, compared with fully and casually naturalised species in the New Zealand flora not listed by DOC as environmental weeds. The degree of difference between these groups varies by plant life form. (Life form and naturalised plant data from Gatehouse (2008).)

from our roadside plots may in part be due to our sampling outside urban centres, in which many ornamentally sourced weeds first establish in the decades following naturalisation (Esler 1988; Williams & Cameron 2006). Even a successful, ornamentally sourced, wind-dispersed weed like moth plant (*Araujia sericifera*), now ‘likely to appear in every garden in Auckland [City]’ (Esler 2004, p. 125), was found on only two nearby plots along one road out from one town (Pukekohe) in the Auckland Region.

We found similar patterns in the plot occupancy of just those weeds present on roadsides (Table 4). The most consistent effects across regions were a positive association between weeds of past agricultural use and roadside occupancy; a negative association of weeds used in forestry with roadside occupancy; and a negative relationship between a species’ date of naturalisation and its roadside occupancy (Table 4). The most consistently detected dispersal mode was for weeds with seeds with adaptations for attachment to vertebrates; this was positively associated with roadside occupancy in four of our five analyses (Table 4). Species classified by Gatehouse (2008) as of solely ornamental use had significantly lower roadside occupancy than other species only in Canterbury (Table 4).

Are roads linear corridors of dispersal?

If roads act as linear corridors of dispersal for most weed species, then we expect the vegetative similarity of weed communities among roadside plots to decrease with increasing spatial separation along each road, even after controlling for differences in habitat and adjacent land use. Within each transect out from a town, plots closer together were more similar vegetatively than distant plots (Mantel tests with Bray–Curtis dissimilarity

of plots by species composition and log(distance), with randomisation restricted to within each 10-km transect: Auckland, $r = 0.12$, $P < 0.001$; Waikato, $r = 0.15$, $P < 0.01$; Wellington, $r = 0.09$, $P < 0.001$; Canterbury, $r = 0.26$, $P < 0.01$). Plots closer together were also more similar environmentally than distant plots (analogous Mantel tests using all environmental variables within and adjacent to plots, Auckland, $r = 0.19$, $P < 0.001$; Waikato, $r = 0.17$, $P < 0.05$; Wellington, $r = 0.17$, $P < 0.001$; Canterbury, $r = 0.21$, $P < 0.05$). After we controlled for the effects of environment on plot vegetative similarity, nearby plots were still more similar vegetatively than distance plots only in Wellington (partial Mantel test: Wellington, $r = 0.07$, $P < 0.05$).

Roads and scenic reserve weediness

For four regions (excluding Canterbury), we collated data from 101 scenic reserves with adjacent roads and 42 without roads adjacent (see results in Table 5). The presence of roads was always associated with woody weeds in the North Island regions of Bay of Plenty and southern King Country, and where there were no adjacent roads, there were no woody weeds noted. The patterns were not as stark in the South Island, where many reserves with roads had no woody weeds, and several reserves without adjacent roads had weeds.

The weeds frequently recorded in Bay of Plenty reserves were Himalayan honeysuckle (*Leycesteria formosa*), blackberry, Japanese honeysuckle (*Lonicera japonica*), barberry (*Berberis glaucocarpa*), buddleia (*Buddleja davidii*), tree lupins (*Lupinus arboreus*), and willows (*Salix* spp.). Recorded once were Scotch broom, *Chamyparis lawsoniana*aeec, *Clematis vitalba*, *Selaginella kraussiana*, and *Tradescantia fluminensis*.

Table 4. Results of minimum adequate GLMs using species traits to predict frequency that environmental weeds occur in roadside plots, excluding species not found in any plot, and analysed independently for each region sampled. The sign (+/–) indicates direction of the effect, and the superscript indicates its statistical significance (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, variable retained in minimum adequate model, $P < 0.15$).

