

Symposium

People and Time Explain the Distribution of Naturalized Plants in New Zealand¹

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Abstract: New Zealand has as many naturalized plant species as natives, and the invasion has yet to slow. The current composition and distribution of the naturalized flora are dominated by the time since species introduction and by human factors such as population density, at spatial scales from region to neighborhood.

Additional index words: Eradication, introduction effort, invasive plant, propagule pressure, weed.

Abbreviations: NZ, New Zealand; SE, standard error of the mean.

INTRODUCTION

New Zealand (NZ) is awash with naturalized plant species (i.e., species introduced purposefully or accidentally by people that now reproduce consistently and sustain populations over many life cycles without direct intervention by people, *sensu* Richardson et al. 2000). The NZ naturalized vascular flora (>2,100 species) is now comparable in size with the native flora (>2,000 species) (Buddenhagen et al. 1998; Williams and Cameron 2005), a result of 160 yr of plant introductions after European settlement (Lee et al. 2000; Williams and Cameron 2005). More than 20% of naturalized species are now recognized as weeds by an NZ government agency or primary industry (Williams and Timmins 2002).

New naturalized plant species continue to be found at a steady rate of more than 12 species/yr (Williams and Timmins 2002), and new weed species annually accrue on industry and government weed lists. The great majority were sourced from the pool of more than 25,000 species currently propagated in NZ (Williams and Cameron 2005) and were introduced before NZ's recent stringent national biosecurity legislation (e.g., <http://www.protectnz.govt.nz>).

Awareness of the magnitude and cost of this invasion is growing (Williams and Timmins 2002), stimulating research to identify the main drivers of plant naturalization: which species, where, and when? Answers are required to improve weed risk assessment models

(Groves et al. 2001) and preemptive weed control and eradication programs.

Recent NZ studies emphasize two dominant and obvious components of plant naturalization: people and time. Which species are most likely to naturalize? Species that propagated most widely, intensively, and for the longest time. Where? Where people planted them, almost always close to where people live. When? Naturalization usually occurs several decades after introduction, even for the most widely planted species; usually many decades (to centuries) more are required for some species to become widespread and abundant in the wild. We have been surprised by just how dominant people and time are for explaining the composition and distribution of NZ's naturalized flora at this early stage of the invasion.

We have found strong correlations between human factors and the composition and distribution of naturalized plant species at three scales: regions, suburbs, and neighborhoods. We introduce these findings and discuss their implications for invasive plant management. Our focus is exclusively on NZ, although the described patterns and processes are not unique to NZ (Mack and Lonsdale 2001; Pysek et al. 2003).

REGIONAL SCALE

The relevant floras of NZ and subsequent updates allowed the distribution of NZ's naturalized flora to be described by the presence or absence of 1,822 species in 10 similarly sized geographic areas on NZ's two main islands (Williams and Cameron 2005, and references within; P. A. Williams, unpublished data). Despite covering 10° of latitude, there is no clear relationship between the number of species in a geographic area and

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the latitude. Instead, this broad snapshot reveals the effects of human activities and time in structuring the naturalized flora.

The number of plant species that naturalized in a geographic area between 1991 and 2000 increases with the human population of an area (in year 2000) (linear regression, $P < 0.001$, $R^2 = 0.98$, Williams and Cameron 2005; P. A. Williams, unpublished data). Not coincidentally, 97% of these species were purposefully introduced for urban horticulture (Williams and Cameron 2005). The population of each geographic area also shows a significant, although weaker, linear relationship with the total naturalized flora of each area ($P < 0.05$, $R^2 = 0.61$).

The majority (53%) of naturalized species are found in $\leq 30\%$ of the geographic areas. The number of areas a species occupies increases linearly with the number of years since the species naturalized (Williams and Cameron 2005; P. A. Williams and H.W.A. Gatehouse, unpublished data). For example, the 237 species that first naturalized before 1870 are now present in an average 77% of the areas ($SE = 1.9\%$), whereas the 705 species that first naturalized in 1971 to 2000 are only present in an average 20% ($SE = 0.6\%$) of the areas. This suggests that it takes most naturalized plants more than a century after naturalization to appear in all ecologically suitable region-scale areas of NZ. This “spread” is not necessarily limited by the dispersal ecology of the species; it is as likely caused by numerous independent and regional naturalizations from propagated plants.

CITY AND SUBURB SCALE

Auckland is the NZ region with the largest population and the largest naturalized flora (Esler 1988; Lee et al. 2000). Within this region, most naturalized plants are concentrated in the Tamaki Ecological District, a 53,800-ha area encompassing Auckland City and parts of the neighboring North Shore City, Manakau City, and Waitakere City. We have been studying the records of plant naturalization in the Tamaki Ecological District, building on Esler's foundation (Esler 1988).

Since 1840, the Tamaki Ecological District has gained about 1,100 fully and casually naturalized species, predominantly of horticultural origin, and has maintained about 400 native species (Duncan and Young 2000; Esler 1988, 1991; E. K. Cameron, unpublished data). Of these naturalized species, 13% are listed in the Auckland Regional Council Pest Management Strategy (<http://www.arc.govt.nz>). These naturalized species are accumulating at just over four species a year, a rate largely constant during the past 100 yr (Esler 1988; E. K. Cam-

eron, unpublished data). The composition and distribution of the naturalized species is again tightly associated with past and present human activities.

