Movement of exotic plants into coastal native forests from gardens in northern New Zealand

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Abstract: The number and abundance of exotic weeds in native forest fragments are known to correlate with the distance to the nearest large town. This is of concern as land near lowland forest is increasingly being subdivided for housing throughout much of New Zealand. We quantified the relationship between settlements and exotic plants for the coastal forests in eastern Northland, New Zealand. Exotic plant species were sampled in 18 coastal forest areas of varying size, and related to attributes of nearby settlements (housing proximity, density, age, and the exotic plant species present). All settlement attributes were significantly related to the number of exotic species present in neighbouring forest fragments, unlike fragment size. The exotic species found in a particular forest area were significantly more likely to be present in the neighbouring settlement than in other settlements. The number of houses within 250 m of a forest area, alone, explained 66.8% of the variation in the number of exotic plant species in these forests. Our results suggest that proximity and size of settlements are currently the dominant factors controlling the number of exotic plant species in these forest areas, rather than ecological conditions within the forests. Properly managing the locations and densities of new subdivisions, as well as the species grown in gardens in existing and new subdivisions near forest reserves, will reduce the weed pressure and subsequent cost of weed control in these reserves.

Keywords: coastal forest; environmental weeds; gardens; housing subdivisions; invasive plant pests.

Introduction

Many naturalised plant species are known to have serious, deleterious impacts on native flora and fauna (e.g. Vitousek *et al.*, 1996; Williams, 1997; Owen, 1998; Ewel *et al.*, 2000; Lee *et al.*, 2000; Standish *et al.*, 2001). Since European settlement of New Zealand, more than 20 000 exotic plant species (i.e. not native to New Zealand) have been introduced (Lee *et al.*, 2000). About 2000 of these have "naturalised" (i.e. formed self-sustaining wild populations, see Richardson *et al.*, 2000), and New Zealand now has about as many naturalised plant species as native plant species (Owen, 1998; Lee *et al.*, 2000, Heenan *et al.*, 2002). This is only the beginning — many of the >20 000 exotic garden species not yet wild are in the process of becoming so (Lee *et al.*, 2000). The implications of this invasion for New Zealand's native flora and fauna are just beginning to be understood (e.g. Timmins, 1997; Ewel *et al.*, 2000; Lee *et al.*, 2000).

Given that New Zealand's naturalised plant species are increasing in number, abundance, and range, we urgently need to keep those exotic species with both known *or* suspected detrimental effects on the natural environment — termed environmental weeds — from invading important forest fragments. To do so, we need to understand where these environmental weeds come from locally, and what factors hinder or enhance their ability to cross the forest fragment boundary and establish.

The majority of New Zealand's recent naturalised plant species originated as ornamental garden plants (Esler, 1988; Buddenhagen *et al.*, 1998; Lee *et al.*, 2000), and gardens act as an important source of exotic plants that spread into native forest fragments. In a study of forest reserves in eight lowland regions of New Zealand, the distance from forest fragments to towns with more than 5000 inhabitants was the best predictor of the number of environmental weed species (Timmins and Williams, 1991).

Few published international studies have quantified the relationships between forest fragment weediness and characteristics of neighbouring settlements. Those that have document strong effects for a variety of vegetation types and settlement attributes. A major source of weed introductions to foredunes of coastal SE Queensland was the adjacent dumping of garden waste (Batianoff and Franks, 1998). Wetlands in Portland, U.S.A., surrounded by agricultural, commercial, industrial and transportation land contain significantly more exotic plant species than areas surrounded by undeveloped land (Magee *et al.*, 1999). The number of exotic species in disturbed habitats on Tiwi Islands, Australia, increased with the age of neighbouring settlements (Fensham and Cowie, 1998), while the proportion of exotic plant species in urban bushland reserves in Sydney, Australia, increased with the age of the surrounding settlement (Rose and Fairweather, 1997). At a larger scale, the degree of invasion of Czech nature reserves by naturalised plants was related positively to the human population density of the region (Pyšek *et al.,* 2002).

