



Department of Conservation biodiversity indicators: 2015 assessment



Landcare Research
Manaaki Whenua

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Summary

Project and Client

- This technical report contributes towards documenting the status of biodiversity in New Zealand's public conservation lands. It underpins the intermediate outcome 'the diversity of our natural heritage is maintained and restored', stated in the Department of Conservation's Annual Report for the year ended 30 June 2015.

Objectives

- The report focuses on the status of biodiversity across public conservation land during the last five years, highlighting two features:
 - Distribution and abundance of woody non-native plants;
 - Areas under greatest pressure from non-native species.

Methods

- We report indigenous dominance and species occupancy (two components of ecological integrity) across public conservation land.
- Standard methods were used for assessing three measures of ecological integrity (one for vegetation, one for bird communities, and one for pest mammals), all reported from an objective assessment with sample points on an 8-km grid superimposed upon public conservation land.
- The measures of vegetation derive from measurements of the sample points in 2009–2014 (919 sample points).
- The measures of bird communities and pest mammals derive from measures at sample points 2012–2015 only (534 sample points). These were combined with vegetation measures from the same plots to derive an aggregated index of pressure.
- A new method, point-of-truth calibration, was used to derive the pressure index.
- Status and trends in vegetation measures and in carbon were analysed in relationship to pest mammals, bird communities, national park status, pest management regimes, and with respect to probable environmental drivers.

Results

The distribution and abundance of woody non-native plant species on public conservation land.

Woody non-native plants occurred on 8.4% of 919 plots sampled across all public conservation land. They occurred most often, and with greatest cover, in areas with low annual rainfall (<1600 mm) and in low-stature vegetation. They occurred most often close to roads and close to non-native forests, and in sites where hares were also common. Plots in

inland Marlborough were especially prone to invasion. Woody environmental weeds were very infrequent in forested areas, especially in high rainfall zones (>2500 mm). Some widespread, common woody environmental weeds could become more common in low rainfall zones under climate change forecasts, especially species such as gorse (*Ulex europaeus*) and prickly hakea (*Hakea sericea*), which are flammable and recolonise rapidly after fire. If regions with 1600–2500 mm rainfall became drier under climate change, current invasions by woody environmental weeds could become more widespread in those regions.

Wilding conifers occurred on 1.8% of plots sampled across all public conservation land. Like other woody environmental weeds, they invaded low rainfall, low-stature vegetation most frequently, but they tended to invade regions with cool minimum temperatures more often as well. They were most concentrated on public conservation land in Nelson–Marlborough and South Canterbury. Lodgepole pine (*Pinus contorta*) was the most frequent invader of plots and, importantly, it was the only woody environmental weed that was recorded in plots in the alpine zone, as small plants, probably not long established. Lodgepole pine could expand in range in the alpine zone under climate change, and it can alter soil nutrients and support, and benefit from fire, which is naturally very uncommon in the alpine zone. Early detection of lodgepole pine in these areas of unique biodiversity is critical.

The areas under greatest pressure from non-native species on public conservation land

Sampling locations with high pressure indices and low pressure indices were distributed throughout New Zealand. Areas of highest pressure occurred in the largely deforested inland Marlborough region, and areas of lowest pressure were in northern Westland and Fiordland. Indices of pressure were generally higher when: rainfall was low or the mean top height of vegetation was low; sampling locations were closer to non-native forests, roads or the public conservation land boundary, and when sampling locations were not in National Parks.

Conclusions

- Areas under high pressure from non-native species on public conservation land are in dry regions with low-stature vegetation. Areas close to roads and non-native forests are under particular pressure. Invasions by non-native woody plants exemplify this pattern, and lodgepole pine can invade alpine ecosystems where no native trees can grow. Forested ecosystems, especially in high rainfall areas, are less invaded. Complementary indices are also needed for native species occupancy, and to identify areas of high endemism in the biota, so that management of areas that are currently under high pressure safeguards areas that are also important for native biodiversity.

1 Introduction

This technical report contributes towards documenting the status of biodiversity in New Zealand's public conservation lands. In providing that information, it underpins the intermediate outcome 'the diversity of our natural heritage is maintained and restored', stated in the Department of Conservation's Annual Report for the year ended 30 June 2015. This year the report focuses on the status of biodiversity in forests on public conservation land during the last five years. Two features are highlighted:

1. *The distribution and abundance of woody non-native plant species.* Woody non-native plants are widespread in New Zealand, and include environmental weeds such as some species of wilding conifer, and other widespread species such as gorse and Scotch broom. A comprehensive overview of where they are most invasive, and whether there are general attributes of the ecosystems that they invade, is so far lacking, and could potentially focus attention on ecosystems that are vulnerable to invasion.
2. *The areas under greatest pressure from non-native species.* Aggregated indices that can be tracked over time are in widespread use in other sectors such as economics and public health. We developed a method to measure *as one value* pressures from multiple non-native species (non-native plants, pest mammals, non-native birds) that is likely to impact upon the ecological integrity of public conservation land. Evaluating whether the ecosystems under greatest pressure share general attributes could potentially direct management to alleviate those pressures.

2 What is the distribution and abundance of woody non-native plant species on public conservation land?

Distribution and abundance of exotic weeds and animal pests considered a threat – Weeds (Measure 2.2.1)

Definition

This measure assesses the presence and abundance of non-native vascular plant species on New Zealand's public conservation land at the national scale. Non-native plant invasion is measured as the number of non-native vascular plant species, the percentage of vascular plant species that are non-native at each location, and the frequency of occurrence of 47 selected species classified as weeds of concern by DOC (Allen et al. 2013a) (Methods are described in Appendix 1.1).

2.1 All woody non-native plant species on public conservation land

Key results for woody non-native plants (all species combined)

Woody non-native plants within sample plots occurred:

- on 8.4% of plots across all public conservation land, much less than the 38.3% of plots invaded by herbaceous non-native plants.
- most often on plots north of Tauranga, on plots throughout the eastern South Island, and on plots around the coast.
- most frequently and with greatest cover in sites with low annual rainfall, in low-stature vegetation, and close to non-native forest. They occurred most often close to roads.
- more frequently in plots where hares were also common.

At least one species of woody non-native plant occurred in 77/919 (8.4%) permanent plots across public conservation land that were measured during 2009–2014 (Appendix 1.1). Considering all woody non-native plants together, their distribution is patchy across public conservation land (Fig. 1a). They occurred:

- at most sample plots north of Tauranga;
- at some plots in the central North Island;
- throughout the eastern South Island, but especially in inland Marlborough;
- at sample plots near the coast, from Wellington southwards.

The distribution of woody non-native plants contrasts with the distribution of all non-native plant species (woody and herbaceous) combined, which occur throughout nearly all public conservation land (Fig. 1b); at least one non-native plant species occurred on 352/919 (38.3%) plots. Seen in this context, it is striking that woody non-native plants were absent from nearly all plots sampled along the axial range of the North Island, and western North Island forests, including Egmont and Whanganui National Parks. With the exception of plots close to the coast, they were absent from the great majority of plots sampled in the western South Island from Kahurangi National Park to Fiordland National Park, and they did not occur in any plots on Rakiura (Stewart Island).

2.1.1 Does the presence and abundance of woody non-native plants vary with distance to nearest public conservation land boundary, roads, and nearby non-native forest?

Woody non-native plants were more likely to be present with (Table 1):

- lower total rainfall
- shorter-stature vegetation
- closer proximity to a non-native forest
- closer proximity to the boundary of public conservation land
- closer proximity to a road

- warmer minimum temperatures
- more northern latitudes.

The abundance of woody non-native plants (cover of all species combined) was generally greatest in plots in the eastern South Island, especially in Marlborough (Fig. 1a). On the plots where they were present, the combined relative cover (percentage of total cover on a plot), comprised of the cumulative cover of woody non-native plants, was 3.5% (95% CI 3.2, 4.0). The abundance of woody non-native plants, as assessed by their cover, was significantly related to just one variable (Table 1). They were more abundant the lower the total rainfall at the plot. Woody non-native plants were not present on the plots with very high annual rainfall, i.e. >4000 mm rainfall (Fig. 2), whereas they occurred across the full range of minimum temperatures.

After accounting for the nine environmental and ecological variables listed in Table 1, residual variation in the presence and abundance of woody non-native plants had some spatial structure (Appendix 1.2). With respect to the presence of woody non-native plants, plots within 100 km of each other share variance that is not explained by the nine fitted environmental and ecological variables in Table 1. With respect to the abundance of woody non-native plants, plots within 75 km of each other share variance that is not otherwise explained. Some of this spatial variance may reflect unmeasured predictor variables, such as land-use history (e.g. pastoralism, mining), that increase the similarity of adjacent plots, relative to other plots in similar environments.

Table 1 Summary of statistical models predicting the presence and abundance of all species of woody non-native plants listed according to the direction of the significant relationships (– for negative relationship, + for positive relationship; NS for relationships with no statistical support; details of analyses and assignment of support levels is described in Appendix 1.3, Tables S1, S2).

Predictor	Presence	Support for Presence Model	Abundance (cover)	Support for Abundance Model
Moisture (total rainfall)	–	Very strong	–	Moderate
Mean top height	–	Very strong	NS	No support
Distance to non-native forest	–	Very strong	NS	No support
National Park	–	Very strong	NS	No support
Distance to Public Conservation Land boundary	–	Very strong	NS	No support
Distance to nearest road	–	Very strong	NS	No support
Latitude	+	Very strong	NS	No support
Minimum Temperature	+	Moderate	NS	No support
Altitude	NS	No support	NS	No support

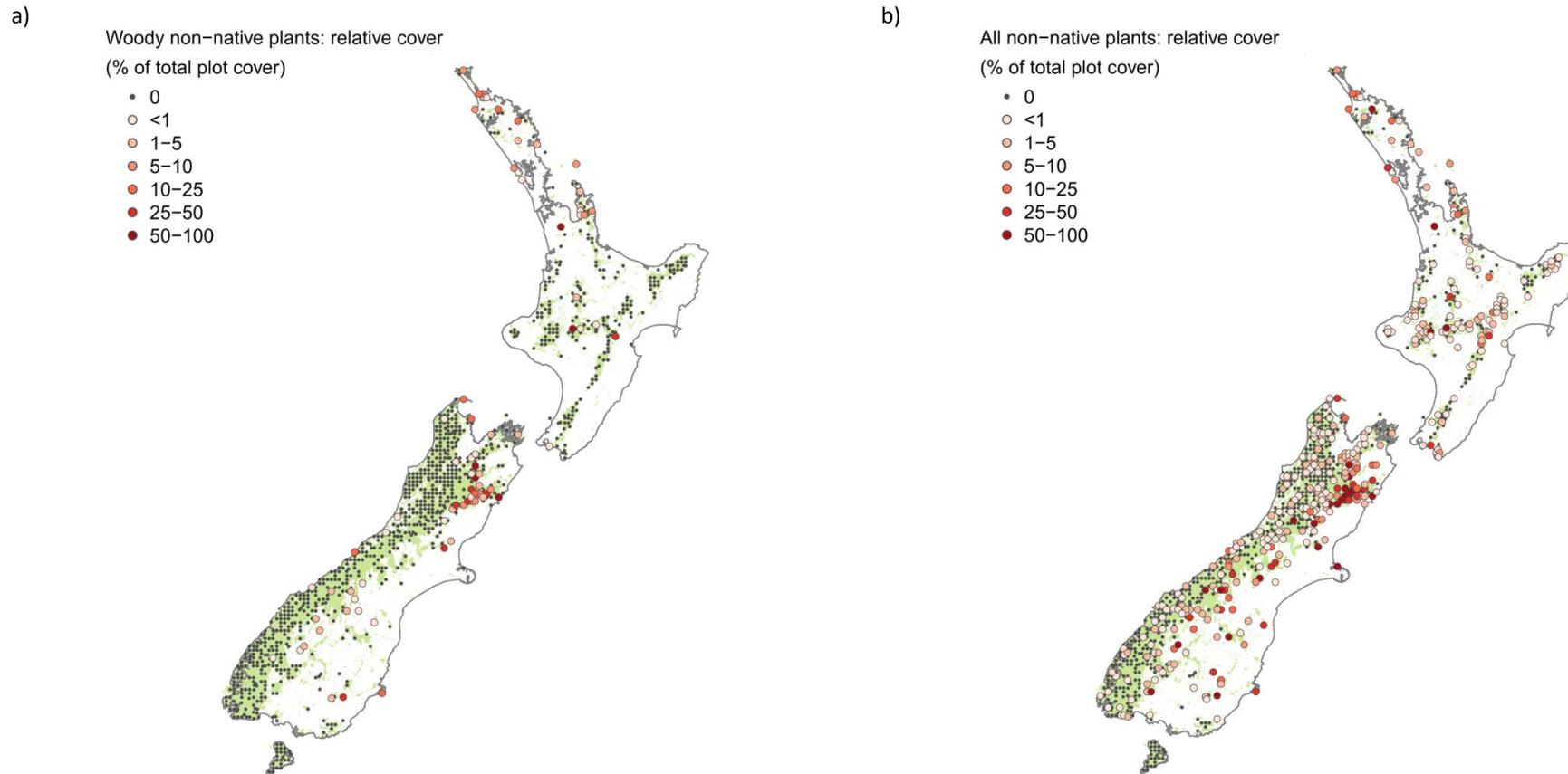


Figure 1 Relative cover (percentage of total cover on a plot) comprised of the cumulative cover of (a) all woody non-native plant species present on a plot, and (b) all non-native plant species, woody and herbaceous, present on a plot.

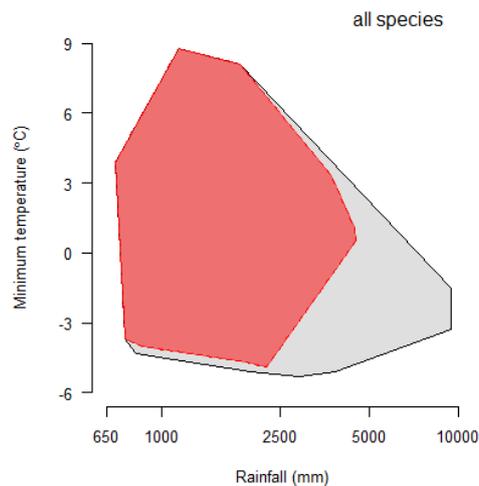


Figure 2 Relationship between occurrence of woody non-native plants and total annual rainfall and minimum temperature. The grey zone represents the envelope within which all 919 sample plots occur, and the red zone represents the envelope within which the 77 sample plots occur on which woody non-native plants were present.

Discussion

The occupancy of public conservation land by woody non-native plants, in terms of both their presence and abundance, is linked strongly to total rainfall: 70 of the 77 occurrences were in plots where total rainfall was <2500 mm, and among those, the sites with the lowest rainfall were especially prone to invasion. Many of the plots that are invaded in low rainfall areas are in areas that were deforested during the last 750 years. Below natural treelines, New Zealand was mostly forested historically, and even its lowest-rainfall areas were dominated by woody vegetation, mostly shrublands (McGlone 1983, 2001). Māori conducted widespread burning of the drier regions (e.g., areas with <1600 mm total rainfall below treeline in the South Island) soon after their arrival; between AD 1280–1600, these areas were largely deforested (McWethy et al. 2010). The low natural fire regime in New Zealand resulted in a native woody flora that is poorly adapted to fire; most native trees are killed by fire. The initial fires, combined with subsequent more-or-less frequent fires, resulted in a highly-flammable seral vegetation of native grasses and some shrubs that created an alternate fire-prone stable state (McWethy et al. 2014). Rates of succession back to native forest in these ecosystems are very slow because of the drastic reduction of seed sources of some species that were formerly prevalent in these regions, especially podocarps, or the slow rate of colonisation from margins (e.g., by beeches, Nothofagaceae, which are likely to be limited by the ectomycorrhizal fungi on which they depend for their ability to take up soil nutrients; Baylis 1980; Dickie et al. 2012). However, since the drier regions of New Zealand supported forest for most of the Holocene, they should continue to do so. The introduction of woody non-native plants by Europeans includes many species that are well suited to invade deforested sites; either transient early-successional species or more persistent species that can form long-term forest canopies. Many of them derive from zones where natural fires, as well as human-caused fires, are frequent and have selected for characteristics that allow them either to survive fire or regenerate rapidly after fire. Areas that were less vulnerable to Māori deforestation by fire (>1600 mm total rainfall) are also invaded by woody non-native plants,

including areas where rainfall is as much as 4000 mm. Inspection of records from some of the wettest plots invaded by woody non-native plants revealed that these have been subject to human disturbance in the recent past (e.g., logging or mining activity). Further determination of past human disturbance could be factored into future models that assess the likelihood of invasion. It also points to the risks associated with any new proposed activities that involve disturbance (e.g., new logging roads).