Trait	Auckland	Waikato	Waikato (Overton)	Wellington	Canterbury
Naturalisation year	—*	—*	—	—**	
Wind dispersal		+**			+
Explosive dispersal		+*	+**	+***	
Vertebrate attachment dispersal	+***		+***		
Water dispersal	—*	—*			
Gut dispersal		+			
Ornamental use only		—			—**
Rural utilitarian use	+*		+**		
Agricultural crop	+***	+***	+***	+***	+*
Forestry crop	—**	—	—	—	—**
Life form		**	*		

Table 5. Presence and absence of habitat class 'exotic scrub/shrubs or 'exotic forest/trees' in relation to the presence or absence of roads bordering the reserves in several scenic reserve survey reports: (a) Taneatua and West Gisborne (Beadel & Shaw 1988; Clarkson & Regnier 1989), (b) southern King Country (Fuller & Edwards 1989), and (c) and (d) Otago and Southland (Allen et al. 1989).

	Weeds present	Weeds absent	χ^2	P
(a) <i>Bay of Plenty</i>				
Roads present	17	0	16.0	0.001
Roads absent	0	5	13.0	0.05
(b) <i>southern King Country</i>				
Roads present	13	0	13	0.001
Roads absent	0	14	13.13	0.001
(c) <i>Otago</i>				
Roads present	27	4	20.18	0.001
Roads absent	7	11	0.88	n.s.
(d) <i>Southland</i>				
Roads present	31	9	12.1	0.001
Roads absent	1	4	2.5	n.s.

A similar list was recorded for southern King Country: Japanese honeysuckle, blackberry, Himalayan honeysuckle, buddleia, barberry, willows, and tree lupin. For Japanese honeysuckle and blackberry, specific mention was made of them being on the roadsides and they were variously described as 'swamping trees', 'spreading into the forest' or 'inundating' native shrubland (Fuller & Edwards 1989). These species formed either pure associations or were variously mixed with bracken (*Pteridium esculentum*) and native broadleaved shrubs. None of the weeds were recorded as invading forest apart from selaginella, and one area of pole totara forest invaded by barberry (Fuller & Edwards 1989).

In Otago and Southland reserves where roads were absent, the following species were recorded: gorse (5 reserves), Scotch broom (2 reserves), larch (*Larix decidua*), Douglas-fir (*Pseudotsuga menziesii*), elderberry (*Sambucus nigra*, 2 reserves), gooseberry (*Ribes uva-crispa*), and Himalayan honeysuckle (Allen et al. 1989). These species are dispersed by gravity, wind, or carried by birds. All would plausibly have been purposefully planted in the vicinity of rural residential houses and all have been naturalised for a long time.

Among the 78 Canterbury scenic reserves surveyed by Kelly (1972), 40 were adjacent to a public road. On average, those reserves with an adjacent road contained more weed species (5.6, SEM 0.6) than those without (3.4, 0.4). This result held in a Poisson GLM model that first took into account six site environmental variables recorded by Kelly (1972): area, distance to nearest reserve, distance to nearest town, annual rainfall, minimum and maximum altitude, and soil fertility, the first four log transformed (adjacent road effect: estimate 0.46, d.f. = 1, deviance = 137, LRT = 16, $P < 0.001$). An analogous GLM on native plant richness in these reserves showed a significant negative effect of an adjacent road (estimate

−21.55, d.f. = 1, deviance = 42038, $F = 18$, $P < 0.001$). Curiously, when we analysed the effects of distance to the nearest road on the weed richness in those reserves without adjacent roads, there was a significant positive effect of distance from roads on weed richness (Gaussian GLM, road distance effect: estimate 0.49, d.f. = 1, deviance = 50, LRT = 23, $P < 0.001$). There was no significant effect of distance to road on native richness in this subset of reserves.

Discussion

We expected strong patterns in roadside weed distributions and abundance relating to the proximity to the nearest town and residential garden, the adjacent land use, and the extent of woody roadside vegetation (Ullman et al. 1995; Overton et al. 2002; Sullivan et al. 2005). We found some statistically significant patterns consistent with these expectations, but our overall impression is of a largely unpredictable system in the early stages of invasion and far from equilibrium.