We investigated the relationship between the number of exotic plants established in Northland coastal native forests and several settlement attributes: housing density, distance to the nearest houses, settlement age, and the number of exotic plant species growing in gardens. This study differs from earlier New Zealand studies (Timmins and Williams, 1991) in its examination of a greater range of settlement attributes at a finer spatial resolution. Coastal forests in Northland were studied because New Zealand Department of Conservation (DOC) staff were concerned about the consequences of expansion of coastal subdivisions there. Also, coastal systems, being naturally frequently disturbed, are likely to be particularly susceptible to rapid exotic plant invasion.

Methods

Study sites

During 5–9 February 2001, we visited areas of coastal native forest familiar to DOC staff and located between Bream Head and Whananaki Inlet, including the northern coast of Whangarei Harbour (latitude 35°34'–35°52' S, longitude 174°21'–174°35' E, elevation 0–100 m). This area of Northland, New Zealand, has a warm-temperate climate with frequent, year-round

Table 1. Sampled forest areas and neighbouring settlements visited in this study, ordered north to south. All sites were visited in February 2001, except for forest sample 3 (1991, K. Bowden, R. Bowden, and G. Bowden), forest sample 10 (1989, R. Parish and P. Anderson, DOC Northland), forest samples 16–18 (1997–1998, W. Holland and M. Maitland, DOC Northland), and settlements 17–18 (1998, W. Holland). Existing species lists from forest sample 4.9 (1991, R. Parish, and 1995, Auckland Botanical Society (Asquith 1995)) were used to complement our current observations. The grid references, from N.Z. Map Series 260 maps, describe the midpoints of each area.

	Forest sample	Area (ha)[1]	Grid ref.	Neighbouring settlement sample	Grid ref.
1	Sheltered Bay	4	QO6 442 272	Sheltered Bay	QO6 441 269
2	Whale Bay, Otito Scenic Reserve	24.5	QO6 467 258	Matapouri and Woolley's Bay	QO6 467 258
3	Tawapou Farm forest, Bowden property	26.5	QO6 496 228	Bowden property houses	QO6 499 234
4	Kukutauwhao Is., Tutukaka Head Reserve	11.5	QO6 507 198	Adjacent to Tutukaka Head (South Gable)	QO6 503 197
5	Coastal slopes between Oturu and Tutukaka Bays	1	QO6 492 196	Oturu Place Development	QO6 492 196
6	Pacific Bay	2	QO6 499 189	Pacific Bay and Pacific Rendezvous Hotel	QO6 499 189
7	Te Maika coastal forest	14	QO6 480 179	Te Maika (east of Ngunguru)	QO6 467 175
8	Below Memorial Reserve, Dolphin Place, Tutukaka	29.5	QO6 502 178	Dolphin Place houses	QO6 502 178
9	Whau Point	29.5	QO6 503 172	Tutukaka Estates "Estate of Grace" development	QO6 499 173
10	Kumi Point	350	QO6 468 150	(No nearby housing)	–
11	Waimahanga walkway, Sherwood Rise	18	QO7 336 053	Sherwood Rise	QO7 333 048
12	Tait property, Waikaraka	162	QO7 364 032	Waikaraka (near Onerahi)	QO7 364 032
13	Kauri Mountain coast	260	QO7 512 018	(No nearby housing)	–
14	Devonshire Park, Scotts Road	5.5	QO7 386 013	Scotts Road housing	QO7 386 013
15	Coastal slopes west of Little Munro Bay	70	QO7 466 957	Little Munro Bay	QO7 469 959
16	Peach Cove to Bream Head, Bream Head	710	QO7 536 940	(No nearby housing)	–
17	Old Woman, Bream Head	710	QO7 538 935	Ocean Beach	QO7 527 946
18	Busby Bay, Bream Head	25	QO7 486 925	Urquharts Bay	QO7 494 936

[1]the approximate area of contiguous forest containing the forest sample

rainfall. It was originally forested (e.g. Wardle 1991), although most of the original forest has been cleared for agriculture, exotic plantation forestry, and urban settlements. We sampled within 18 coastal forest areas at a range of distances from settlements, and varying in size from 1 ha to 710 ha (average 136 ha, Table 1).