Models that forecast the consequences of human-caused climate change project warming of minimum temperatures by up to 2 °C (McGlone et al. 2010). The representation of woody non-native plants across the full range of current minimum temperatures (Fig. 2) implies that there is already a broad range of taxa that could occupy an altered range of minimum temperatures. If the upper bound of current minimum temperatures was to increase, some woody non-native plants that have already naturalised, for example Bangalow palm, *Archontophoenix cunninghamiana* (Cameron 2000), could become more widespread or locally abundant (over much of its native range in Australia, minimum temperatures are >10 °C). For example, in an evaluation of four climate models under two scenarios of increasing atmospheric concentrations of CO₂, the area of potentially suitable habitat for Bangalow palm in New Zealand increases by up to 169 % (Sheppard 2013). Models also forecast reduction in total annual rainfall in drier regions and increasing rainfall in wetter regions (McGlone et al. 2010). Reduction in rainfall, potentially coupled with increasing fire, could favour rates of invasion by woody non-native plants, not just in the largely deforested regions with currently <1600 mm total rainfall, but also in the regions with currently 1600–2500 mm total rainfall. Conversely, if currently wetter regions (especially if not subject to human disturbance by roads or mining) are mostly resistant to invasion by woody non-native plants, that trend could well continue.

In general, woody non-native species were more likely to be present the shorter the stature of the surrounding vegetation. This underscores the resistance of forested ecosystems to invasion by woody non-native plants, relative to other vegetation types. There are exceptions to this rule; for example, broadleaf privet (*Ligustrum lucidum*) is a shade-tolerant tree (Hoyos et al. 2010) that invades the understoreys of some warm temperate rain forests in northern New Zealand (Smale & Gardner 1999), although it was not found on any of the 919 plots measured on public conservation land during 2009–2014. Broadleaf privet and some other currently uncommon woody non-native plants could become long-persistent components of some New Zealand forests (Williams 2011). However, more typically, most of the widespread woody non-native plants in New Zealand invade low-stature vegetation (Dansereau 1964, Lee 1998), including adjacent to tall native forest, or canopy gaps (such as treefalls) within native forests. Often these woody non-native plants do not persist as succession proceeds, and more shade-tolerant native tree species replace them. This can be the case with gorse (*Ulex europaeus*, Wilson 1994; Sullivan et al. 2007), Scotch broom (*Cytisus scoparius*, Partridge 1992), and other woody non-native plant species (McQueen 1993). Low shrublands where woody native species are prevalent can also be invaded by woody non-native species, and the presence of other woody species can be a prerequisite for successful invasion by bird-dispersed non-native species. For example, non-native hawthorn (*Crataegus monogyna*) was slow to invade a montane grassland in the inland South Island, but as the native shrub matagouri (*Discaria toumatou*) became more common, providing perches for hawthorn's main disperser, the non-native blackbird (*Turdus merula*), the rate and extent of hawthorn invasion increased rapidly (Williams et al. 2010).

Some of the woody non-native species that invade low stature vegetation are fire-adapted and fire-promoting (Perry et al. 2014). These include many pine species, *Hakea* species, and gorse. These species are highly flammable, and either resprout or reseed vigorously after fire, with their seed germination often promoted by smoke or high temperature (Craine et al. 2006). In contrast, most native New Zealand plants, especially trees (those usually >5 m tall), do not survive fire (Perry et al. 2014). Even though many of the pyrogenic non-native species are not shade-tolerant, their ecology could mean that in drier, fire-prone regions, rather than being shaded out by native species, frequent fires could be promoted by their presence, their dominance could increase over time, and native woody species may become less common. Climate change models predict that fire frequency will increase in eastern regions of New Zealand (IPCC 2007), where woody non-native species are already most frequent and abundant on public conservation land (Fig. 1).

The greater frequency of woody non-native species close to the boundary of public conservation land and to roads confirms earlier trends across all non-native plants (woody and herbaceous) from subsets of the plots from the same sampling system (MacLeod et al. 2012; Bellingham et al. 2013), and is consistent with evidence from regional studies in New Zealand (Sullivan et al. 2005, 2009; Wisser & Buxton 2008). It appears that the most important characteristics influencing the number of non-native species in reserves are proximity to towns and distance from roads (Timmins & Williams 1991). It underscores the role of existing roads as vectors for plant invasions within protected areas (McKinney 2002), and this would be probable consequence of any new roads proposed within protected areas (e.g., a proposed road from Hollyford to Haast, partly through the north of Fiordland National Park).

Woody non-native species were more likely to be present in more northerly sites and those with warmer minimum temperatures. This is likely to result from both greater introduction effort, related to a larger human population, and a larger species pool of woody non-native species. Greater introduction effort has been shown to result in greater rates of invasion of woody non-native species (cf. Sullivan et al. 2005). The large pool of species, which originates particularly from gardens, has increased at a linear rate for nearly 200 years (Williams & Cameron 2006): Auckland is notable as one of the world's "weediest" cities (Esler 1988). The larger pool of species in northern New Zealand is also a function of a warmer climate; some of the woody non-native species that invaded plots are likely to be restricted to regions with warmer minimum temperatures (e.g., queen of the night, *Cestrum nocturnum* (Esler & Astridge 1987), and downy hakea, *Hakea gibbosa* (Enright 1989), both found on single plots in the current survey).

Repeated measures of the same plots will reveal the circumstances in which woody non-native species persist or are transient, and where they come to dominate. Some of the woody non-native species are functionally distinct and may have legacy effects even if they do not persist. For example, non-native gorse and the native tree, kānuka (*Kunzea ericoides* s.l.), both colonise open sites (such as abandoned pasture). Gorse is a leguminous shrub which has symbiotic bacteria in nodules in its roots that can fix atmospheric nitrogen, which is in turn translated into nitrogen-rich plant material, and nitrogen-rich litter and nitrates leach from its root zone (Egunjobi 1969; Magesan et al. 2012). In contrast, kānuka lacks symbionts that fix nitrogen. There is evidence that the forests that grow to overtop and displace gorse differ from those that develop under kānuka (Sullivan et al. 2007).

Repeated measurements are especially needed in warm temperate region where the pool of woody non-native species is greatest. For example, Williams (2008) considered that there were 100 terrestrial non-native plants that potentially threaten ecosystems in Northland, and that populations of five non-native trees in Northland at early invasion stage have begun to increase exponentially. The rate at which woody non-native plants are invading public conservation land in warm temperate regions is unclear. Public conservation land in the warm temperate region in warmer regions is generally much more fragmented than in cooler regions, especially in the South Island. Since distance to roads and edges of public conservation land are general predictors of likelihood of invasion, we could expect that the combined effects of a greater pool of invasive woody non-native plant species and greater fragmentation are likely to result in frequent invasions in the warm temperate region.

2.1.2 Are woody non-native plants less frequent and less abundant in National Parks relative to other conservation lands (taking into account environmental covariates)?

Over and above the predictions based on environmental variables, woody non-native species (all species combined) were no more likely to be present in National Parks than in other public conservation land (delta AIC = -0.37 , no support; Appendix 1.1). Similarly, the abundance of woody weeds in National Parks vs. other public conservation land showed no significant difference over and above and beyond predictions based on environmental variables (delta AIC = -0.90 , no support).

Discussion

New Zealand's National Parks occur mostly in high-rainfall zones and most of them are largely forested below natural treeline. These are the zones less likely to be invaded by woody non-native plants (Table 1). Conversely, regions that are heavily invaded by woody non-native plants, such as public conservation land in inland Marlborough (Fig. 1a), are generally not in National Parks. Therefore, it is unsurprising that National Park status offers no predictive power about where woody non-native plants occur, or are abundant, over and above other environmental predictors.

Woody non-native plants do occur in National Parks, and in some communities they can be abundant, for example, gorse in coastal dune communities in Westland National Park (Wardle 1977) and Fiordland National Park (Johnson 1982), heather (*Calluna vulgaris*) in subalpine communities in Tongariro National Park (Chapman 1988, Chapman & Bannister 1990), and two species of *Hakea* in young successional communities in Abel Tasman National Park (Williams 1992a, b). In these communities, these species are likely to have enduring ecosystem effects. Successions on dunes under gorse and kānuka are likely to be different because of the nitrogen-fixing symbionts associated with gorse (Smale et al. 1994; McQueen et al. 2006). Species of *Hakea* have cluster roots that are an adaptation for nutrient acquisition from nutrient-poor soils (Shane & Lambers 2005), and these nutrients may be inaccessible to most co-occurring native plants. As a result, *Hakea* species can be dominant in successions, although the longer-term nature of these successions in New Zealand is unknown. Additionally, both gorse and *Hakea* species are fire-adapted and fire-promoting (see Section 3.1), so their presence in National Parks could be an ignition source that

promotes fire in communities that would not support fire so readily without them, with the likelihood that these species could expand locally as a result of any fires.

2.1.3 Are higher densities (e.g., cover, basal area) of woody non-native plants associated with the presence or high densities of vertebrate pest species?

There was a positive relationship between the presence of woody non-native plants and both the presence and abundance of lagomorphs (i.e., mostly brown hares and less frequently European rabbits) (Table 2). Nearly 28% of plots with lagomorphs present also had woody non-native plants, compared with just 6% of plots without lagomorphs present.

In contrast, there was a negative relationship between the presence of ungulates (i.e., deer and goats) and the presence of woody non-native plants (Table 2): only 8% of plots with ungulates present also had woody non-native plants, compared with 16% of plots without ungulates present. There were no significant relationships between the presence of woody non-native plants and either the presence or abundance of possums. The abundance of woody non-native plants was unrelated to either the presence or abundance of any of the three pest mammal groups.

Table 2 Summary of statistical models predicting the relationships between the presence and abundance of all species of woody non-native plants and the presence and abundance of three groups of pest mammals, i.e., brushtail possums, ungulates (deer, goats, etc.), and lagomorphs (brown hares and European rabbits), listed according to the direction of the relationships (– for negative relationship, + for positive relationship; NS for relationships with no statistical support; details of analyses and assignation of support levels is described in Appendix 1.1).

Dependent variable	Predictor	Possum	Ungulate	Lagomorph	Explanation
Presence / absence of woody non-native plants	Pest mammal presence/absence	NS	– moderate support	+ very strong support	Woody non-native plants are more likely to occur in sites where hares are present, and sites where ungulates are absent
Presence / absence of woody non-native plants	Pest mammal abundance	NS	NS	+ very strong support	Woody non-native plants are more likely to occur in sites where hares are more abundant
Abundance of woody non-native plants	Pest mammal presence/absence	NS	NS	NS	Woody non-native plant abundance (where present) is unrelated to pest animal presence
Abundance of woody non-native plants	Pest mammal abundance	NS	NS	NS	Woody non-native plant abundance (where present) is unrelated to pest animal abundance

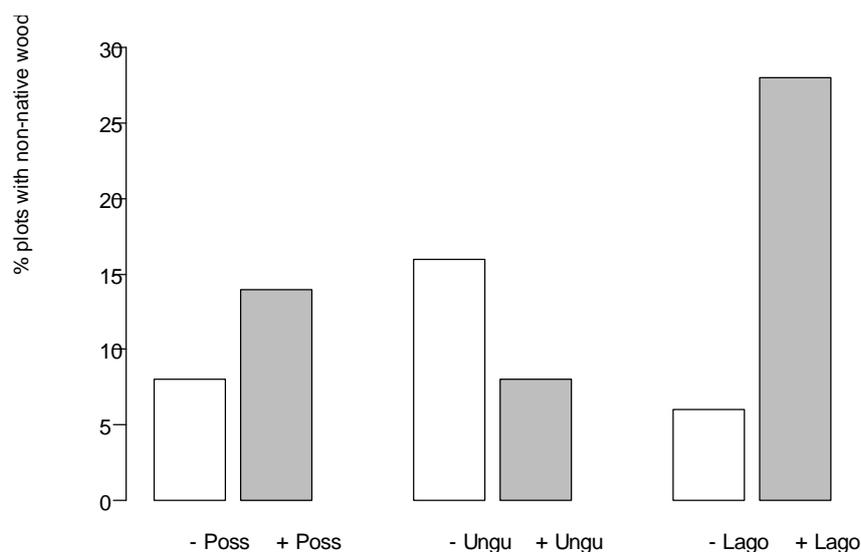


Figure 3 The percentage of sample plots with woody non-native plants according to the presence or absence of possums (poss), ungulates (ungu) and lagomorphs (lago). Differences in proportions were tested for using general linear models (see Table 2)

Discussion

The coincidence of lagomorphs and woody non-native plants is almost certainly attributable to both preferentially invading non-forested ecosystems. Brown hares and especially European rabbits seldom occur in New Zealand's natural forests (Norbury & Flux 2005; Norbury & Reddiex 2005). In an earlier assessment of the plots across public conservation land (79 plots in non-forested ecosystems and 76 in forested ecosystems), lagomorphs were detected at only one forested ecosystem plot. In contrast, hares occurred at 41 (52%) of the non-forested ecosystem plots, while rabbits were much more restricted in extent, and occurred at only two (3%) of those locations (Bellingham et al. 2013). In the current assessment of plots on public conservation land, woody non-native plants were more frequent and abundant in shorter vegetation, that is, in non-forested ecosystems (Section 2.1.1). The implications of the co-invasion of non-forested ecosystems by lagomorphs, especially hares, and woody non-native plants require more investigation. In alpine zones, especially, we do not know whether hares browse seedlings of lodgepole pine, which invades above natural treelines (as shown in the current assessment in the eastern South Island; section 2.2). Above treelines, hares graze the plants that comprise most of the biomass (*Chionochloa* spp. and *Celmisia* spp.) and remove new growth on native woody plants in these zones (Flux 1967). If hares reduce the biomass of resident vegetation, then this could result in reduced competition for newly established woody plants, such as lodgepole pine. However, in other non-forested ecosystems, there is no evidence that competing resident vegetation retards establishment and growth of lodgepole pine in New Zealand (Ledgard 2006) or elsewhere (Anderson & Romme 1991). This remains to be investigated in alpine zones in New Zealand.

Many other woody non-native plants (as well as lodgepole pine) invade non-forested ecosystems below treeline, and hares and, to a lesser extent rabbits, occur in many of these ecosystems. Some non-forested ecosystems below treeline on public conservation land are changing in composition from grassland, comprised of native and non-native herbaceous species, towards shrublands, comprised of native and woody non-native species (Walker et

al. 2009, Wiser et al. 2011). It is unclear how grazing by hares and, locally, rabbits may determine which woody species dominate in succession. Some native woody plants that invade grasslands below treeline are grazed by hares, notably species of the native legume *Carmichaelia* (Norbury & Flux 2005), and selective elimination of *Carmichaelia* species can retard the rate of succession (St John et al. 2012). In contrast, little is known about effects of grazing by hares or rabbits on woody non-native species in non-forested ecosystems below treeline in New Zealand. Hares graze seedlings of the non-native legume Scotch broom in these ecosystems (Williams 1998), but did not graze briar in a site where it was dominant in the eastern South Island (Blay 1989). The grazing regime of hares and rabbits and its capacity to influence succession needs to be evaluated in a landscape context; a recent study showed that increased rabbit abundance in fertilised pastures adjacent to grasslands largely dominated by native plant species, results in rabbits “spilling over” into the adjacent grasslands (Norbury et al. 2013). The consequences of inflated numbers of rabbits on the relative performance of native vs. woody non-native species in successions in non-forested ecosystems below treeline are unknown.