Roadsides as weed habitats

We estimate that about 150 environmental weed species occur on roadsides on the outskirts of towns in the landscapes we sampled. These were disproportionately early naturalisations that were stock-dispersed, and of past and/or current agricultural use (Table 4). Total roadside weed richness reflects habitat within the plots and aspects of adjacent land use (Ullman et al. 1995; Overton et al. 2002; see also Williams & Wiser 2004). Roadsides, together with riparian margins and other 'waste' areas, contain patches of wild habitats that in combination act as reservoirs for weeds in otherwise intensively managed rural landscapes. Nevertheless, our data are ambivalent about weeds using

roadsides as linear dispersal corridors independently of the adjacent land. Instead, weed communities on roadsides typically reflect the surrounding land and the weed populations on that land. There will undoubtedly be exceptions to this rule. A New Zealand example is Kaffir lily (*Schizostylis coccinea*) in mid-Canterbury, which is spreading along irrigation ditches beside roads (Webb et al. 1988, JJS, pers. obs.). This uninterrupted continuity of the same habitat along roadsides is unusual.

Our species accumulation curves (Fig. 1) suggest greater sampling would not have found many more of the 200 environmental weeds that were absent from our plots. Given the variety of wild habitats on roadsides, we expect this reflects a current lack of nearby propagule sources for these species in the landscapes we sampled. This is supported by our strong association of roadside occupancy with species' dates of naturalisation. Nevertheless, contrary to our expectations (Timmins & Williams 1991; cf. Botham et al. 2009), we found only a weak gradient in ornamentally sourced weeds out from towns into surrounding rural and wildland landscapes (Figs 2, 3). The ornamentally sourced weeds we found tended to be close to buildings and parks. This suggests the cultivated sources of these wild plants were within a few hundred metres away, rather than in gardens several kilometres away in the nearby towns, consistent with Sullivan et al. (2005). This role of propagule pressure in species distributions at local scales was well documented by Levine (2001) in an analogous riparian system. It is unclear whether many ornamental weed species restricted to roadsides would be able to sustain their populations without the support of propagules from nearby cultivated sources, particularly in the face of competition from more abundant species, e.g. pasture grasses, dispersing onto the roadsides from the adjacent land.

Despite the usual dominance of species from adjacent land, roadsides are not simply extensions of adjacent habitats (e.g. Angold 1997; Parendes & Jones 2000). Roadsides are usually perpetually disturbed and with altered soil conditions, especially close to the carriageway. They usually have high light levels, especially adjacent to high-use roads (Parendes & Jones 2000). This proximal roadside zone is a very specialised habitat that in temperate zones of the Southern Hemisphere is occupied by ruderal species mainly from Eurasia, but varying according to the local climatic conditions (Wilson et al. 1992; Ullman et al. 1995; Pauchard & Alaback 2004). In Australia, tropical grasses often establish on roadsides and then spread to adjacent open woodland (Amor & Stevens 1976; Milberg & Lamont 1995). In general, woody weeds are less common on roadsides than herbaceous weeds, but species like pines and eucalypts (Healey 1969) can be common on roadsides with reliable available moisture and low disturbance rates. Such species as *Cotoneaster* spp. (PAW, pers. obs.) are most common on roadside batters, which tend to be less disturbed by mowing and spraying than flat areas.

Even if weeds are present on roadsides and can persist there as wild populations, they still may not penetrate into the surrounding vegetation. Filtering effects may be particularly strong in climatically severe environments even where the adjacent short vegetation might appear to be open to invasion. Herbaceous roadside weeds tend to be ephemerals unable to penetrate adjacent native vegetation, while successful invaders tended to be less ephemeral (Winqvist 2003) and functionally akin to the native species (Godfree et al. 2004). In prairie vegetation with both native and exotic ruderal species, native species are less likely to be found on roadsides than exotic species (Larson 2002). Similar patterns probably occur in New Zealand, but there are very few of either ruderal native species (Wardle 1991) or ruderal environmental weeds (6; Fig. 4) on roadsides.