Data collection

We recorded the vegetation in sampled forest areas and in housing areas within 250 m of the forest boundary. In addition to our own sampling, we used existing plant species lists from five of the forest areas and two of the settlements (Table 1).

Rather than attempt to survey the entirety of each forested area, we searched for all the common exotic plant species, using a reasonably consistent search effort of 15–90 minutes per site, depending on site terrain and accessibility. Our species lists are samples rather than censuses of the exotic plants in these forest areas. We refer to the areas we sampled as "forest samples," being comparable-sized samples within each forest area. We use the term "exotic species" throughout rather than "naturalised species," as there was not adequate information to assess whether each species we recorded was part of a self-sustaining wild population ("naturalised" *sensu* Richardson *et al.*, 2000), or was dependent on propagule pressure from nearby cultivated plants ("casual alien species" of Richardson *et al.,* 2000).

We listed exotic vascular plant species in the areas of the settlements neighbouring each forest area, by walking and slowly driving along the streets and roads neighbouring each forest sample, and noting the exotic plant species occurring in and around houses and gardens. All known and potentially naturalised plants were included, with the exception of lawn species. We subsequently excluded from our garden lists all species not found in any of our forest samples.

For each settlement, we noted the number of exotic plant species (excluding lawn species) present in the visible portion of the gardens of 10 random houses within each settlement sample. When fewer than 10 houses were present within 250 m of a forest sample, all house gardens were recorded. From this, we calculated the average number of exotic plant species in the properties of each settlement, and called this value the "garden index" of a settlement.

We counted the number of houses within 250 m of each forest sample, and noted the distance between the forest boundary and the nearest house. The age of the oldest house was estimated based on housing style and building materials, using the following categories: <1900, 1900–1945, 1945–1980, 1980–present. We also noted the landform, parent material and dominant aspect of each site.

We later used 1:50 000 topographic maps (N.Z. Map Series 260 maps QO6 and QO7) to estimate the density of housing at greater distances from each forest sample. The number of marked buildings and the area (square millimetres on map) of residential housing (mapped as a blocks of grey) were recorded for 250–500 m and 500–1000 m away from each forest sample. To calculate the total housing densities, we conservatively estimated the mapped residential areas to include two houses per one square millimetre. The maps are dated 1988, but may provide a better index of potential "weed pressure" than more up-to-date maps, as it takes time to establish gardens in new subdivisions, and for the garden species to then move into forest areas.

We also used these maps to estimate the area (in hectares) of contiguous natural forest that included each forest sample. These forest areas were bounded by ocean, roads, other land uses (rural, urban), or vegetation types (e.g. coastal wetlands). Forest area size was included because weed invasion increases with decreasing forest fragment size (Timmins and Williams, 1991). Forest size could therefore confound any relationship we observed between settlement proximity and forest fragment weediness.

Data analysis

Two statistical methods, multiple regressions and Mantel tests, were used to assess the influence of settlement characteristics on the number and identities of exotic plant species in the coastal forest samples. The multiple regressions and multiple correlations were performed on SPSS Version 6.1.1 for Macintosh. All Mantel tests were run using the R Package 4.0 for Macintosh (Casgrain, 2002).

The relationships between the number of exotic plant species in each forest sample (the dependent variable) and the recorded (independent) variables of their paired settlement sites were assessed using stepwise multiple regressions ($P < 0.05$ to enter and $P > 0.10$ to remove). The eight variables included were: (1) number of exotic species in settlements also present in at least one forest sample; (2) the garden index of a settlement; (3) the minimum distance between the boundary of the forest sample and the nearest house; (4) the number of houses counted within 250 m of a forest sample; (5) the estimated number of houses 250–500 m from each forest sample; (6) the estimated number of houses 500–1000 m from each forest sample; (7) the maximum settlement age; and (8) the area of contiguous native forest. These variables were log transformed, when appropriate, to meet the assumptions of regression analysis. A multiple correlation analysis was used to reveal the degree of correlation among the many settlement variables.

To test whether the addition of plant list data to our observational data biased our results, we performed parallel regression analyses on the subset of the data without these list data. This produced comparable, and often significant, relationships, with similar regression slopes and intercepts. For simplicity, only the results from the full dataset are reported here.