The lack of overlap between plots where ungulates (i.e., deer and goats) were present and plots where woody non-native plants were present has no obvious explanation. For example, ungulates occur in both forested and non-forested ecosystems throughout New Zealand (Bellingham et al. 2013), so non-overlap cannot be attributed to ungulates being more frequent in forests. Recent research has highlighted the role of ungulates, as well as possums, as indirect facilitators of non-native conifer invasions, as dispersers (via dung) of non-native ectomycorrhizal fungi into soils of non-forested ecosystems (Wood et al. 2015). These fungi enhance the establishment and growth of seedlings of non-native conifers, and confer little benefit on the growth of seedlings of native beech (Nothofagaceae), which require native ectomycorrhizal fungi (Dickie et al. 2010).

2.1.4 Are higher densities (e.g., cover, basal area) of woody non-native plants associated with high abundance of herbaceous non-native plants?

Of 919 plots across public conservation land, 45% had at least one non-native plant species present. The presence of woody non-native and herbaceous non-native plants were strongly, positively associated (delta AIC herbaceous = -99.9, very strong support; Appendix 1.1; Fig. 4). Woody non-native plants were found on 77 plots, and on 68 of these (88%) a herbaceous non-native plant was also found. In contrast, plots without a woody non-native plant were much less likely to have a herbaceous non-native plant (33%; Fig. 4).

Plots that had at least one stem of a woody non-native plant that was ≥ 2.5 cm diameter at 1.3 m height were also more likely to have at least one herbaceous non-native plant (delta AIC = -21.7, very strong support). Thirty sample plots had tagged woody stems (≥ 2.5 cm diameter at 1.3 m height) on them and 24 of these (80%) also had a herbaceous non-native plant present. In contrast, 31% of plots without tagged woody non-native stems had herbaceous non-native plants present.

These two analyses suggest a strong association between the presence of woody and herbaceous non-native plant species. Furthermore, in those plots where woody non-native plant species were found, the cover of herbaceous non-native plant species was associated with the cover (delta AIC = -5.61, moderate support), and stem density (delta AIC = -3.59; weak support) of woody non-native plant species, but not the basal area (delta AIC = -0.78, no support).

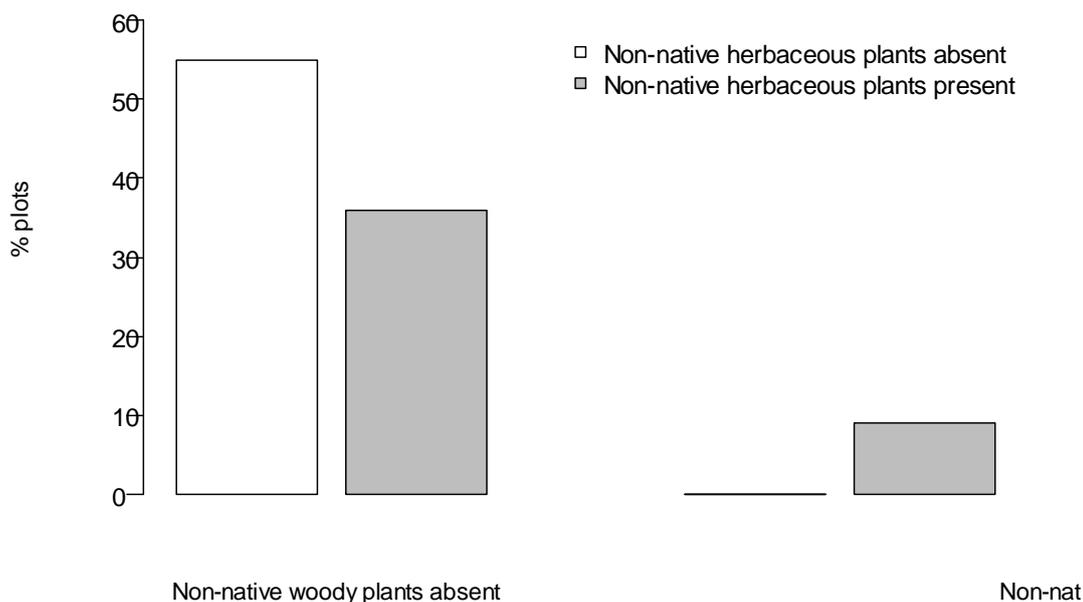


Figure 4 The percentage of sample plots with non-native herbaceous plants present or absent, according to whether non-native woody plants were present or absent.

Discussion

There was a clear relationship that herbaceous non-native plants were usually present when woody non-native plants were present, but not *vice versa*. There are two probable explanations for this. The first is that the landscapes into which woody non-native plants can invade are generally invadable, especially in areas that are or have been subject to human habitat modification. The most invadable sites are deforested landscapes that are close to forest margins, roads, and some probable sources of invasion propagules such as conifer plantations. Many herbaceous non-native plants in New Zealand are most frequent and abundant in these sites (e.g., Wilson et al. 1992; Tomasetto et al. 2013). Woody and herbaceous non-native plants could invade these sites simultaneously, although the invasion of some long-established herbaceous non-native plants, such as sheep's sorrel, *Rumex acetosella* (Moore 1954; Harris 1970; Williams 1980), sometimes will have preceded invasion by non-native woody plants. Several herbaceous non-native plants invade forest understoreys in New Zealand (Standish et al. 2001; Williams et al. 2003; Wiser & Allen 2006), whereas woody plants generally are less successful invaders in forested regions (Fig. 1). This is probably the main reason that woody non-native plants were not always present where herbaceous non-native plants were present.

Another possible explanation for the relationship between the presence of woody non-native plants and herbaceous non-native plants is habitat modification by the former. Pyrogenic woody invaders could favour non-native herbaceous species that either resist fire or seed readily after fire. Nitrogen-fixing woody non-native species, such as gorse and Scotch broom, contribute N-rich litter to ecosystems. This could favour establishment and growth of other non-native species (e.g., blackberry, *Rubus fruticosus*, was more commonly found in successions on old fields under nitrogen-fixing gorse than under native kānuka, which does

not fix nitrogen; Sullivan et al. 2007). Pines and their associated, largely non-native, ectomycorrhizal fungi can make limiting nutrients more available to other species, and this also can favour some herbaceous non-native plants. For example, lodgepole pine invasion increases the soil concentrations of mineral N and available P, which is associated with invasion by non-native grasses and herbs (Dickie et al. 2014). Longer-term records from the same plots will reveal whether co-invasion or habitat modification is the predominant means by which the pattern shown here arises.

2.2 Wilding conifer species on public conservation land

Key results for wilding conifers:

Wilding conifers were:

- on 1.8% of sample plots across public conservation land.
- throughout New Zealand, but were most concentrated in sample plots in Nelson–Marlborough and South Canterbury.
- most often close to non-native forests, in drier locations, in non-forested habitats, and close to roads and the boundary of public conservation land.
- absent from sample plots across National Parks.

Lodgepole pine was the most widespread wilding conifer species. It was the only woody non-native plant that occurred on plots above natural treelines, where it occurred as small individuals, presumably at an early stage of invasion.

Eight species of non-native conifers (hereafter wilding conifers) occurred in 17 (1.8%) of 919 plots across public conservation land. Lodgepole pine was the most widespread of the wilding conifers, in 8 plots (0.9%). Other wilding conifers in the Pinaceae included the widely planted economic species radiata pine (*Pinus radiata*, 4 plots) and Douglas fir (*Pseudotsuga menziesii*, 2 plots), as well as other pines, *Pinus nigra*, maritime pine (*Pinus pinaster*), and *Pinus patula*, and also Lawson’s cypress (*Chamaecyparis lawsoniana*, Cupressaceae) and Japanese cedar (*Cryptomeria japonica*, Taxodiaceae) (each of these species on single plots).

Wilding conifers were distributed in plots throughout most of the latitudinal range of public conservation land, towards the east of both islands, and with concentrations in two areas in the eastern South Island; Nelson–Marlborough and South Canterbury (Fig. 5). Lodgepole pine alone occupied a subset of the plots, concentrated in inland Marlborough and inland South Canterbury, and also in inland Hawke’s Bay (Fig. 6a). All plots in which lodgepole pine occurred on public conservation land occurred in areas mapped by the Department of Conservation as areas in which its presence was known or likely (Fig. 6b). In contrast, one of the two records of Douglas fir from the plots was mapped by the Department of Conservation as being in area from which it was either suspected or modelled to be absent (data not shown).

Wilding conifers: relative cover
(% of total plot cover)

- 0
- <1
- 1-5
- 5-10
- 10-25
- 25-50
- 50-100

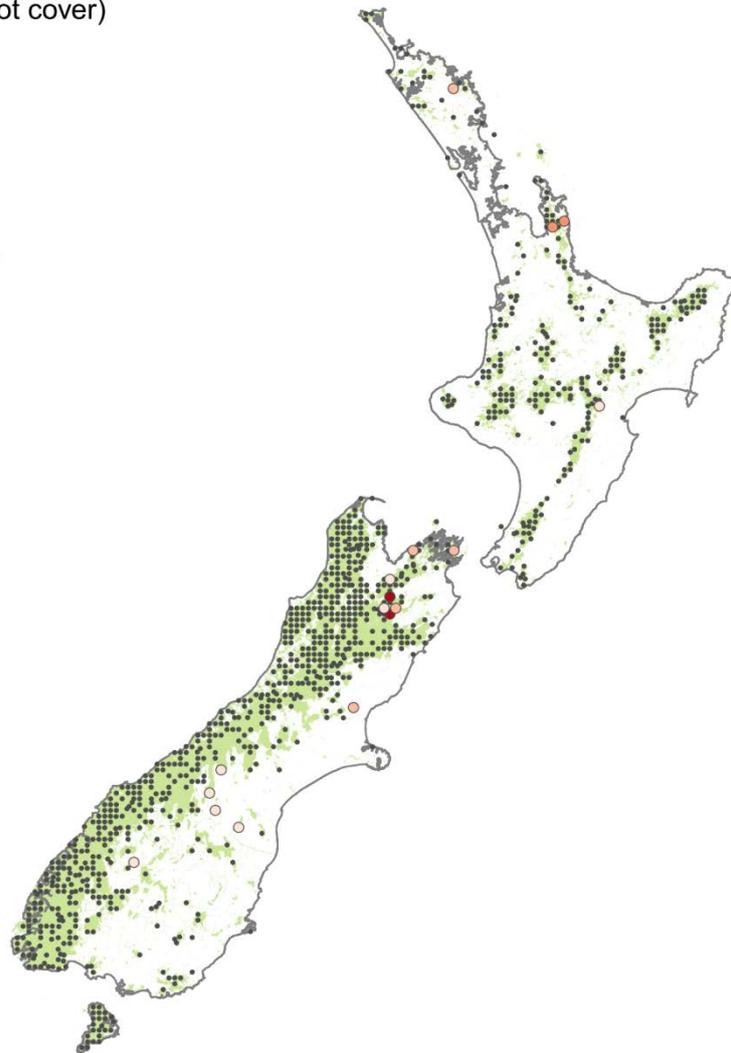


Figure 5 Relative cover (percentage of total cover on a plot) comprised of the cumulative cover of all woody non-native conifer species (wilding conifers) present on a plot.



Figure 6 (a) Relative cover (percentage of total cover on a plot) of lodgepole pine (*Pinus contorta*) on plots, and (b) presence of lodgepole pine in plots on public conservation land, overlying a map of known or probable presence, and known or modelled absence of lodgepole pine, determined by the Department of Conservation.

2.2.1 Does the presence of non-native conifers vary with distance to nearest public conservation land boundary, roads and nearby non-native forests?

Wilding conifers in general, and lodgepole pine alone, were more likely to be present in plots closer to a non-native forest, in a drier location, and with shorter-statured vegetation. They were absent from plots in National Parks (Table 3). Wilding conifers were also more likely to occur close to the boundary of Public Conservation land and close to roads, and lodgepole pine was more likely to occur at plots at higher altitudes with lower minimum temperatures (Table 3), all outside National Parks (even though high altitude, low minimum temperature sites are frequent in National Parks).

In general, all wilding conifer species were present in plots that where annual rainfall was <2500 mm (Fig. 7a), which is drier than the zone occupied by all woody non-native plants (Fig. 2). Plots with the warmest minimum temperatures were not invaded by wilding conifers (Fig. 7a), again in contrast to the overall pattern among woody non-native plants (Fig. 2). Compared with all wilding conifer species, lodgepole pine was present in plots over a narrower environmental range and in areas that had among the coolest minimum temperatures (Fig. 7b).

Table 3 Summary of statistical models predicting the presence of all species of wilding conifers, and of lodgepole pine alone, listed according to the direction of the relationships (– for negative relationship, + for positive relationship; NS for relationships with no statistical support; details of analyses and assignation of support levels is described in Appendix 1.3, Tables S3, S4).

Predictor	All wilding conifers	Support	Lodgepole pine	Support
Mean top height	–	Strong	–	Very strong
Rainfall	–	Very strong	–	Weak
National Park	–	Very strong	–	Moderate
Distance to non-native forest	–	Very strong	–	Very strong
Distance to Public Conservation Land boundary	–	Moderate	NS	No support
Distance to nearest road	–	Weak	NS	No support
Minimum Temperature	NS	No support	–	Very strong
Altitude	NS	No support	+	Very strong
Latitude	NS	No support	NS	No support

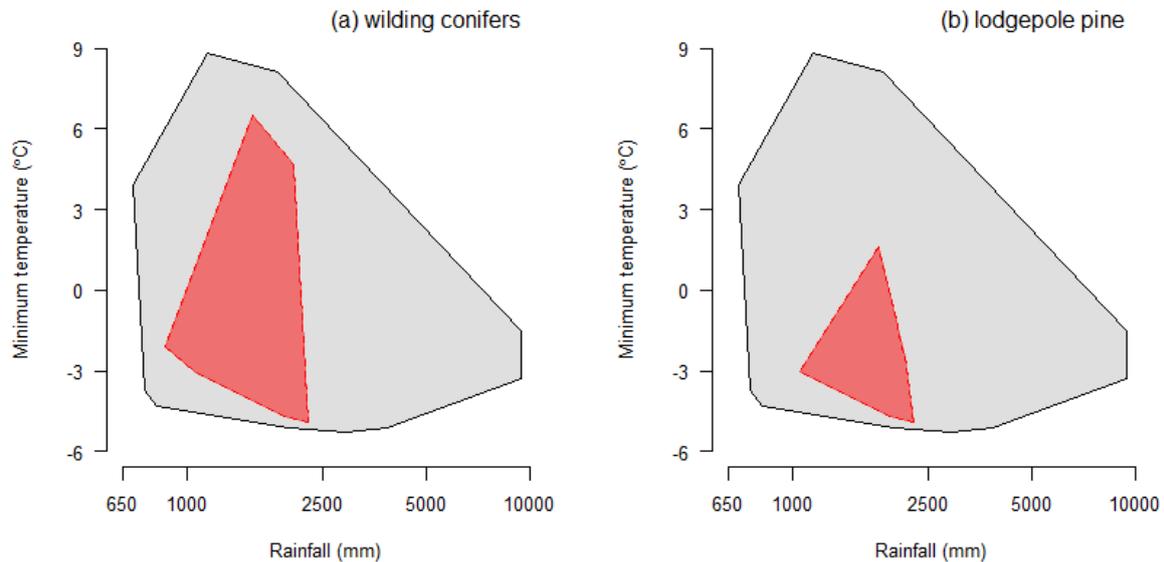


Figure 7 Relationship between (a) occurrence of all non-native conifers (wilding conifers) and (b) lodgepole pine (*Pinus contorta*) and total annual rainfall and minimum temperature. The grey zone represents the envelope within which all 919 sample plots occur, and the red zone represents the envelope within which wilding conifers (including lodgepole pine) or lodgepole pine alone was present.

Discussion

Conifers outside their native range begin their invasions from plantations onto land nearby (e.g., Buckley et al. 2005, Simberloff et al. 2010). It is unsurprising that the extensive sampling of public conservation land confirms this is the mode of invasion for an individual species (lodgepole pine) and for wilding conifers in general. Some of the plantations that are sources of these invasions occur on public conservation land (e.g., in the Craigieburn Range, and in the Leatham Valley in Marlborough), and others are adjacent to it. The association of lodgepole pine with high altitude sites is likewise expected in this context; the original introductions of this species were intended to control erosion at high altitude sites (Craigieburn Range, Leatham Valley, central North Island volcanic region, Kaweka Range; Ledgard 2001).