In contrast, where filtering effects are weak, the distribution of weeds along roadsides may instead reflect the beginning of invasion into the surrounding vegetation. In Europe, herbaceous or shrubby 'hinterland' vegetation may be invaded for up to 50 m (Gelbard & Belnap 2003) or 100 m beyond the road verge (Tyser & Worley 1992) and evergreen woody exotics in Massachusetts, USA, invaded deciduous forests to at least 120 m from roadside plantings (Forman & Deblinger 2000). This effect is colourfully illustrated in our study by the spread of Russell lupins (*Lupinus polyphyllus*) from stony roadsides into degraded tussock grassland of the Mackenzie Basin, although riverbeds also function as major linear corridors for spread.

In other situations, the mismatch between roadside invaders and the adjacent vegetation may be readily apparent. Ruderal species are confined to roadsides or for short distances into adjacent disturbed forest in environments both dissimilar (Wester & Juvik 1983) and similar to New Zealand (Pauchard & Alaback 2004). Most Eurasian ruderal species are excluded from forests in New Zealand, and roadside margins are more likely to be invaded by shrubs and vines with similar life form to the native species (Williams et al. 2001a).

Roadside exotic floras are strongly influenced by altitudinal and climatic gradients in New Zealand (Wilson et al. 1992; Ullman et al. 1995) and in Chile (Pauchard & Alaback 2004). Because their environmental responses were similar to those recorded in Europe, Ullman et al. (1998) suggested colonisation of all available roadside sites by the exotic species had occurred, despite the relatively short time since their introduction to New Zealand. Even if this is largely correct for the widespread species Ullman et al. (1998) studied, it is unlikely to apply to our sampled DOC weeds or to naturalised species generally, given our strong relationship between time since naturalisation and roadside occupancy, and because so many new naturalisations are found on roadsides (Williams & Cameron 2006). Roadsides frequently offer the first and nearest chance in an otherwise intensively managed

landscape for a species to colonise beyond the bounds of horticulture. Indeed, 25% of new naturalisations between 1989 and 2000 were collected from roadsides and tracks (Williams & Cameron 2006), although this will be due at least in part to sampling bias.

Creation of an environment favourable to weeds begins with road construction itself, in a range of environments worldwide (Greenberg et al. 1997; Mullerova 2000; Godefroid & Koedam 2004). Construction often results in heightened water-table levels on roadsides facilitating the establishment of wetland weeds (Buckley et al. 2003), while in dry regions, runoff provides moisture or nutrients that stimulate weed growth (Williams & Groves 1980) to a greater extent than native species (Cale & Hobbs 1991; Angold 1997; Perez-Fernandez et al. 2002). Both these phenomena were seen during our study although our sampling did not aim to quantify the relationship. Salt (NaCl) is frequently used overseas to prevent ice on roads and there is a large literature on its effects, including on weed growth (Detwyler 1971), but salt is not used in New Zealand.

Several roadside maintenance procedures – grading, cutting or mowing, and herbicide spraying – all stimulate weed growth, e.g. *Acacia* (Spooner et al. 2004). Such conditions can be very local, e.g. the bare areas created by repeated spraying around road markers that are colonised by *Sedum acre* and *Verbascum thapsus* in the Mackenzie Basin (PAW, pers. obs.).

More generally in our study, elsewhere in New Zealand (Ullman et al. 1998), and overseas, exotic grasses are amongst the most common roadside species (Tyser & Worley 1992; Milberg & Lamont 1995; Appleby 1998; Kim & Lee 2000; Gelbard & Belnap 2003; Hoffmann et al. 2004), because they benefit from the altered environment, and roadside management, more than some other life forms, e.g. woody species (Angold 1997). In the pakihi vegetation of Westland, New Zealand, roads facilitate weed establishment and spread by altering the drainage (*Carex ovalis*) and increasing nutrients through disturbance (*Holcus lanatus*) (Williams et al. 1990).