The 144 species that naturalized in the Tamaki Ecological District between 1985 and 2000 were found disproportionately often in suburbs (census units) with the highest densities of people and buildings, as recorded in the NZ census of 1996 (<http://www.statistics.govt.nz>) ($P < 0.001$, E. K. Cameron and J. J. Sullivan, unpublished data). Furthermore, the population densities of suburbs in 1945 explained 4.5 times more variation than those in 1996. This suggests that plant propagation patterns half a century ago may be driving plant naturalizations today, especially because an increasing proportion of new naturalizations in this area are woody plants. For example, 6.3% of the 48 species that naturalized in the area before 1870 are woody vs. 40.4% of the 47 species naturalizing between 1985 and 2000 (Esler 1988; E. K. Cameron and J. J. Sullivan, unpublished data). Newly naturalized plants also were collected significantly more frequently in richer suburbs (socioeconomic deprivation values per census unit were estimated from the 1996 census by Crampton et al. 2000) after socioeconomic status had been corrected for suburb population.

Even within a 53,800-ha area of largely open and frequently disturbed urban and suburban habitats, it still takes most plant species more than 50 yr to become abundant. The average date of first naturalization (colated for each species from herbarium records) is 1913 ($SE = 2.58$, $n = 308$) for the abundant or widespread species, 1952 ($SE = 2.37$, $n = 339$) for the scarce or restricted species, and 1976 ($SE = 1.54$, $n = 270$) for the rare or casually naturalized species (Esler 1988; E. K. Cameron and J. J. Sullivan, unpublished data).

NEIGHBORHOOD SCALE

The proximity to individual houses also strongly influences the distribution of naturalized plant species. For example, in a study on the eastern fringes of Whangarei City, Northland, we found that the number of houses < 250 m from native forest patches, ranging from no houses to > 100 houses, explained two-thirds of the variation between patches in the number of naturalized plant species (Sullivan et al. 2005).

Distance to houses is equally important in explaining the spatial distribution of newly naturalized plants nationwide, presumably because most newly naturalized plants are recent descendents of propagated garden plants. Of all first collections of plant species that naturalized in NZ between 1985 and 2000, 91.5% are found

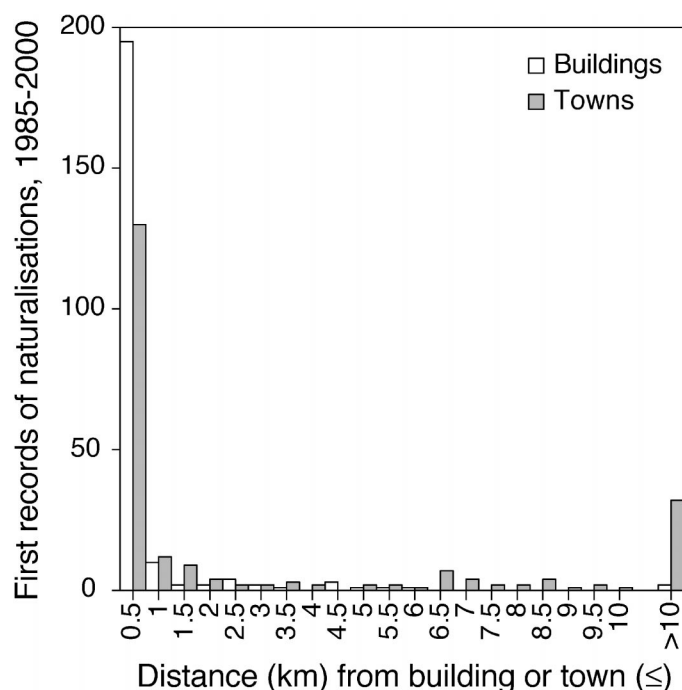


Figure 1. The proximity to the nearest building and town of the first collections of all 224 plant species that naturalized in New Zealand between 1985 and 2000. The distances to buildings and towns are sourced from NZMS260 topomaps.

within 1 km of the nearest building and <1% are found >10 km from the nearest building (Figure 1). In comparison, 67% of collections were within 2 km of a town. Although based on herbarium collections, it is unlikely that this pattern represents a bias in collecting effort because NZ botanists frequently collect native plants from remote areas of the country.

IMPLICATIONS FOR PREEMPTIVE CONTROL OF NEW WEEDS

A cost-effective method of managing invasive plants is the prompt detection of species at the beginning of naturalization, followed by a swift, sustained control or eradication program if weed risk assessments show a high probability of weediness (Braithwaite 2000; Mack and Lonsdale 2002). Our findings suggest that surveillance efforts should target areas with the most people because this is where most future naturalizations (including those of future invasive species) will occur, both nationally and regionally. Most species that naturalize have been propagated in the country for many decades, which complicates control efforts.

If, as our results suggest, people and time are dominant forces shaping the current distribution and composition of NZ's naturalized flora, then it may be feasible

to estimate when and perhaps where species currently only in propagation may naturalize. This, combined with NZ's weed risk assessment systems (Timmins and Owen 2001; Williams and Newfield 2002; Williams et al. 2002), would be a valuable tool for invasive plant management. NZ currently lacks the necessary coordinated knowledge of the introduction dates and the past and present popularity of propagated species (Mulvaney 2001), although this has been collated for subsets of species and the appropriate information is available in herbaria and libraries. Together with simple ecological characteristics, such a data set also would allow for a rigorous estimation of the relative importance of time, human factors, and ecological factors for explaining which of NZ's large pool of propagated species have naturalized and when and where they first naturalized.

At this early stage in the invasion of NZ, the naturalized flora is far from equilibrium with edaphic, climatic, and ecological conditions, and its composition and distribution seem to be largely dictated by recent history. Nevertheless, our documented correlations among people, time, and the current composition and distribution of NZ's naturalized flora do not preclude strong, parallel effects of species ecology. One aspect of what makes a popular garden plant is its ability to grow well in local conditions.

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