The capacity of non-native conifers to invade non-woody ecosystems outside their native range is also well documented, especially in grasslands, in New Zealand (Hunter & Douglas 1984; Ledgard 2001) and elsewhere (Simberloff et al. 2010). Lodgepole pine and wilding conifers are present most frequently in short vegetation (such as grasslands) in the widespread sampling of public conservation land, showing that non-forested ecosystems are preferentially invaded. Grasslands below natural treeline in New Zealand, many of which were induced by Māori deforestation caused by fire (McGlone 2001), are invaded rapidly by wilding conifers, whereas tree species from adjacent natural forests (especially beech, Nothofagaceae spp.) invade slowly. There is evidence that the more rapid invasion of non-native conifers into these grasslands is facilitated by co-occurring non-native mycorrhizal

fungi that enhance growth and nutrient uptake by the conifers, and these fungi occur more frequently in the grasslands than the native mycorrhizal fungi that are needed by the beeches (Dickie et al. 2010).

Conifer invasion of low-stature vegetation need not be confined to grasslands on public conservation land; for example, radiata pine invades bare landslides among rain forests (Sullivan et al. 2006) and it occurred on lowland plots on public conservation land. While non-native conifers can invade primary successional surfaces, such as landslides, many can also invade shrublands that develop during secondary successions after fire or abandoned agriculture. For example, secondary successions dominated by native mānuka (*Leptospermum scoparium*) and kānuka on former agricultural land in Abel Tasman National Park are invaded, and overtopped, by radiata pine and maritime pine (Esler 1961; Sanson 1978). Douglas fir also occurred on two of the widespread Tier One plots; it is more shade tolerant than lodgepole pine (e.g., Waring et al. 1982) and can invade forest understoreys in New Zealand (Dehlin et al. 2008) as well as grasslands (Wood et al. 2015). Moreover, the non-native ectomycorrhizal fungi that Douglas fir and other introduced Pinaceae require for growth and survival are also now widespread in many New Zealand ecosystems (Orlovich & Cairney 2004). These factors, along with ongoing introduction effort (Richardson et al. 1994), make it likely that Douglas fir will invade more plots in future, where its rapid growth rates (Waring et al. 2008) could result in its dominance over native species colonising the same site. Douglas fir is also long-lived, often surviving c. 450 years and sometimes over 600 years in its native range (Black et al. 2008), in contrast to some of the native tree species with which it co-occurs (e.g., typically 300 years for mountain beech; Wardle 1984), so once established it could exert long-term ecosystem effects.

Some of the invasive pines in New Zealand have high periodicity in their production of heavy seed crops (mast seeding) between years. In their native ranges, these include lodgepole pine (Smith et al. 1990) and ponderosa pine (*Pinus ponderosa*; invasive in New Zealand but not yet recorded on the plots; Silvertown 1980). The seeds produced by these species are consumed by rodents in their native ranges (Silvertown 1980). In New Zealand, many native tree species, but especially beech (Nothofagaceae) also exhibit mast seeding (Allen & Platt 1990; Webb & Kelly 1993). Mast seeding by New Zealand beeches drives irruptions of introduced rodents (Choquenot & Ruscoe 2000). These irruptions in turn cause populations of their introduced mammalian predators, notably stoats, to increase, and these prey upon native birds (King 1983). It is unknown whether introduced rodents in New Zealand consume seeds of introduced pines; a study of the diet of ship rats in a radiata pine plantation comprised mostly insects, but it was conducted in winter when radiata pine seeds were least abundant (Clout 1980). Wilding pines can provide habitat for native insectivorous birds (e.g., rifleman, *Acanthisitta chloris*; Norton & Forbes 2013), but if rodents do consume pine seeds in New Zealand, and their populations respond to mast seedings, this could have important implications for New Zealand native birds in ecosystems dominated by wilding pines and in native-dominated ecosystems adjacent to them. Moreover, temperatures that strongly predict the likelihood of masting by Nothofagaceae in New Zealand (Kelly et al. 2013) also predict masting of ponderosa pine in its native range (Moreira et al. 2015), but whereas time from flowering to ripe seed production in Nothofagaceae is at most 9 months (e.g. Richardson et al. 2005), the time from cones being pollinated to ripe seed production in ponderosa pine is 15–18 months (Oliver & Ryker 1990). Thus, where there are extensive areas of wilding pines that may mast, such as lodgepole and ponderosa pine, adjacent to beech forest, there is the potential that rodent outbreaks driven by beech mast seeding in one year may be sustained by pine mast seeding the following year, with potential impacts on bird populations across the

landscape. Such situations occur in the Craigieburn Range, Leatham Valley, and Kaweka Range (Ledgard 2001). The early maturation of lodgepole pine in New Zealand, with cone production on individuals as young as 3 years old (Benecke 1967), also means that seeds that could initiate rodent outbreaks are available much earlier than in developing beech stands, where earliest flower production is on 20-year-old individuals (Wardle 1984).

2.2.2 What is the extent and abundance of woody non-native plants above treeline?

Non-native woody plants occurred nationally in 18 plots that were above 900 m elevation, and we investigated which of these plots were above a natural treeline, by evaluating the surroundings of each plot and treelines in Google Earth. Delineation of probable treelines at each locality was based on studies that have determined treelines and their stability throughout New Zealand (e.g., Wardle 1985a, 2008; Harsch et al. 2012; Cieraad et al. 2014). Of the 18 plots, 14 are probably below natural treelines. Seven of these plots that are probably below natural treelines were in Molesworth, inland Marlborough, where treelines are among the highest in New Zealand (1530 m; Cieraad 2011), but also where deforestation through Māori fires was extensive 750–600 years ago, and where more fires since European colonisation c. 150 years ago further reduced forest cover (McGlone & Basher 1995).

Of the remaining four plots, three are certainly above natural treelines and one may be. Lodgepole pine was the only woody plant species to invade plots that were certainly above natural treeline. Two of these plots were in inland Marlborough and the other in inland Canterbury. The other plot that may be above treeline was in Tongariro National Park, and heather was present in that plot (Chapman & Bannister 1990). Treelines are hard to define in much of Tongariro National Park because of the effects of periodic volcanic eruptions. In the three plots invaded by lodgepole pine in alpine habitat, its total cover was low (occupying <1 m² cover within a 400 m² plot in all cases) and its height was <2 m in all cases.

The area of alpine habitat in New Zealand is 24 338 km² and if we assume that nearly all this habitat is contained within public conservation land (c. 80 000 km² in total), then c. 30% of public conservation land is alpine habitat. Some of this habitat could be invaded by lodgepole pine (Wardle 1985b; results above). If we assume that lodgepole pine is restricted to areas with a rainfall ≤2500 mm (Fig. 7b) and is unlikely to invade sites above 2000 m elevation, then a liberal estimate of the alpine habitat that lodgepole pine could invade is 16% of public conservation land. This estimate is based on the proportion of Tier One plots that are c. 900–2000 m elevation, with rainfall ≤2500 mm (i.e., 220 plots from the network of 1342 plots). Treelines are much higher than 900 m in some regions of New Zealand (see above), so we also calculated a conservative estimate, by setting treeline at 1400 m elevation. The conservative estimate of alpine habitat that could be invaded by lodgepole pine is only 5% of public conservation land (i.e., 68 plots fall within this area). Of the two estimates, the liberal estimate is closer to the areal extent of alpine habitat in the Land Cover database. Hence, using the liberal estimate, 3/220 (1.4%) plots within the alpine habitat that is environmentally suitable for invasion were invaded by lodgepole pine.

Discussion

Lodgepole pine was the only woody non-native plant that was detected in plots that are undoubtedly above natural treelines in New Zealand, and all three cases were in the eastern South Island, in the rain shadow of the Southern Alps. This is consistent with experiments that showed that transplanted seedlings of lodgepole pine survived and grew 150 m above a native mountain beech (*Fuscospora cliffortioides*) treeline in the eastern South Island, and that it was one of only two apparently cold-tolerant non-native trees (with mountain pine, *Pinus mugo*) that could do so (Wardle 1985b). Other experiments in the eastern South Island have shown that transplanted mountain beech seedlings can survive above their own treeline only if they are sheltered, whereas transplanted seedlings of lodgepole pine survived and grew successfully without shelter (Harsch 2010). These experimental studies, along with the natural occurrence of lodgepole pines in the plots above treeline reported here, show that ongoing invasion into zones above current natural treelines in the eastern South Island is to be expected as long as seed sources are present. Moreover, the current invasions are likely to consolidate locally and could form a new forested zone comprised of lodgepole pines in the currently mostly treeless alpine zone (Lee 1998; McGlone et al. 2010). This would probably have major consequences for native and non-native biodiversity above and below ground. Above ground, increasing biomass and leaf area could change competitive relationships, especially rendering habitat unfavourable for shade-intolerant plant and animal species. Below ground, there is evidence in New Zealand that lodgepole pine invading below natural treelines causes major shifts in soil nutrient cycling, indicated by increased bacterial dominance and nitrate and plant-available phosphorus in soils, which are likely to be mediated by the pine's ectomycorrhizal fungal symbionts (Dickie et al. 2014). Once this is underway, removing the pines can have adverse consequences for native biodiversity because non-native grasses can colonise the altered soils more readily than native plant species (Dickie et al. 2014). So far, lodgepole pine invasion above treeline shows no clear association with other non-native plant species. This could be, in part, because the current cover (abundance) of lodgepole pine in the plots where it occurs is not great.

Fires occur very uncommonly above treeline in New Zealand and the rate of recovery of alpine native plant communities after fire is very slow (Calder & Wardle 1969). The establishment of lodgepole pine could alter the fire disturbance regime because it is a pyrogenic species that is highly flammable (Jolly et al. 2012, Cobar-Carranza et al. 2014), and lightning strikes that seldom cause ignition in less flammable native plant communities are more likely to ignite canopies of lodgepole pine. Not only could this result in fire damage and slow recovery of vegetation above treeline, but it could result in fire damage to treeline communities, for example of mountain beech, which is killed by fire (Wiser et al. 1997). Lodgepole pine typically regenerates rapidly from seed beneath or beyond its own burned canopies (e.g., Chappell & Agee 1996); hence, after fire in lodgepole pine communities above treeline in New Zealand, we might expect expansion into adjacent burned native alpine vegetation and also downslope into burned beech forest below treeline. Below treeline, mountain beech can gradually recolonise areas where its canopies have been killed by fire (Wiser et al. 1997), but in areas colonised by both lodgepole pine and mountain beech, we would expect that the much more rapid growth rates of lodgepole pine (Ledgard 2001) would lead to its dominance, at least in the medium term.

Nearly all the potential alpine habitat that lodgepole pine could invade in the eastern South Island (and potentially in the central and eastern North Island) is on public conservation land. The evidence suggests that legacy effects of these pines, even once removed, might be

detrimental for native biodiversity and that an unchecked invasion of these pines could promote fire that would engender a positive feedback for its invasion. This suggests a need for the rapid removal of invasive lodgepole pines from above treeline and adjacent sources in the areas that these plots occur, especially if any of these alpine zones coincide with known “hotspots” of native biodiversity. For example, the Leatham Valley, where one of the invaded plots occurs, is an area with a large number of endemic alpine *Veronica* (*Hebe*) species, some with very narrow ranges (Heads 1997; Bayly & Kellow 2006). Throughout New Zealand’s alpine habitat, the same native plant genera are often widespread, but turnover in species within these genera is such that there is often very low overlap in species between any two alpine areas (Richardson et al. 2012). Invasion and ecological transformation by lodgepole pine in one alpine area physiognomically similar to another (e.g., Richardson et al. 2012) could result in local loss of diversity of native biota.

In all cases where lodgepole pine had invaded plots above treeline, it was of low cover and the seedlings or saplings were short (<2 m tall). Because of this, detecting these invasions would be difficult by remote means. Because the lodgepole pines were small, the plots serve as an early warning of an invasion.

2.2.3 Are non-native conifers less frequent in National Parks relative to other conservation lands (taking into account environmental covariates)?

Wilding conifers generally (all non-native conifers, including lodgepole pine) were absent from plots in National Parks and hence were statistically less likely to be present in National Parks than in other public conservation land after accounting for environmental variation (delta AIC = -2.33, weak support; Appendix 1.1), but the same was not true for lodgepole pine alone (delta AIC = -0.03, no support).

Discussion

Most of the areas below natural treeline in New Zealand’s National Parks are in native forest cover, and most wilding conifers, except to some degree Douglas fir and Japanese cedar, are too intolerant of shade to invade closed evergreen forests (see section 2.1). Permanently open sites below treeline in National Parks are invaded by wilding conifers, for example, by maritime pine and radiata pine in Abel Tasman National Park into otherwise largely native shrublands (Esler 1961; Sanson 1978) and coastal cliffs (J.M. Hurst et al., unpublished data), and by radiata pine and Douglas fir in Kahurangi National Park on inland cliffs (J.M. Hurst et al., unpublished data). Open sites, such as inland or coastal cliffs, are seldom detected by the sampling regime of regularly spaced plots that we report. Permanently open sites that support wilding conifers can be the inocula for invasions into areas that are deforested by natural disturbances such as floods, earthquakes, volcanoes, and landslides (Allen et al. 2013b). Extensive deforested areas below natural treeline are uncommon in New Zealand’s National Parks. One example is in the rain shadow region of Tongariro National Park, and wilding conifers, including lodgepole pine, have invaded this region, including its volcanic dunes (<http://www.landcareresearch.co.nz/publications/factsheets/rare-ecosystems/inland-and-alpine/volcanic-dunes>), which is of particular concern because these are an endangered, naturally uncommon ecosystem (Holdaway et al. 2012).

The plots above treeline that were invaded by lodgepole pine were not in National Parks, but similar habitats, above a treeline of mountain beech, are west of, but otherwise close to the invaded sites, at Aoraki/Mount Cook National Park and Nelson Lakes National Park. Since most seed sources of lodgepole pine are to the east of these National Parks, prevailing westerly winds could diminish the likelihood of invasion above treeline in these National Parks. However, less frequent easterly winds can also transport dust in a westerly direction across the Southern Alps and into Westland (Marx & McGowan 2005), so it is likely that infrequent westward dispersal of lodgepole pine could occur into these areas. Therefore continued measurement of these and other networks of plots in alpine regions of National Parks close to potential seed sources should continue, especially since detection in the early stages of invasion (i.e., before they become detectable by remote means, when they have high cover) would mitigate the ecological damage that they could cause. Lodgepole pine invasions have occurred in alpine regions of Tongariro National Park and have been subject to control since the 1970s (Cooper 1984).

2.3 Other widespread woody non-native species on public conservation land

Twenty-nine species of woody non-native plants (in addition to the 8 species of wilding conifers) were found across the plots. Six of the 29 species were in the legume family (Leguminosae), and three each in the protea family (Proteaceae), rose family (Rosaceae), and willow family (Salicaceae). The most widespread individual species occurred on at least 8 plots (i.e., $\geq 0.87\%$ of the 919 plots). These were:

- briar (*Rosa rubiginosa*, Rosaceae) (22 plots)
- gorse (*Ulex europaeus*, Leguminosae) (16 plots)
- Scotch broom (*Cytisus scoparius*, Leguminosae) (11 plots)
- prickly hakea (*Hakea sericea*, Proteaceae) (8 plots).

Briar occurred on plots on public conservation land in the eastern South Island, with greatest concentrations and cover in inland Marlborough, and inland South Canterbury and Otago (Fig. 8a). Gorse occurred on plots throughout New Zealand, more frequently in the west and often near the coast (Fig. 9a). Scotch broom occurred on inland plots from the central North Island southwards, most frequently in the north-eastern South Island (Fig. 10a). Prickly hakea occurred on plots in warm temperate regions of New Zealand, mostly north of Tauranga but also at a site in Abel Tasman National Park (Fig. 11).