Mantel tests were used to assess whether the presence and absence of exotic species in each forest sample was correlated with the presence and absence of the same species in neighbouring settlement samples. Mantel tests are randomisation tests that compare two or more dissimilarity matrices of equal size, and can easily be modified to test a variety of different data designs (Sokal and Rohlf, 1995). Significance is evaluated by comparing a calculated Mantel *Z*-statistic for the observed data with a distribution of *Z*-statistics calculated for numerous random permutations of the data (Sokal and Rohlf, 1995).

A Mantel test, using 999 randomisations, was set up to ask whether there were significantly fewer "unshared" species combinations between paired forest-settlement sites than between random combinations of sites. "Unshared species" for a pair of sites are those species present in one site but not the other. The more vegetatively similar two sites are, the fewer unshared species they will have. Hence, this analysis tests whether there was a significant correlation between the exotic species present and absent in forest samples and in their neighbouring settlement sites.

A similar Mantel test was set up to test whether, overall, settlements and forest samples were more

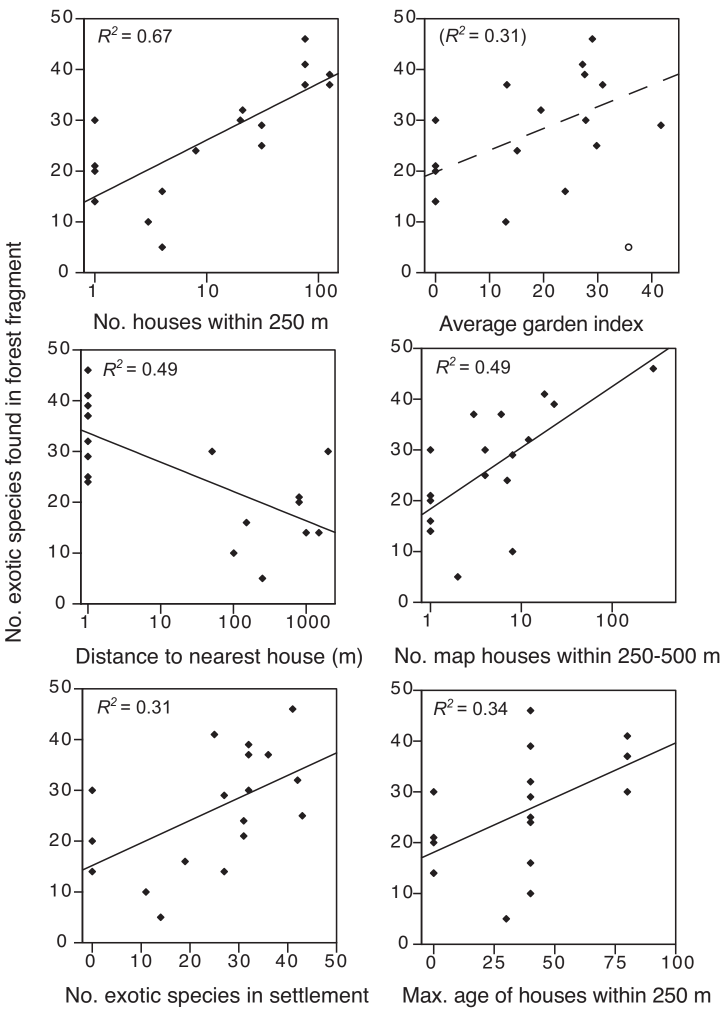

Figure 1. The relationships between the six most important settlement attributes and the number of exotic species in natural coastal forest fragments of eastern Northland. Plotted are the univariate regression lines, with their R^2 values. All univariate regressions were significant at the $P = 0.05$ level or less (values follow Table 2), although, because of correlations between these variables, the stepwise multiple regression result is more appropriate (see Results). The circle on the garden index graph is from forest fragment 3 (see Table 1), which was noted as having been recently weeded when the species list was gathered. This outlier is excluded from the regression line and corresponding R^2 value. The regression line is dotted and the R^2 bracketed to highlight that this relationship is dependent on the exclusion of this outlier. Note that some x-axes are on a log-scale.

dissimilar with respect to exotic species than settlements were from other settlements and forest samples were from other forest samples. A partial Mantel test was run to take this effect into account before running the above test.