Road-mediated dispersal

By their very nature, roads provide a means of access to the landscape for a range of moving objects from animals to trucks, each of which may carry weed seeds that are deposited randomly by the wayside or in specific places. In this way, a species may invade faster along roadsides than through the landscape as a whole (Guthrie-Smith 1953; Shuster et al. 2005). This may be reflected in the greater naturalised species richness and abundance alongside the most developed roads (Tyser & Worley 1992; Gelbard & Belnap 2003) where traffic volumes are greatest, although more developed roadsides may also have more altered and frequently disturbed roadside habitats and higher densities of buildings and gardens. Despite this, we found

no detectable difference between major and secondary roads on roadside weed richness and composition in any of the four regions we sampled. Traffic volumes typical of major roads outside of New Zealand towns may be insufficient to enhance frequent short-distance dispersal of propagules capable of attaching to vehicles.

Many seeds and whole seed heads are capable of being carried attached to vehicles. Small seeds, especially, are carried by tyres and in soil adhering to vehicles (Clifford 1959; Wace 1977; Schmidt 1989), as we also found. Consequently, seeds on vehicles come from a wide range of habitats, including urban areas. Although relatively few of these species grow commonly on roadsides, seeds of most roadside weed species are also found on vehicles (Wace 1977; Schmidt 1989). Vehicles transport not only small seeds of agricultural crop species or their associated weeds, predominantly grasses, but also urban horticultural species that are mostly dispersed by wind (e.g. *Buddleja davidii*) or animals (e.g. *Pyracantha* spp.) (Wace 1977). Vehicles as dispersal agents can be of concern to natural areas managers, e.g. the weeds of roadsides in Kakadu National Park (Cowie & Werner 1993) were found in the mud and tyres of vehicles (Lonsdale & Lane 1994). Traditional car washes are cosmetic only, and do nothing to halt the spread of weeds by vehicles, so it is unlikely anything can be done about seeds on private motor vehicles other than in special cases, or by keeping vehicles out of sensitive areas altogether (Wace 1977; Parendes & Jones 2000). The alternative strategy of ignoring the vectors and concentrating on finding founder populations of weeds in high-risk areas was suggested by Lonsdale and Lane (1994). This is probably the best approach in New Zealand too, although it may be impractical for finding weeds spread by 'off road' vehicles on wilderness tracks.

Road users and maintenance practices, particularly the use of roadside slashers, are important dispersers of roadside weeds and numerous websites are devoted to codes of best practice to minimise this (e.g. Tyers et al. 2004). Species reliant on vegetative spread benefit particularly from this practice, e.g. domestic hops (*Humulus lupulus*) in the Buller catchment, Nelson (PAW, pers. obs.). Domestic stock are still responsible for dispersal of agricultural weed seeds overseas (Tyser & Worley 1992; Pauchard & Alaback 2004), as they were prior to the advent of stock transporters in New Zealand (Guthrie-Smith 1953). Although stock droving is now little practised in New Zealand, stock can still disperse weeds when they are transported from one place to another (N. Ledgard, pers. comm.). This potential weed spread can be minimised by appropriate quarantine measures (Tyser & Worley 1992).

Active dispersal of plants on roadsides by people, such as for erosion control and garden waste dumping, has led to some major plant invasions, e.g. Japanese honeysuckle in the USA (see Williams et al. 2001b). In New Zealand, the invasion of banana passion vine (*Passiflora* spp.) in

New Zealand appears to have been helped considerably by people throwing half-eaten fruit from cars (Williams & Buxton 1995) while Russell lupin dispersal in the Mackenzie Basin has been greatly facilitated by purposeful spread of seeds (D. Scott, pers. comm.). Populations of some feral fruit tree species are dependent on continuous seed input from passing cars (Smith 1986) and this applies in New Zealand where apple (*Malus × domestica*) and peach (*Prunus persica*) trees are scattered through the lowlands even though they do not appear to regenerate naturally (PAW and MCS, pers. obs.). Such dispersal is often clumped around picnic grounds and other access points close to roads, as are weeds in illegally dumped garden waste (Sullivan et al. 2005, pers. obs.).

Conclusion

Sections of roadside are among the patches of suitable habitat often used by environmental weeds as they leapfrog their way across landscapes. Because of this, protecting valuable conservation reserves from weed invasion would undoubtedly benefit from weed control along adjacent roadsides, especially in conjunction with control in other adjacent suitable weed habitats.

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