Compared with the national distribution of briar, it is striking that it was not found on any plots on public conservation land in the North Island, although its presence there is confirmed by either herbarium records or other plot records, and by expert opinion (Fig. 8b). This may be because its principal habitat of dry, cold regions, mostly below treeline, is seldom found on public conservation land in the North Island. The occurrence of gorse and Scotch broom on public conservation land occurs throughout the ranges of both species (Figs. 9b, 10b). Tier One plots on public conservation land confirmed expert opinion of the presence of briar in 14 $10\text{ km} \times 10\text{ km}$ grid squares, and of its expected absence in another three grid squares. Tier One plots also confirmed expert opinion of the presence of gorse (one grid square) and Scotch broom (two grid squares).

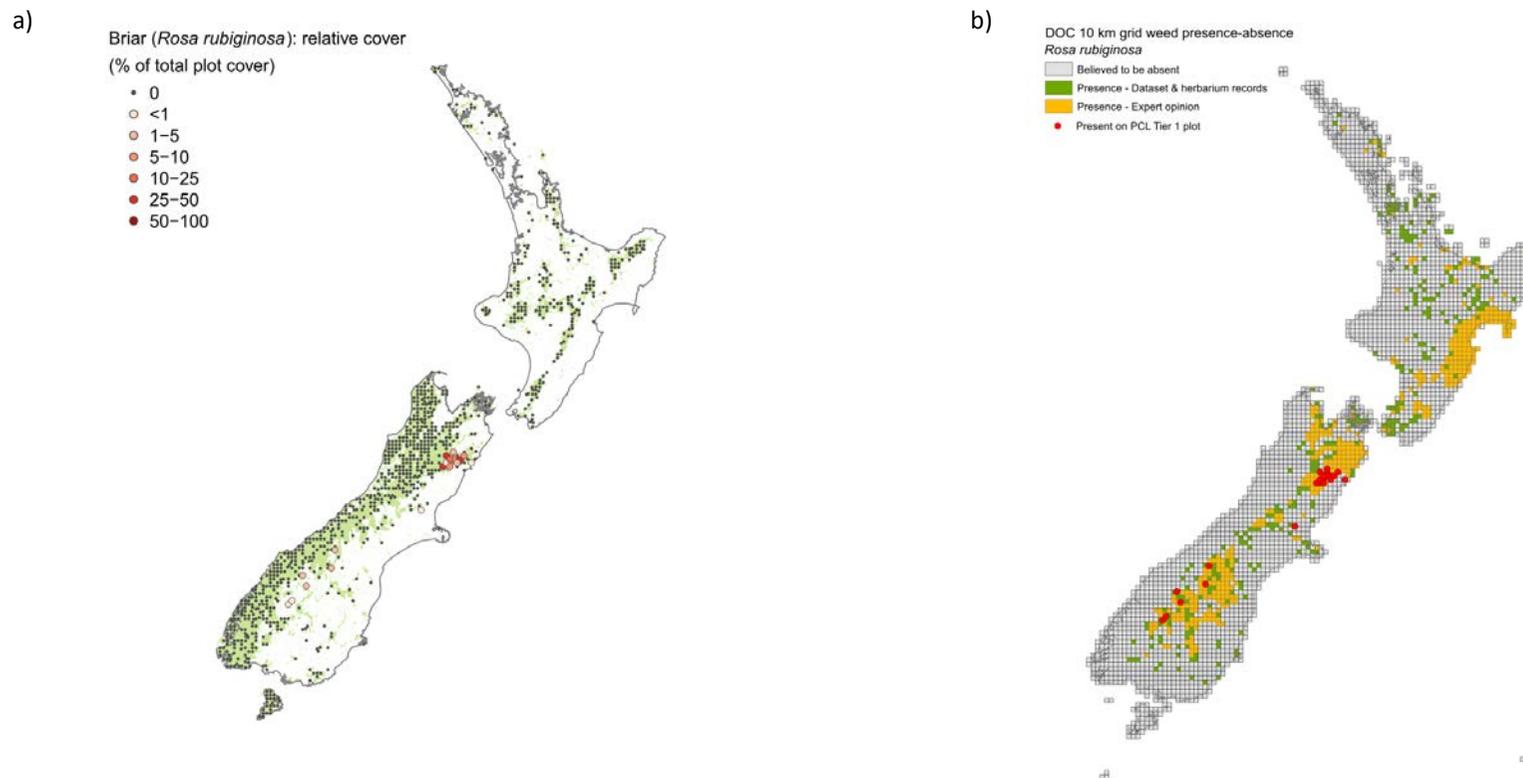


Figure 8 (a) Relative cover (percentage of total cover on a plot) of briar (*Rosa rubiginosa*) on plots, and (b) presence of briar in plots on public conservation land, overlying a map of 10 km × 10 km cells in which its presence is known (from herbarium specimens and/or other plot records), likely, or believed to be absent (based upon expert opinion), determined by the Department of Conservation.

a)

Gorse (*Ulex europaeus*): relative cover
(% of total plot cover)

- 0
- <1
- 1-5
- 5-10
- 10-25
- 25-50
- 50-100



b)

DOC 10 km grid weed presence-absence
Ulex europaeus

- Believed to be absent
- Presence - Dataset & herbarium records
- Presence - Expert opinion
- Present on PCL Tier 1 plot

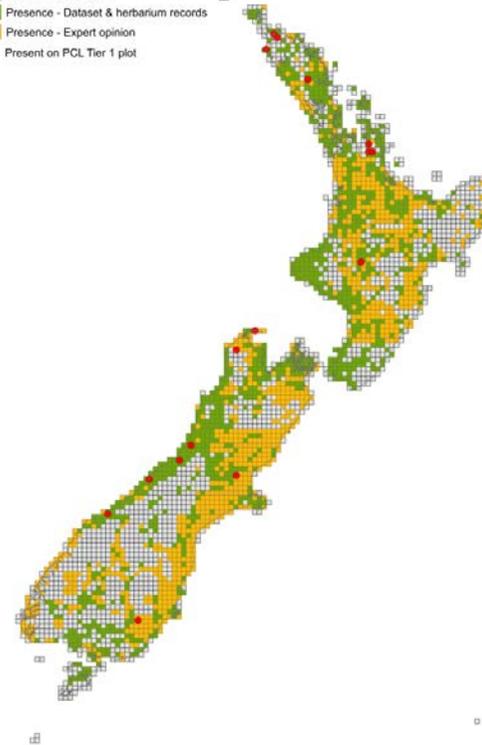


Figure 9 (a) Relative cover (percentage of total cover on a plot) of gorse (*Ulex europaeus*) on plots, and (b) presence of gorse in plots on public conservation land, overlying a map of 10 km × 10 km cells in which its presence is known (from herbarium specimens and/or other plot records), likely, or believed to be absent (based upon expert opinion), determined by the Department of Conservation.

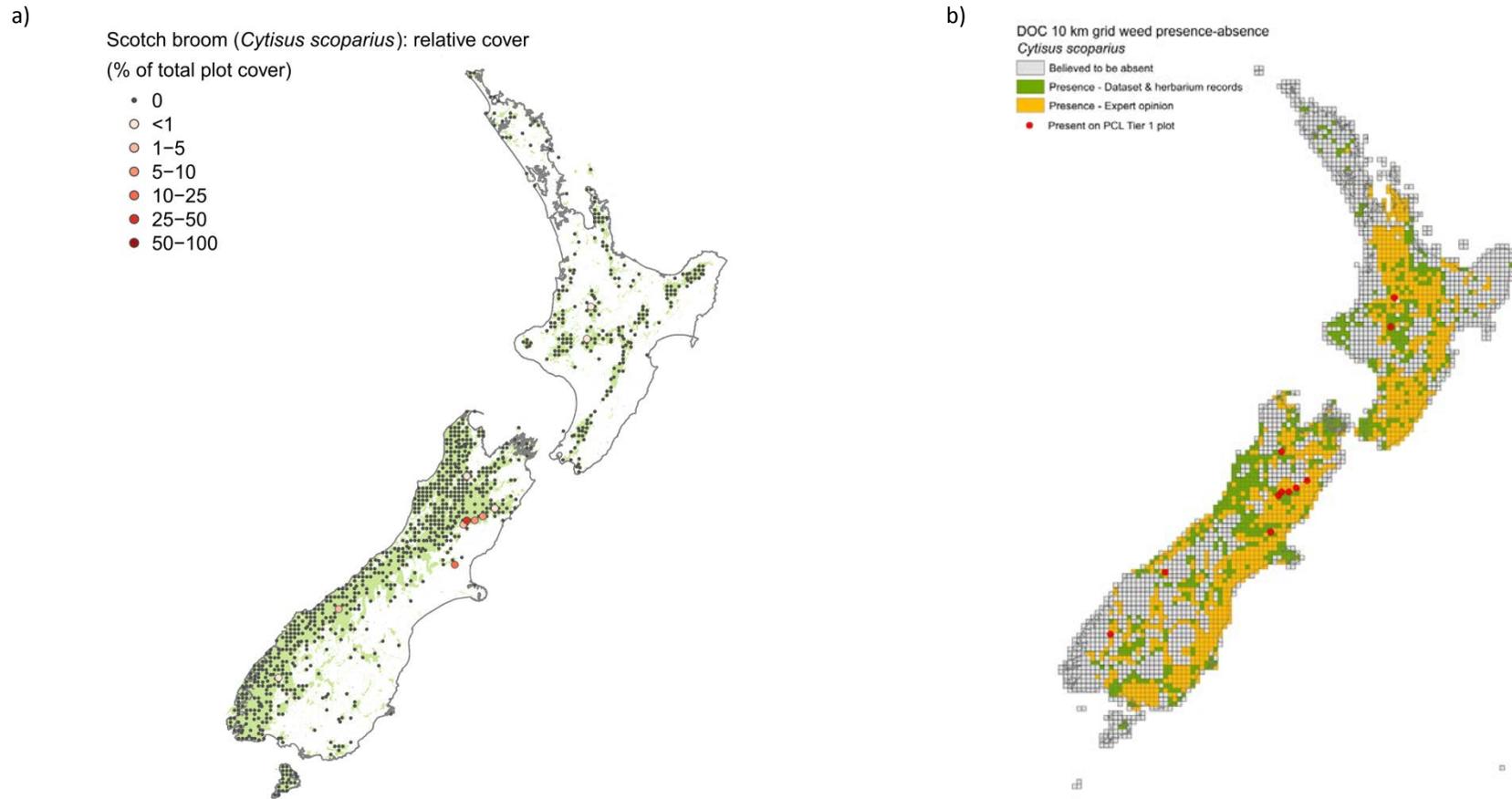


Figure 10 (a) Relative cover (percentage of total cover on a plot) of Scotch broom (*Cytisus scoparius*) on plots, and (b) presence of Scotch broom in plots on public conservation land, overlying a map of 10 km × 10 km cells in which its presence is known (from herbarium specimens and/or other plot records), likely, or believed to be absent (based upon expert opinion), determined by the Department of Conservation.

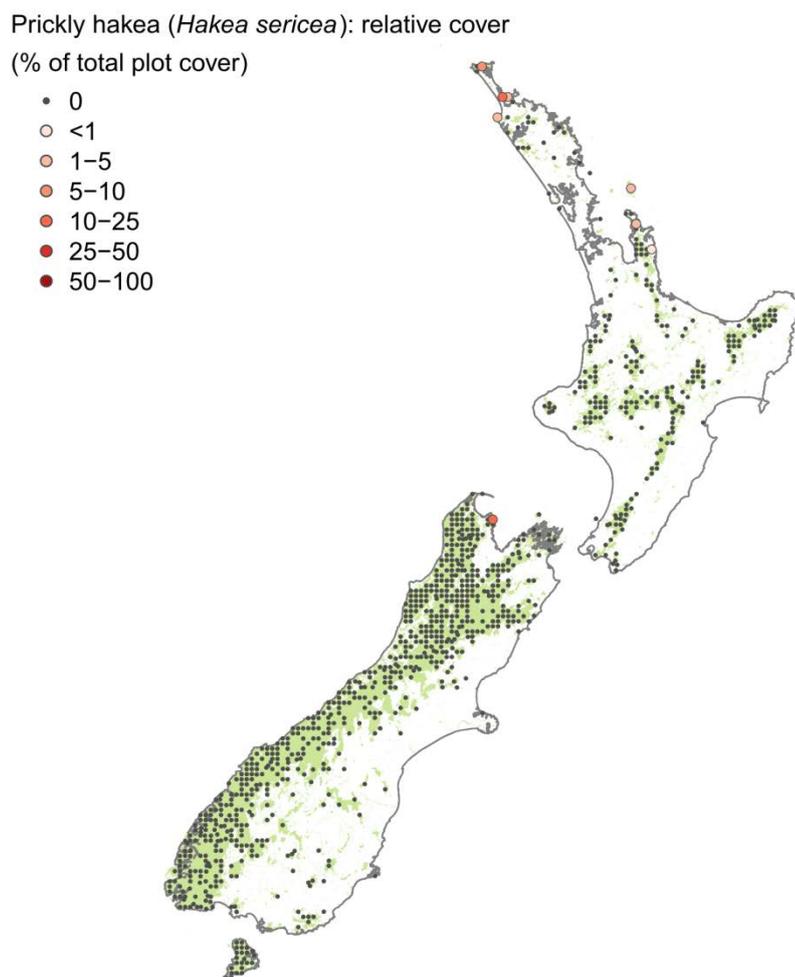


Figure 11 Relative cover (percentage of total cover on a plot) comprised of prickly hakea (*Hakea sericea*) on plots on public conservation land.

2.3.1 Does the presence of widespread woody non-native species vary with distance to nearest public conservation land boundary, roads, and nearby non-native forests?

All four of the most widespread woody non-native species occurred most frequently in lower stature resident vegetation (Table 4). Briar, gorse and prickly hakea were more likely to be present the closer the plots were to a non-native forest. Gorse, Scotch broom and prickly hakea were also more likely to be present if the plots were close to a road, and gorse and prickly hakea if the plots were close to the boundary of public conservation land. Gorse and prickly hakea were most frequently present in low-elevation, more northerly plots. Briar, gorse and prickly hakea were also more likely to be present in plots in low rainfall regions.

The four most widespread woody non-native species show strikingly different relationships with respect to total rainfall and minimum temperatures (Fig. 12). Briar occurred on the plots

with the lowest rainfall and the coldest minimum temperatures (Fig. 12a). Although the plots on which gorse and Scotch broom occurred covered a similar gradient of rainfall, gorse extended into much warmer regions than Scotch broom, and Scotch broom extended into much cooler regions than gorse (Figs. 12b, c). Prickly hakea occurred on plots in warm regions across a narrow range of rainfall, and not in dry regions (Fig. 12d).

None of the four species (gorse, Scotch broom, briar or prickly hakea) were more or less likely to be present in National Parks relative to other public conservation land, once other environmental variables had been accounted for (delta AICc values all <2).

Table 4 Summary of statistical models predicting the presence of four widespread woody non-native plant species, listed according to the direction of the relationships (– for negative relationship, + for positive relationship; NS for relationships with no statistical support; details of analyses and assignation of support levels is described in Appendix 1.3, Tables S5, S6, S7, S8).