Results

More exotic plant species in coastal forests near settlements

There was a strong relationship between settlement characteristics and the number of exotic plant species in neighbouring forest samples. In the best regression model, the number of houses within 250 m of the forest sample alone explained 66.8% of the variation in the number of exotic plant species in forest samples (P <0.001, slope = 10.5, intercept = 16.5). Forest samples with about 100 houses within 250 m of their boundary contained, on average, more than twice as many exotic plant species as forest samples with fewer than five houses close by (Figure 1).

The relationships between the six most important settlement attributes and the number of exotic species in the forest samples are shown in Figure 1. The independent effects of these settlement variables in the dataset cannot be differentiated because the variables are highly correlated with one another (Table 2). This problem was anticipated, as we had only 18 pairs of sites, and eight independent variables of interest. When univariate regressions were performed separately with each independent variable, every settlement variable was significantly (P < 0.05) related to the number of exotic plant species in forest sample (see Figure 1 for the regression lines, and Table 2 to calculate the R^2 values). Only the size of the contiguous forest area containing the sampled area was not significantly related to the number of exotic plant species in our forest samples (Table 2).

Overall, 185 exotic plant species were found in the forest samples; 127 of these were also found in at least one settlement. Most (67%) of the remaining 58 species are species of grasslands and/or agricultural lands, which either do not commonly occur in settlements, or occur commonly only in settlement lawns, which we did not record. Some of the other species recorded in forest samples but not in settlements can occur in settlements (e.g. *Banksia integrifolia*, *Buddleja davidii*, *Carica pubescens*, *Hakea salicifolia*), and were either not visible or uncommon/absent in the settlements we sampled.

The above regression results conservatively use the full list of 185 species. Regression results from analysing only the 127 shared species are consistently better than above, with the best model explaining 73.2% of the variation using only the number of houses within 250 m of the forest sample (slope = 10.52, intercept = 12.21, P <0.0001).

Exotic plants are shared by forests and neighbouring settlements

Mantel tests show that forest samples and neighbouring settlements are also likely to share the *same* exotic species. The particular exotic plant species found in a forest sample were significantly more likely to be found in the neighbouring settlement than in other

Table 2. The matrix of Pearson's correlation coefficients for all variables used in the multiple regressions. "Forest" is the dependent variable, and all other variables are independent variables in the multiple regression results reported in the text. P-values are indicated as follows: n.s. = not significant (P > 0.05), * P < 0.05, ** P < 0.01, *** P < 0.001.

	H < 0.25	H 0.25–0.5	H 0.5-1.0	nearest H	age	garden	# exotics	area
H 0.25-0.5	0.74 ***							
H 0.5-1.0	0.70 **	0.73 **						
nearestH	-0.92 ***	-0.75 ***	-0.69 **					
age	0.83 ***	0.49 *	0.59 *	-0.72 **				
garden	0.81 ***	0.64 **	0.69 **	-0.80 ***	0.72 **			
# exotics	0.71 **	0.56 *	0.80 ***	-0.76 ***	0.54 *	0.59 *		
area	-0.60 **	-0.51 *	-0.54 *	0.58 *	-0.67 **	-0.69 **	-0.42 n.s.	
forest	0.82 ***	0.70 **	0.51 *	-0.70 **	0.58 *	0.55 *	0.55 *	-0.36 n.s.

* H < 0.25, H 0.25–0.5, H 0.5–1.0 = $\log_{10}$(number of houses within 250 m, 250–500 m, and 500–1000 m of a forest sample, respectively); nearest H = $\log_{10}$(distance from forest sample boundary to nearest house (m)); age = estimated maximum age of settlement (years); garden = average garden index of houses with 250 m (measured in number of non-lawn species per garden); # exotics = number of all exotic plant species (minus lawn species) found in the area of settlement within 250 m of a forest sample; area = $\log_{10}$(area of contiguous native forest that includes the forest sample); forest = the number of all exotic plant species found in a forest sample.