Predictor	Briar	Gorse	Scotch broom	Prickly hakea
Mean top height	– (Very strong)	– (Very strong)	– (Strong)	– (Moderate)
Distance to non-native forest	– (Very strong)	– (Very strong)	NS	– (Moderate)
Distance to nearest road	NS	– (Very strong)	– (Weak)	– (Strong)
Rainfall	– (Very strong)	NS	– (Strong)	– (Moderate)
Minimum Temperature	– (Very strong)	+ (Very strong)	NS	+ (Very strong)
Distance to Public Conservation Land boundary	NS	– (Very strong)	NS	– (Strong)
Altitude	NS	– (Very strong)	NS	– (Very strong)
Latitude	NS	+ (Very strong)	NS	+ (Very strong)
National Park	– (Very strong)	NS	NS	NS

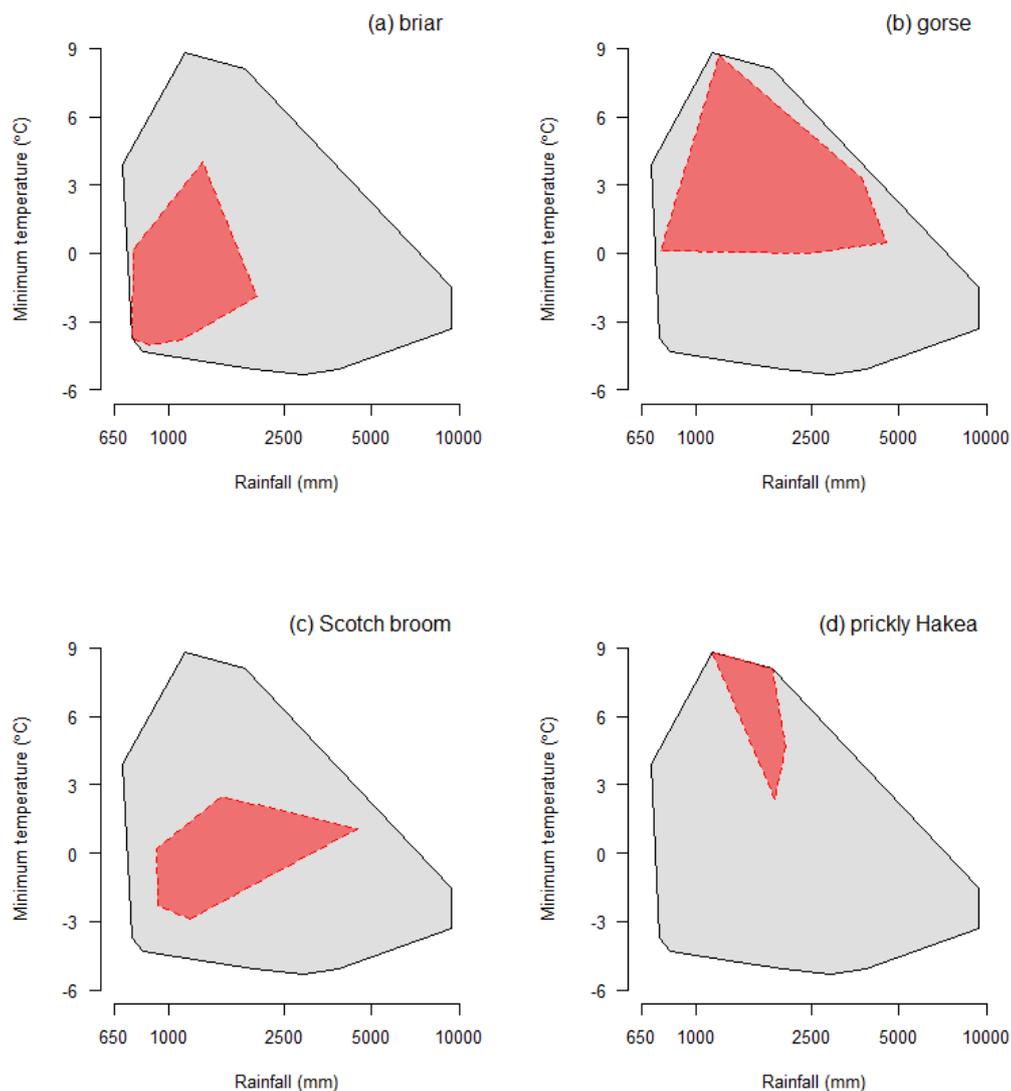


Figure 12 Relationship between occurrence of (a) briar (*Rosa rubiginosa*), (b) gorse (*Ulex europaeus*), (c) Scotch broom (*Cytisus scoparius*), and (d) prickly hakea (*Hakea sericea*) and total annual rainfall and minimum temperature. The grey zone represents the envelope within which all 919 sample plots occur, and the red zone represents the envelope within which each individual species was present.

Discussion

All four of these widespread invasive species invade low stature ecosystems most frequently. This is consistent with their ecology; both of the legume shrubs, gorse and Scotch broom, typically invade open vegetation from old fields (Partridge 1992; Wilson 1994), to braided rivers (Williams 1981; Drake 2011), and open coastal habitats, including dunes (Sykes & Wilson 1991).

The more frequent presence of prickly hakea in low-altitude, moderate rainfall, more northerly sites is to be expected due to its warm temperate native range in south-eastern

Australia and its invasive ranges elsewhere, for example, in South Africa (Richardson et al. 1987). Gorse was also more frequently present in low-altitude, more northern sites across the plots on public conservation land, yet it is widely distributed throughout all latitudes of New Zealand, including throughout the South Island (Bascand & Jowett 1982), covering 3.5% of New Zealand's land area (Rees & Hill 2001). Its coincidence close to plots at more northern latitudes may reflect greater fragmentation of natural ecosystems at more northern latitudes, and proximity of seed sources; for example, gorse was more likely to be present at sites close to roads (it was originally planted as hedges, including along roads) and close to non-native forests. Non-native conifer plantations were shown to be frequent sources of gorse and other woody non-native species invasions at the edges of adjacent natural forests (Sullivan et al. 2006). Equivalent plot-based data from outside public conservation land would enhance the ability to predict the sites most frequently invaded. Similarly, improved evaluation of past human habitat modification (even at fine scales, such as former logging roads close to plots, and improved fire history) could result in improved predictions of sites that could be subject to ongoing invasion by these widespread woody species.

Climate change models that predict warming of minimum temperatures by up to 2 °C (McGlone et al. 2010) are likely to increase the range of habitats that are invasible by prickly hakea, which is currently confined to northern, warm temperate climates (Fig. 12d). Conversely, the cool temperate range occupied by briar (Fig. 12a) may be constrained, although its current occupancy of these sites may render it competitive in the face of new invasive woody plants (non-native and native), even as temperatures warm (Sato et al. 2007). However, in some sites within its cool temperate range, briar is being overtopped by taller non-native woody species, such as sycamore (*Acer pseudoplatanus*) and hawthorn (Williams 2011), that are from similar cool temperate native ranges, and it may not persist if it is shaded. The coincidence of declining rainfall in the regions of New Zealand that already have low rainfall, and increased likelihood of fire (both natural and human-caused) is also likely to favour some of these species: all but briar are pyrogenic and benefit from fire by resprouting and recruiting from seed. Therefore, climate change is likely to result in consolidation and probable spread of these species from current points of invasion, unless they are subject to control now.

3 Where are the areas under greatest pressure from non-native species on public conservation land?

Distribution and abundance of exotic weeds and animals pests considered a threat – Weeds and Pests (Measure 2.2.1)

Definition

This measure assesses the presence and abundance of non-native vascular plant species on New Zealand's public conservation land at the national scale. Non-native plant invasion is measured as the number of non-native vascular plant species, the percentage of vascular plant species that are non-native at each location, and the frequency of occurrence of 47 selected species classified as weeds of concern by DOC (Allen et al. 2013a). The measure also assesses the distribution and abundance of pest mammals: wild ungulates (feral goats *Capra hircus*, and seven deer taxa, Family Cervidae), lagormorphs (brown hares *Lepus europaeus* and European rabbits *Oryctolagus cuniculus*), and brushtail possums (*Trichosurus vulpecula*), on New Zealand's public conservation lands at a national scale. It measures occupancy (percentage of sampling locations occupied) and relative abundance of pest mammals. (Methods are described in Appendix 1.1)

Demography of widespread animal species – Birds (Measure 5.1.2)

Definition

This measure assesses the status of communities of widespread and common bird species on New Zealand's public conservation land at a national scale. It measures bird species richness (the number of species present), occupancy (the percentage of sampling locations occupied by a given species) and density (the number of individuals of a given species within a hectare). It also considers bird species grouped according to their origin (endemic, native or introduced) or their threat status (threatened, at risk, not threatened; Robertson et al. 2013), with native and endemic species pooled in relation to threat status.

3.1 An index of pressure on public conservation land

Key results for aggregated index of pressure on public conservation land.

- Sampling locations with high pressure and low pressure were distributed throughout New Zealand.
- Areas of highest pressure occurred in the largely deforested inland Marlborough region.
- Areas of lowest pressure were in northern Westland and Fiordland
- Indices of pressure were generally higher when:
 - rainfall was low or the vegetation was of low stature
 - sampling locations were closer to non-native forests, roads or the public conservation land boundary
 - sampling locations were not in National Parks.

An aggregated *index of pressure* was constructed to partly inform on the indigenous dominance component of ecological integrity (full methods are described in Appendix 1)¹. Seven attributes were selected to be aggregated into an index of pressure for each sampling location: (1) percent of plant species that are non-native, (2) percentage of foliar cover from non-native plant species, (3) ungulate faecal pellet indices (FPI), (4) lagomorph FPI, (5) possum trap-catch indices (TCI), (6) percentage of bird species that are non-native and (7) percentage of individual birds counted that are non-native. These attributes are based on the relationship between non-native mammals, native vegetation, and weeds and birds measured as part of Tier1 monitoring (Fig. 13).

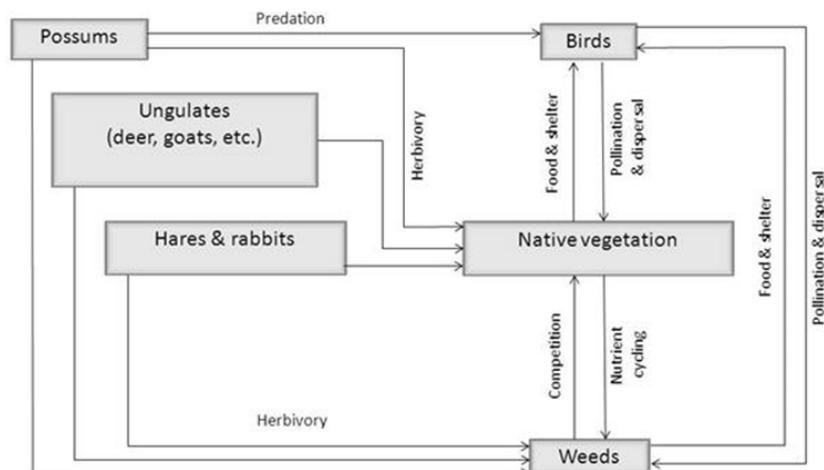


Figure 13 Relationship between non-native mammals, native vegetation, weeds and birds that are measured as part of Tier 1 sampling (adapted from Marburg and Allen 2010).

¹ The methodology for combining attributes is relatively new and is an ongoing area of research. Furthermore, this is the first time we have implemented this approach. Therefore, we expect that construction of the pressure index will likely require further refinement, research and development.

The index of pressure is a value between 0 and 1, where sampling locations with a value of 0 have very low pressure while those with a value of 1 have very high pressure. Of the 534 Tier 1 sampling locations that have had data collected for all seven attributes, the estimated pressure index values ranged from 0.02 to 0.85, with a mean of 0.3 (Fig. 14).

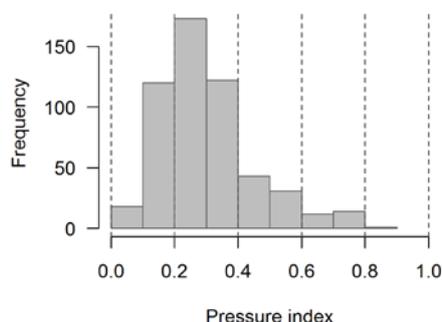


Figure 14 Distribution of the predicted pressure index for 534 sampling locations. The dashed vertical lines are breakpoints that match the breaks in the map shown in Figure 3.

Pressure index values tended to be higher (Table 5) when:

- mean annual rainfall was low
- the vegetation was of low stature
- distance to non-native forests was small
- locations were not in National Parks
- locations were closer to the public conservation land boundary
- locations were closer to the nearest road
- locations were further north

There was no evidence of a relationship between pressure index values and elevation nor minimum temperature.

Table 5 Summary of models explaining the pressure index scores to the direction of the relationship for models fitted with just the one explanatory variable (– for negative, + for positive and NS for relationships with no support; details of analyses in Appendix 1).

Predictor	Direction of relationship	Strength of evidence
Moisture (total rainfall)	–	Very strong
Mean top height	–	Very strong
Distance to non-native forests	–	Very strong
National Park	–	Very strong
Distance to Public Conservation Land	–	Very strong
Distance to nearest road	–	Very strong
Latitude	+	Moderate
Minimum Temperature	NA	None
Altitude	NA	None

The spatial distribution of pressure index indicates some clusters of low and high values. Sampling locations in the inland Marlborough region were generally high whereas sampling locations in the western part of Fiordland and northern Westland were low (Fig. 15). Some of this spatial distribution can be partly accounted for by the environmental covariates above. However, after fitting a model with all nine covariates to account for as much variation as possible, some residual clustering remains (Fig. 16). This may indicate one or more unknown environmental factors were influencing pressure but were not included in the model.

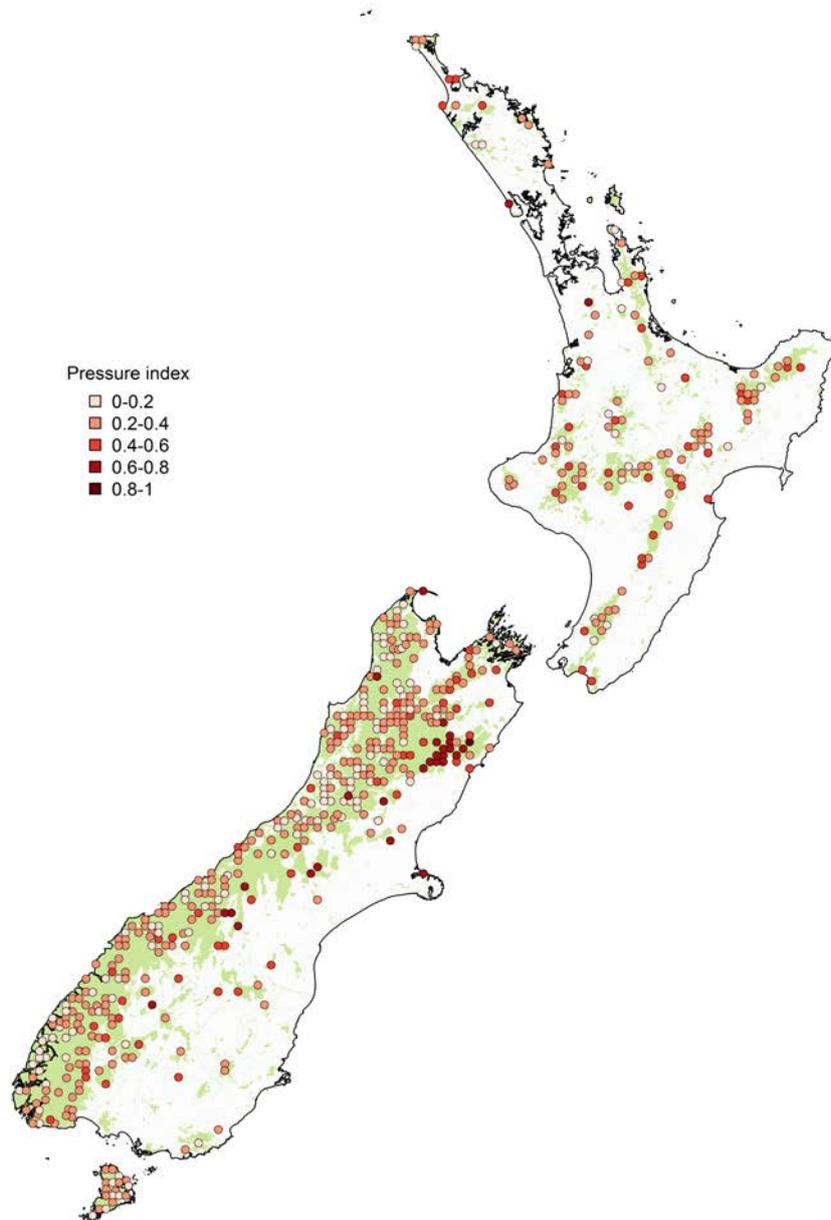


Figure 15 Spatial distribution of pressure index values for each of 534 sampling locations where information for all seven attributes is available. The green shaded area is public conservation land.

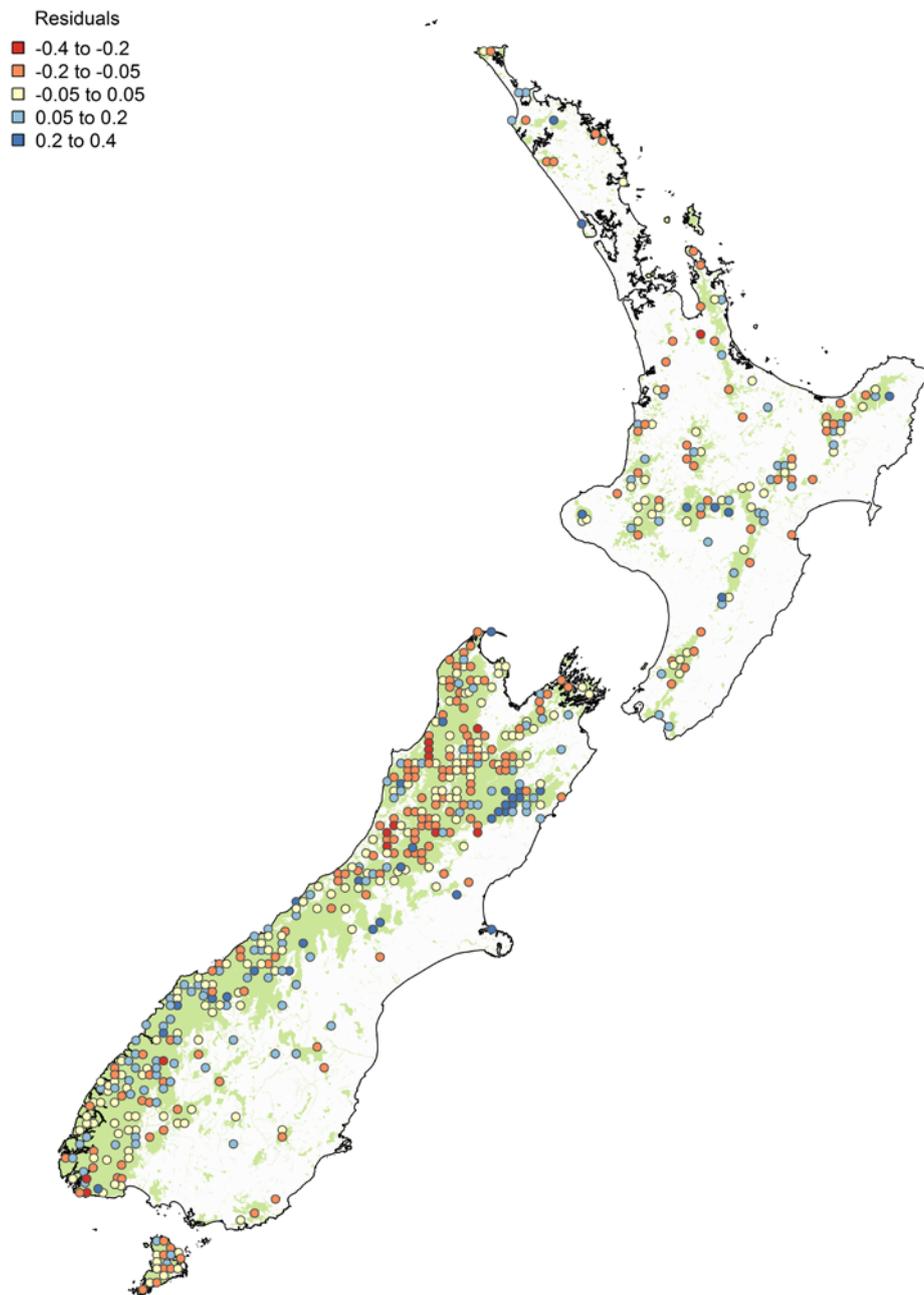


Figure 16 Spatial distribution of residuals for all 534 sampling locations where information for all seven attributes is available after fitting a model with all nine environmental variables.

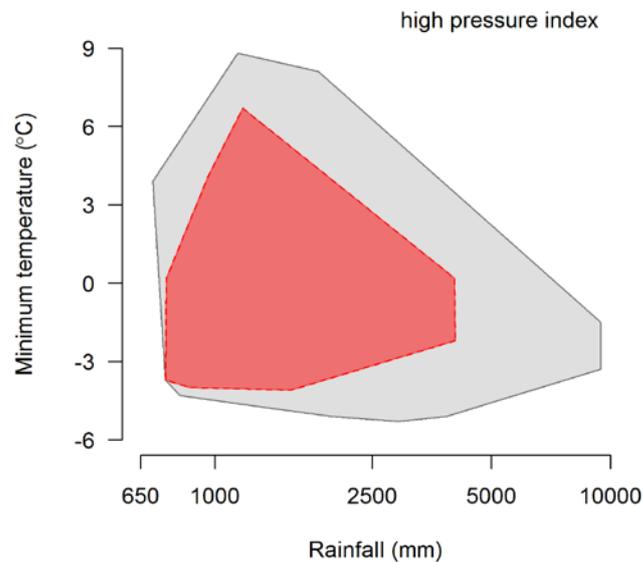


Figure 17 Relationship between the sampling location with a value >0.6 and total annual rainfall and minimum temperature. The grey zone represents the envelope within which all 919 sample plots occur, and the red zone represents the envelope within which the 28 sampling locations with a pressure index of >0.6 occur.

Discussion

An aggregated pressure index

The aggregated pressure index is an indicator of the potential loss of indigenous dominance. The pressure index presented here is the first in a series of indices that are needed to develop a view of ecological integrity across public conservation land. There is a need for a complementary index that addresses indigenous dominance directly. To build a more comprehensive view of ecological integrity, complementary indices are also needed for native species occupancy. This is necessary to identify areas that are important for native biodiversity that are under pressure from non-native species but which are also important areas for native biodiversity can be identified and, where so that appropriate remedial action can be taken. It would be wrong to use the pressure index alone as a means of allocating resources, without, for example, information about species occupancy. The two following examples illustrate why. In largely-deforested inland Marlborough there are distinct concentrations of high pressure indices, which are consistent with the general pattern of greatest cumulative pressure from introduced mammals, non-native plants, and non-native birds in drier regions with short-stature vegetation. Inland Marlborough is also a region of high endemism in the flora (Burrows 1965; McGlone et al. 2001); for example, it has one of the highest levels of endemism in the New Zealand grass flora (Connor 2002), and is also an important area of richness for some lichens (Heads 1997). Seen in these terms, remedial action to relieve the high pressure exerted in this region could be a priority for management. Conversely, north Westland, including Papatōia National Park, is a region of generally low

pressure and is a major region of native species richness in caddisflies (Trichoptera) and some stoneflies (Notonemouridae, Plecoptera; Heads 1997). Seen in these terms, maintaining the current low pressure exerted in this region could be a priority for management.

The pressure index presented here is not a comprehensive assessment of pressures on points at a national scale. The scale of assessment, in space and time, is not amenable for the collection of data on some key pressures that vary rapidly during and between seasons, as well as inter-annually and which are known to affect some components of biodiversity severely. These pressures include rodents and mustelids that prey upon native birds (Innes et al. 2010), and non-native social wasps that prey upon a range of native invertebrates (Beggs & Wardle 2006). These pressures will be assessed in managed sites in the future (DOC's Biodiversity Monitoring and Reporting System's Tier Two plots) at appropriate temporal and spatial scales, and will add to understanding of cumulative pressures that affect ecological integrity.

The ultimate value of the pressure index (and associated indices related to ecological integrity) will be in the change in the index with time. This is comparable with other aggregated indices used to assess economic performance (e.g., consumer price index; NZX 50 index) or human welfare (e.g., New Zealand deprivation index; Salmond et al. 2007), in which trends, rather than current values, have greatest relevance. Like these aggregated indices, the pressure index presented here has no identifiable threshold values that can be assigned to particular plots or regions, and both plots and regions require further interpretation to ascertain the reasons for their scores.

Calculation of an aggregated index: Point of Truth Calibration

The Point of Truth Calibration (PoTCal) approach requires only a single elicitation of each sampling location used for constructing the *expert emulator* (Appendix 2). This feature makes it direct and relatively quick to score. Furthermore, by engaging with multiple experts from a range of backgrounds, the final metric is inherently inclusive and consultative (Sinclair et al. 2015). However, this does not mean that all experts agree with the modelled pressure index values: the PoTCal approach models the central tendency of the expert opinions and some experts differ markedly in their assessment of some sampling locations.

The finding that the predicted scores were all below 0.85 reflects the fact that the calibration site with very high attribute values that was given to each expert to train the model (see Appendix 2) had attribute values that have not been (or are unlikely to be) encountered in one location in the field. We anticipate that that the model will therefore be able to deal with the full range of sampling locations that will be encountered in future sampling years.

The *expert emulator* can be used to 'score' all future sampling locations. Furthermore, any future modification/recalibration of the expert model can be used to derive an improved random forest model that can easily be used to back-calculate the pressure index values from sampling locations that have already been measured.

Other expert-scoring methods are available and in use in many situations. However, these are often based on point-scoring approaches where experts are asked to convert the individual measured attribute values (e.g. Trap-Catch-Index, Weed Cover) into point-scores; the point scores across all attributes are then assigned weights and combined (summed) to generate a

final score. These approaches have been severely criticised (Hubbard 2009) as they are very sensitive to the choice of threshold values used to convert attributes into points and particularly to the relative weights of the attributes. The PoTCal approach has a number of advantages over those methods, including needing only a single score to be elicited from each expert for each sampling location, allowing experts to apply all of their knowledge about the location, incorporating variation among experts, and avoiding the need for experts having to consider complex interactions and non-linear relationships (Barry & Lin, 2010)

National variation in the pressure index across public conservation land

There are clear reasons for disproportionate pressure in some plots. Those plots that are close to roads, the edge of public conservation land, and non-native forests have greater likelihood of invasion (e.g., by non-native plants, including environmental weeds; Sullivan et al. 2009). This is reflected in the diminishing pressure indices the further a plot is from these sites. Some edges of public conservation land adjoin not only non-native forests (including conifer plantations) but also pastoral farming or other grasslands where deer and ungulates may forage preferentially, using adjacent forest mainly for shelter (e.g., Forsyth et al. 2010). A recent study has shown that fertilising pastures adjoining public conservation land boosts rabbit abundance in the pastures, and their increased populations in turn “spill over” into largely native grasslands and shrublands in public conservation land (Norbury et al. 2013). Better quantification of the surrounding matrix of land uses around public conservation land, especially where it is most fragmented (much of the North Island and the eastern South Island, Fig. 3), is likely to yield better predictive capability about pressure on public conservation land. For example, the extent of invasion by non-native plant species in fragmented habitats mostly dominated by native plants was strongly related to the surrounding matrix (Wiser & Buxton 2008), and the same is also apparent in braided river beds (Williams & Wiser 2004).

There are greater numbers of native bird species wherever public conservation land is forested, whereas non-forested sites sometimes have greater numbers of non-native birds (Bellingham et al. 2013), and forested regions are generally not invaded by woody non-native plants (section 2.1). Similarly, hares and rabbits seldom occur in forests on public conservation land (Bellingham et al. 2013). Therefore, it is unsurprising that pressure index increased with decreasing vegetation stature, since it comprises attributes of non-native bird and plant dominance, and abundance of hares and rabbits. Since New Zealand’s remaining natural forests are also generally in regions with high rainfall (Wardle 1991), it is likewise to be expected that pressure indices are least in the forested regions with the greatest rainfall, for example, public conservation land throughout the western South Island (Fig. 3). Against that, other attributes that comprise the index are typically greater in natural forests, for example, the frequency and abundance of possums (Bellingham et al. 2013). Possums are abundant in many forests in the western South Island (e.g., Coleman et al. 1980), which is probably one reason that some level of pressure is still apparent, although pressure indices there are low (Fig. 3).

Determining the factors that are linked to greater pressure indices in some plots could be further improved. Past human disturbance (e.g., formation of old logging roads, localised clearance of forest and subsequent succession) is related to some of the attributes that contribute to the pressure index (e.g. increased likelihood of invasion by non-native plants), but its relationship with other attributes is unknown. The effect of historical disturbance is

important in some areas and may explain the observed clustering of residuals. Improved means of quantifying this disturbance could be used in future (e.g., as it has been used as a means of predicting national carbon stocks in forests and shrublands; Mason et al. 2012). Disturbance (natural or human-caused) can result in successional communities in which plants consumed preferentially by deer and goats are most abundant (Mason et al. 2010) and in which the effects of deer and goats, as well as of possums, in reducing palatable plants can be most pronounced, even causing localised elimination of some palatable species (Smale et al. 1995; Bellingham & Lee 2006).

The carrying capacity and abundances of the introduced herbivorous mammals (that contribute to the pressure index) is variable across public conservation land. They will be determined by climatic drivers (temperature and rainfall), soil fertility at fine and broad scales (e.g., Forsyth et al. 2015), and interactions with topographic variation (e.g., the preference of goats for north-facing sunny aspects; Parkes 2005, and the relative abundance of red deer (*Cervus elaphus scoticus*) vs. rusa deer (*Cervus timorensis*), determined by availability of sunny sites; Allen et al. 2015).

Drivers of the composition of bird communities, and of non-native bird presence and abundance require more investigation. Although native bird species outnumber non-native bird species in forests (but not always in non-forested areas of public conservation land), the reasons for this are not always clear. It is clear that the pressure of predation by some introduced carnivorous mammals is a strong driver persistence of populations of some native bird species (Innes et al. 2010). In the most extreme cases, any predation pressure, other than by kiore (*Rattus exulans*), is too great (e.g., for both tieke species, *Philesturnus* spp.; Worthy & Holdaway 2002). Other native bird species, including kākā (*Nestor meridionalis*; Moorhouse et al. 2003; Innes et al. 2010), can coexist with some introduced mammalian predators (e.g., ship rats *Rattus rattus* and Norway rats *Rattus norvegicus*) but not others (e.g., mustelids and possums). Maps of presence and absence of rodents and mustelids have some predictive value (e.g., mustelids are absent from Aotea and Rakiura), but are otherwise coarse predictors. The derivation of the pressure index presented did not include measures of rodent and mustelid occupancy or abundance. However, it does measure abundance of possums, which are predators, at least on some of the larger species such as kākā, kererū (*Hemiphaga novaeseelandiae*) and North Island kōkako (*Callaeas wilsoni*). Competition for resources between native and non-native birds has been little investigated; Kearvell et al. (2002) suggested that native kākārīki species (*Cyanoramphus* spp.) may compete with non-native finch species for seeds in beech forests, but direct evidence is lacking. We are unaware of any research in New Zealand that has investigated links between the composition and abundance of bird communities and drivers of the resource base on which birds (either as herbivores or predators) depend, namely, climatic drivers (temperature and rainfall), soil fertility, and topographic variation. Climate may limit some species directly (e.g., ruru, *Ninox novaeseelandiae*, can be limited by cold winter temperatures; Greene et al. 2013). Along a transition from forest to non-forest, there is evidence that several non-native bird species can be present in secondary forest resulting from past disturbances, but that fewer species occur in old-growth native forests, especially where the native bird community is species rich (Kikkawa 1964; McCallum 1982). At a national scale, non-native bird species richness declined as forest structure increased towards old-growth stands (Bellingham et al. 2014). Other links between bird communities and habitat structure and quality (including the contribution of dead wood; Richardson et al. 2009, and the resources available to nectivores; Innes et al. 2010) remain to be explored.

Most components of the pressure index are subject to management by DOC in at least some areas of public conservation land, for example, widespread control of possums, localised control of goats, and localised control of some non-native plant species (especially some of the 328 species that are designated as environmental weeds; Howell 2008). These could be reasons that pressure indices at local scales in some plots could be lower than expected in sites that might otherwise be expected to be invaded (e.g., short-stature vegetation close to roads). On the other hand, other components of the pressure index are seldom subject to management. Some widespread environmental weeds, such as the grasses browntop (*Agrostis capillaris*) and cocksfoot (*Dactylis glomerata*; Howell 2008), are not subject to control over most of their ranges across public conservation land. Non-native birds are seldom subject to control on public conservation land; the few species that are controlled occur most frequently on other than public conservation land (e.g., rook, *Corvus frugilegus*; Porter et al. 2008; Canada goose, *Branta canadensis*; Spurr & Coleman 2005). Intensification of control efforts at some of the sample plots could result in reduction of the pressure index at that plot; conversely, reduction in control efforts elsewhere could see increases in the pressure indices of other plots.