Table 3. Environmental weed species present in one or more of the forest samples and/or settlements, as listed in the Regional Pest Management Strategy (Northland Regional Council, 1995) and/or the National Plant Pest Accord (2001). The site numbers follow Table 1. Common names follow Nicol (1997).

Species	Common name	Forest samples	Settlement samples
Acmena smithii	monkey apple		1,2,4,6,8,9,10,13,14,16
Anredera cordifolia	Madeira vine		13,14
Araujia sericifera	moth plant	2,12,17	2,11,16,17
Asparagus asparagoides	smilax	13,14,17	1,13,14
Asparagus scandens	climbing asparagus	1,2,11,17	1,11,13,14
Bartlettina sordida	bartlettina		13
Cestrum parqui	green cestrum	17	11
Chrysanthemoides monilifera	bone-seed	4	1,4,5,8,11
Cortaderia selloana	pampas grass	1,2,3,4,5,6,7,8,9,10,11, 12,13,14,15,16,18	2,3,4,7,8,10,11,13,14,16
Cotonoeaster glaucophyllus	cotoneaster	2,11,13,17	1,2,4,5,8,10,11,13,16,17
Dipogon lignosus	mile-a-minute		13
Elaeagnus X *reflexa*	elaeagnus	16	2,10,14,16
Erigeron karvinskianus	Mexican daisy	2,11,15	2,8,13,14,17
Euonymus japonicus	Japanese spindle tree	11	4,5,8,10,13,14,16,17
Gunnera tinctoria	Chilean rhubarb		7
Hedychium spp.	wild ginger	1,2,11,16,17	1,2,5,7,8,9,10,11,13,16,17
Ipomoea indica	blue morning glory	8	8,17
Jasminum polyanthum	jasmine	2,17	6,8,13,16
Lantana camara	lantana	5,11,14	5,8,10,11,14,16
Ligustrum lucidum	tree privet	10,11	2,4,10,11,14,16
Lonicera japonica	Japanese honeysuckle	2,5	2,9,16
Nephrolepis cordifolia	tube ladder fern		1,2,5,8,13,14,16,17
Passiflora mixta	banana passionfruit		14
Passiflora mollissima	banana passionfruit	11	5,7
Plectranthus ciliatus	plectranthus		2,10,11
Plectranthus ecklonii	blue spur flower	1	1,3,8,11,16
Plectranthus grandis	blue spur flower		13,14
Polygala myrtifolia	sweet pea shrub	10	13,14
Prunus campanulata	Taiwan cherry	5,11,17	5,17
Selaginella kraussiana	selaginella		14
Senecio mikanioides	German ivy	2	13,14,16,17
Senecio petasitis	velvet groundsel	2,11,15,16	1,11,16,17
Tradescantia fluminensis	tradescantia	1,2,11	1,2,6,11,13,14,16,17
Vinca major	periwinkle	2,5	2,13

more distant settlements (Matrix A versus Matrix B, P <0.01, see Appendix 1 for matrix details). This result applies both directly, and in a partial Mantel test that accounts for forest samples being overall vegetatively more like other forest samples than they are like settlements (Matrix A versus Matrix C, P < 0.001; Matrix A versus Matrix B taking Matrix C into account, P <0.01).

These results again use all 185 exotic plant species found in the forest samples. The inclusion of lawn species recorded from forest samples but not from settlements makes this test conservative.

Observations of weed dispersal and establishment

Among the species found in the forest samples were 65% of the 32 plant species listed as forest invasives in the Northland Regional Pest Management Strategy (RPMS; Northland Regional Council, 1995), and 16% of the 91 species listed in the National Pest Plant Accord (MAF Biosecurity Authority, 2001) (Table 3). More of these listed environmental weeds were found in the gardens of settlements — together, forest samples and settlements contained 87% of the RPMS forest invasives and 26% of the species listed in the Accord (Table 3).

Freshly dumped garden waste was observed in, or on the boundary of, five of the forest samples, amounting to 45% of forest samples with one or more houses within 250 m. These dumpings included many environmental weeds, including six (19%) of the RPMS forest invasives: *Asparagus asparagoides*, *Agapanthus praecox, Ligustrum sinense, Nephrolepis cordifolia*, *Senecio mikanioides,* and *Tradescantia fluminensis*. Only two sites contained evidence of weed control (sites 8 and 3 on Table 1), while two others had exotic species that had been recently planted (sites 2 and 14 on Table 1).

Access disturbances such as tracks and boardwalks were observed in 11 (61%) of the forest samples. Natural slips were observed in seven (39%) forest samples, as is expected for coastal ecosystems frequently disturbed by storms. Several environmental weed species were observed establishing in these disturbed areas, particularly *Ageratina riparia*, *A. adenophora, Cortaderia selloana* and *Erigeron karvinskianus*.

While close proximity to settlements was strongly related to high numbers of exotic species in forest samples, this did not mean that isolated forest samples were protected from environmental weeds. This is illustrated by our discovery of a single individual *Araujia sericifera* (moth plant) growing on a coastal face near the Kauri Mountain reserve (site 13). This site was separated from the nearest houses by at least 1.5 km of well-grazed farmland.

Discussion

It is clear from our results, and those of an earlier study (Timmins and Williams, 1991), that natural vegetation close to settlements in New Zealand tends to contain many more exotic plant species than natural vegetation far from settlements. The number of exotic plant species in areas of natural vegetation also increases with the age of neighbouring settlements and the species richness of their gardens. Reliably distinguishing the relative importance of the different settlement variables would require either a much larger dataset or, preferably, more in-depth studies of the factors that limit the dispersal and establishment of the most important environmental weeds species.

While we have only documented correlations for the above relationships, we believe they reflect strong casual links between the settlement variables and neighbouring coastal forest variables. We base this on several factors: the strength of the regressions results; the association between the species found in settlements and neighbouring forest samples; and the intrinsic nature of settlements as places of intense human activity, most importantly, gardening.

Many more naturalised plant species are found in urban areas than in agricultural or wild areas, both in New Zealand (Esler, 1988; Lee *et al.*, 2000) and elsewhere (e.g. Catling and Porebski, 1994; Rapoport, 2000). This is not surprising since most recently naturalised plants were introduced as ornamental garden plants (Esler, 1988; Batianoff and Franks, 1998; Reichard and White 2001). For example, 74% of New Zealand's terrestrial environmental weed species were deliberately introduced for ornamental purposes (Buddenhagen *et al.*, 1998). Many attractive environmental weeds continue to be grown ornamentally in gardens (*pers. obs.* Northland and Auckland regions), including species now banned from sale, propagation and distribution (MAF Biosecurity Authority, 2001).

In addition, settlements have many open areas of high disturbance and high light (e.g. roadside and railway verges, abandoned sections, cemeteries), and these conditions favour the establishment of many naturalised plant species. Rapoport (2000) combined datasets from around the world to show that degree of disturbance explains 55% of the total variation in the proportion of naturalised species at a landscape scale, and was far more important than annual precipitation or mean annual temperature in predicting this aspect of weediness.

Settlements also contain many naturalised plant species because they are connected to other settlements by roads, and many such plants grow well along roadsides and/or are easily transported by vehicles, both inadvertently and deliberately (e.g. Tyser and Worley, 1992; Lonsdale and Lane, 1994; Parendes and Jones, 2000). Studies of seeds present in the sludge of car wash settling tanks in Australia (Wace, 1977), and seeds found in mud on cars in Germany (Schmidt, 1989), show that almost all plant species growing along roadsides can be carried between settlements by cars.

Weeds are moved from settlements into forest areas both by natural dispersal and by people. Many frugivorous bird species, both native and naturalised, readily move between forest areas and the gardens and amenity plantings of neighbouring settlements (e.g. Bass, 1990; Williams and Karl, 1996). One of the most important human weed-dispersal mechanisms is the dumping of garden waste (Esler, 1988; Batianoff and Franks, 1998; Heenan *et al.*, 2002). We found dumpings in nearly half the Northland forest samples with houses within 250 m. Seeds of exotic plants are also likely to be inadvertently carried into forest areas on clothing, the soles of shoes and in dog hair (Mack and Lonsdale, 2001). More people and pets are likely to walk through forest areas near settlements than through those far from settlements.

While the strong relationship between rates of human visitation and weediness of forest fragments has been well demonstrated (e.g. Macdonald *et al.*, 1989; Lonsdale, 1999), few studies have quantified the importance of inadvertent human dispersal and human disturbance of habitats on the growth and spread of naturalised plant species (Mack and Lonsdale, 2001).

Inside forest fragments, vegetation is disturbed by human activities such as tracks and trampling of understorey vegetation off tracks, which facilitate weed establishment (e.g. Rapoport, 2000; Parendes and Jones, 2000; Mack and Lonsdale, 2001). For example, Norway maple (*Acer platanoides*), an invader of deciduous forests of Massachusetts, U.S.A., is disproportionately abundant along the sides of forest tracks and paths, unlike the native American sugar maple (*A. saccharum*), which it outcompetes (Anderson, 1999). Increasing attention is also being paid to how the deposition of anthropogenic particulates and gases in wild areas can alter soil nutrients and pH, and so alter species communities and ecosystem processes (e.g. Vitousek *et al.*, 1997; Weiss, 1999; Driscol *et al.*, 2001).

Taken together, these processes and our results suggest that properly managing the locations and densities of new subdivisions, and the species grown in gardens in existing and new subdivisions near forest reserves, would substantially reduce the weed pressure, and subsequent weed control costs, in these reserves.

While our results apply to managing suites of garden escapes turned environmental weeds, they may not apply to environmental weeds from other sources. For example, the pampas grass *Cortaderia selloana* is at least as common on farmland and along roadsides and waste ground as it is within most settlements (Timmins and Williams, 1990), and with its many light, wind-dispersed seeds, it can move quickly across landscapes. We would therefore not expect a strong relationship between a forest fragment's proximity to settlements and the presence or absence of pampas grass within that forest fragment, although nearby settlements may still exacerbate a local pampas grass problem. Effectively managing the spread of pampas grass into forest fragments in Northland and elsewhere (e.g. into tree fall gaps and other disturbed forest microhabitats) requires knowledge of the processes limiting the dispersal and establishment of pampas grass.

Exceptions aside, an effective method for dramatically slowing the invasion of most naturalised plants into forest reserves is the proper management of new subdivisions, and the encouragement of responsible gardening by those living near reserves. In the future, the trend we document could even be reversed, if enough community groups take responsibility for environmental weeds in their neighbourhood forest reserves and keep nearby gardens and parks weed free.

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Appendix 1. Matrix structure used in the Mantel tests (see Methods for further details).

Matrix A (Data matrix)

	F_1	S_1	F_2	S_2	...	F_{18}	S_{18}
F_1	0	$x_{1,2}$	$x_{1,3}$	$x_{1,4}$	...	$x_{1,35}$	$x_{1,36}$
S_1		0	$x_{2,3}$	$x_{2,4}$	...	$x_{2,35}$	$x_{2,36}$
F_2			0	$x_{3,4}$	...	$x_{3,35}$	$x_{3,36}$
S_2				0	...	$x_{4,35}$	$x_{4,36}$
...					...	...	...
F_{18}						0	$x_{35,36}$
S_{18}							0

where F_i = the i^{th} forest site, S_i = the i^{th} settlement site, and $x_{i,j}$ = the number of unshared species between the site in row i and column j.

Matrix B (codes for a comparison between the dissimilarity of forest-settlement pairs versus the dissimilarity of random combinations of sites)

	F_1	S_1	F_2	S_2	...	F_{18}	S_{18}
F_1	0	0	1	1	...	1	1
S_1		0	1	1	...	1	1
F_2			0	0	...	1	1
S_2				0	...	1	1
...					...	...	...
F_{18}						0	0
S_{18}							0

Matrix C (codes for a comparison between the dissimilarity of combinations of forest-settlement sites and combinations of forest-forest or settlement-settlement sites)

	F_1	S_1	F_2	S_2	...	F_{18}	S_{18}
F_1	0	1	0	1	...	0	1
S_1		0	1	0	...	1	0
F_2			0	1	...	0	1
S_2				0	...	1	0
...					...	...	...
F_{18}						0	1
S_{18}							0