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Appendix 1 – Appendix material related to the distribution and abundance of woody non-native plant species on public conservation land

Appendix 1.1 Methods used to evaluate Measure 2.2.1 Distribution and abundance of exotic weeds and animal pests considered a threat – Weeds

Field data collection

Field surveys were undertaken using a regular sampling framework across New Zealand's public conservation land. This framework builds upon a national infrastructure established to measure carbon, vegetation structure and composition – the Land Use Carbon Accounting System (LUCAS; MfE 2014) network of permanently marked 20 × 20 m plots (0.04 ha) in native forests and shrublands. These were established at regular sampling points on an 8-km grid superimposed upon areas designated as native forests or shrublands in the Landcover Database (LCDB1). A subset of 180 of the sampling points used existing permanent 20 × 20 m plots within the National Vegetation Survey databank (Wiser et al. 2001), most of which were established in the 1970s and 1980s. These plots were used in lieu of establishing a new sample plot if the closest existing plot was within a 2-km radius from the 8-km grid point (Peltzer et al. 2014). The LUCAS vegetation plots were measured between 2001 and 2006, and remeasured between 2009 and 2014. DOC's Tier One component of its Biodiversity Monitoring and Reporting System employs the same plots from this network that are in native forests and shrublands on public conservation land, and extends the 8-km grid to establish additional permanent 20 × 20 m plots in vegetation across all public conservation land. There are more than 1311 possible sampling points on public conservation land (covering North, South and Stewart Islands). Each of DOC's Tier One sample points has a permanent 20 × 20 m plot at its centre, from which all data used to evaluate Measure 2.2.1 were collected. Data used to inform other measures, i.e., on mammal pests and common birds, are collected within a much larger area (331 × 331 m; 10.96 ha), using a design that radiates out from the edges of the central 20 × 20 m vegetation plot (Fig. S1; Allen et al. 2013). We evaluated data for Measure 2.2.1 collected between 2009 and 2014 from 919 vegetation plots across all public conservation land.

The cover of each vascular species that occurred within each 20 × 20 m vegetation plot was assessed and recorded in cover classes (<1%, 2–5%, 6–25%, 26–50%, 51–75%, 76–100% cover of a 400 m² plot; Hurst & Allen 2007) within each vertical height tier in which its foliage occurred (tiers are <0.3 m, 0.3–2 m, 2–5 m, 5–12 m, 12–25 m, >25 m). The presence of each vascular species that occurred as an epiphyte was recorded.

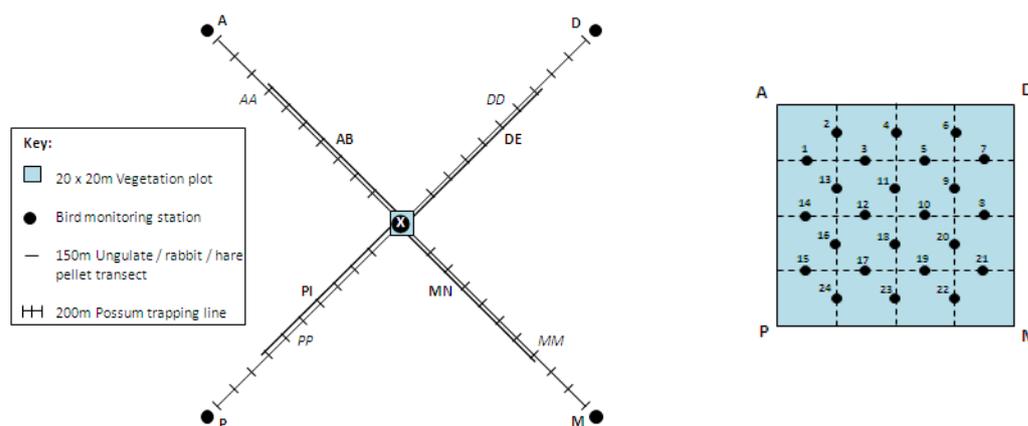


Figure S1 Layout of the animal-survey sampling units in relation to the vegetation plot at each sampling location, along with an outline of the 20×20 m vegetation plot and each of the 24 (0.75 m²) seedling subplots within it.

Assigning biostatus

The biostatus (native vs. non-native) of all vascular species in all plots was assessed as according to Ngā Tipu o Aotearoa (<http://nzflora.landcareresearch.co.nz/>), seeking further advice from experts if in doubt. We used preferred names at the species-level of Ngā Tipu o Aotearoa, i.e., we did not consider distinctions at the subspecies or variety level to their species-level equivalent but do consider most hybrids as distinct taxon concepts. We determined those non-native plant species that are woody according to their assignment in the National Vegetation Survey databank (<https://nvs.landcareresearch.co.nz/>) as “Tree” and “Shrub” growth forms, i.e., we do not include some woody lianas (e.g., old man’s beard, *Clematis vitalba*, and kiwifruit, *Actinidia deliciosa*), which are aggregated with herbaceous non-native species, for the purposes of this report.

Data analysis: general approach

We analysed variation in the presence/absence data for all woody non-native species combined, all wilding conifer species combined, and five widespread individual species (briar, gorse, Scotch broom, prickly hakea, and lodgepole pine). In the case of all woody non-native plant species, we also analysed variation in the percentage of total cover contributed by woody non-native plants (% cover) where they were present. Total cover and cover of woody non-native plant species were calculated as the sum of the midpoints across all tiers (see above).

Our decision to model the presence/absence data separately from the percentage of total cover data was a practical solution to overcome the challenge of zero-inflated continuous data. The data for each species is a single response variable (i.e., percentage cover). This variable contains many values of zero where the species is absent, and a small number of non-zero values that follow a gamma distribution (i.e., they are all positive, continuous and strongly left-skewed with a few high values). The percentage cover data thus reflect two

distinct ecological processes. Presence indicates that a species has successfully dispersed to and established at a site. Non-zero abundance data estimate the performance of that species at a site once it is present. Hurdle models are used for such data as these acknowledge the two stages of a process that are reflected in the data. There are no readily available analysis packages that can model both processes simultaneously as a gamma hurdle model, and best practice is to split the data into two separate analyses. The first analysis models the presence or absence of the observed response variable (i.e. the presence or absence of a species) using a binomial (logistic) model with a logit link. The second analysis models the continuous non-zero data values (i.e. % cover of woody weeds where they were present), using a gamma distribution with a log link.

We modelled variation in the percentage cover where present for all woody non-native plant species combined only, because there were too few presences (<25) in the other species.

Variation in woody non-native plants was modelled in relation to mean canopy top height (m), distance to nearest non-native forest (km); whether or not a plot was in a National Park; distance to the nearest boundary of PCL (km); distance to the nearest road (km); latitude (decimal degrees); minimum temperature (°C); elevation (m); and mean annual total rainfall (mm). Non-native forest was designated using two LCDB4 land cover classes, Deciduous Hardwoods and Exotic Forest. Deciduous Hardwoods are defined as: ‘exotic deciduous woodlands, predominantly of willows or poplars but also of oak, elm, ash or other species. Commonly alongside inland water (or as part of wetlands), or as erosion-control, shelter and amenity plantings’. Exotic Forest is defined as: ‘Planted or naturalised forest predominantly of radiata pine but including other pine species, Douglas fir, cypress, larch, acacia and eucalypts. Production forestry is the main land use in this class with minor areas devoted to mass-movement erosion-control and other areas of naturalised (wilding) establishment’.

Full vegetation data (i.e., relevé, stems, saplings and seedlings) and predictor variable data were available from 919 plots.

We tested how well each of the nine variables accounted for variation in the presence or abundance of each species or species group. For each species (or species group) we ran ten models, one for each predictor and a null (intercept-only) model. Our goal was to assess the strength of support for each predictor relative to the null model. This was achieved by calculating the difference in AICc between the null model and each fitted model (**called ‘delta AICc Null’**). Models with a delta AICc Null >-2 are equivalent to the null model and have no support; models with a delta AICc Null of -2 to -4 have weak support; models with a delta AICc Null of -4 to -7 have moderate support; models with a delta AICc Null of -7 to -10 have strong support; and models with a delta AICc Null of -10 or more have very strong support.

Data analysis: National Parks

We ran two models to test whether the presence or abundance of woody non-native plants differed between National Parks and other PCL while accounting for environmental covariation. The first used only four environmental predictors (rainfall, minimum temperature, latitude and elevation) to model variation. The second model used the four environmental predictors and National Park to model variation. These two models were compared using AICc to determine whether inclusion of National Park as a predictor

increased the support for the model. This approach tests whether the National Park variable contains additional information that accounts for variation in the presence or cover of the weed, above and beyond environment. We did not include distance to road, mean top height, distance to non-native forest or distance to PCL in these models because we did not consider these to be environmental variation. Mean top height is an attribute of the vegetation (and in many instances, a product of the environmental variation). Distances to various human constructs are not environmental variation, but are often part of the reason that land has been designated as National Park. Hence their inclusion seemed circular.

Data analysis: non-native pest animals and herbaceous non-native plant species

Variation in the presence and abundance of all woody non-native plants was also modelled in relation to the presence and abundance of three groups of non-native pest mammals (possums, ungulates and lagomorphs). We used the same model framework as for environmental predictors (i.e. a binomial model for the presence of woody non-native plants, and a gamma model for the abundance of woody non-native plants). Variation in the presence and abundance (cover, stem density and basal area) of all woody non-native plants was modelled in relation to the presence and abundance (cover) of herbaceous non-native plant species. As for non-native pest mammals, we used binomial models for predicting the presence of woody non-native plants, and gamma models for the abundance of woody non-native plants. Where the cover of herbaceous non-native plants was used a predictor, we log-transformed the data while preserving zeros. The basal area, stem density and cover of woody non-native plants were all log-transformed for analyses.

Comparisons with other distributional data for individual species:

1. Lodgepole pine (*Pinus contorta*): The map of current distribution is based on the 2007 distributions generated as part of DOC's Biodiversity Data Inventory. The 2007 extents were extended in 2015, limited to areas of previous or current non-native forest (based on LCDB4 and previous iterations) within 1km of three point datasets: DOC/LUCAS Tier 1 plots (good spatial accuracy), MPI inventory of wilding conifer sites (coarser spatial accuracy), and DOC's Bioweb database (from which some of the original 2007 data was derived), all further checked against DOC's operational activities (wilding control) (data provided by Richard Earl, DOC, Christchurch).
2. Briar (*Rosa rubiginosa*), gorse (*Ulex europaeus*), and Scotch broom (*Cytisus scoparius*): Maps are distributions of presence and absence within 10km square grid (data collated by Clayton Howell, DOC, Wellington).

Appendix 1.2 Is there spatial correlation in the residual variation from models predicting the presence and abundance of all non-native woody plant species?

The 8-km grid was designed such that each sample point would be spatially independent from all other points. However, in reality, landscapes share features at scales of many hundreds of kilometres and because of this, sample points that are close to each other are likely to be more similar to each other than distant sample points, *even after accounting for the similarity in environments between sample points.*

We investigated whether there was evidence for spatially correlated variance in the residuals from the models fitted in Table 1 (shown in detail in Tables S1 and S2). For the presence of woody non-native plants, we fitted a full model using all nine predictors to account for as much variation in the dependent variable as possible (a ‘full environment model’). The residuals from this model were used to determine whether there was spatial correlation among sample points not accounted for by our predictor variables.

We first fitted an intercept-only model to these residuals using *gls* and plotted a variogram of the fitted values using the easting and northing for each sample point. A variogram displays the variance between any two sample points relative to the distance between those sample points. Points close together typically have lower variance and variance typically increases with distance up to a distance beyond which variance no longer increases. We used our variogram to estimate two parameters. The first was the ‘range’, which is the distance at which variance among samples no longer continues to increase. The second parameter was the ‘nugget’, which is the estimated variance at a distance of 0. We estimated the range to be 100 km and the nugget to be 0.7. These parameters were used to specify a covariance structure that was added to the intercept-only *gls* model using a spherical spatial correlation structure (*corSpher()*). We compared the AIC between the *gls* model with and without this spatial correlation structure to evaluate whether inclusion of explicit spatial structure substantially improved the model fit. The AIC of the first model was 1644 and the AIC of the model with spatial structure was 1596 (fitted value of range was 109 km and nugget was 0.82), suggesting that plots within c. 100 km of each other share variance that is not explained by the nine predictors.

We repeated this procedure for the abundance of woody non-native plants. The AIC of the first model was 150 and the AIC of the model with spatial structure was 128 (fitted value of range was 75 km and nugget was 0.01), suggesting that plots within 75 km of each other share variance that is not explained by the nine predictors..

Appendix 1.3 Detailed results

Table S1 Summary of statistical models predicting the presence of woody weeds (all species) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
Rainfall	2	-0.002	-218.4	440.8	-90.43	V strong	1.00
MeanTopHeight	2	-0.171	-225.3	454.6	-76.56	V strong	0.00
DistNonNativeForest	2	-0.195	-232.9	469.7	-61.46	V strong	0.00
NationalPark	2	-1.838	-250.1	504.3	-26.94	V strong	0.00
DistRoad	2	-0.115	-250.3	504.7	-26.54	V strong	0.00
DistPCLEdge	2	-0.225	-252.8	509.6	-21.56	V strong	0.00
Latitude	2	0.172	-256.3	516.7	-14.54	V strong	0.00
MinTemp	2	0.118	-261.1	526.3	-4.95	Moderate	0.00
Elevation	2	-0.001	-262.8	529.7	-1.54	No support	0.00
NULL	1	–	-264.6	531.2	0.00	–	0.00

Table S2 Summary of statistical models predicting the abundance of woody weeds (all species) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
Rainfall	2	0.000	-144.9	295.9	-4.70	Moderate	0.63
MeanTopHeight	2	-0.024	-146.8	299.6	-0.98	No support	0.10
NULL	1	–	-148.3	300.6	0.00	–	0.06
DistRoad	2	0.017	-147.4	300.8	0.19	No support	0.05
DistPCLEdge	2	0.021	-147.9	301.9	1.27	No support	0.03
Latitude	2	0.015	-148.0	301.9	1.32	No support	0.03
DistNonNativeForest	2	-0.013	-148.0	301.9	1.33	No support	0.03
Elevation	2	0.000	-148.2	302.4	1.75	No support	0.02
MinTemp	2	0.006	-148.2	302.5	1.85	No support	0.02
NationalPark	2	-0.024	-148.3	302.6	1.99	No support	0.02

Table S3 Summary of statistical models predicting the presence of wilding conifers (all species) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
DistNonNativeForest	2	-0.880	-63.26	130.5	-40.81	V strong	1.00
Rainfall	2	-0.001	-76.09	156.2	-15.16	V strong	0.00
NationalPark	2	-16.996	-77.93	159.9	-11.47	V strong	0.00
MeanTopHeight	2	-0.128	-78.68	161.4	-9.97	Strong	0.00
DistPCLEdge	2	-0.262	-81.52	167.1	-4.30	Moderate	0.00
DistRoad	2	-0.103	-81.84	167.7	-3.66	Weak	0.00
Altitude	2	0.001	-83.17	170.4	-0.99	No support	0.00
NULL	1	–	-84.67	171.4	0.00	–	0.00
Elevation	2	0.092	-84.12	172.2	0.90	No support	0.00
MinTemp	2	-0.098	-84.17	172.4	1.01	No support	0.00

Table S4 Summary of statistical models predicting the presence of *Pinus contorta* (lodgepole pine) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
Elevation	2	0.003	-37.04	78.1	-15.74	V strong	0.52
MinTemp	2	-0.792	-37.51	79.0	-14.80	V strong	0.32
DistNonNativeForest	2	-0.520	-38.76	81.5	-12.30	V strong	0.09
MeanTopHeight	2	-0.255	-39.16	82.3	-11.51	V strong	0.06
NationalPark	2	-17.227	-42.76	89.5	-4.30	Moderate	0.00
Rainfall	2	-0.001	-43.10	90.2	-3.63	Weak	0.00
NULL	1	–	-45.92	93.8	0.00	–	0.00
DistPCLEdge	2	-0.054	-45.77	95.5	1.71	No support	0.00
DistRoad	2	-0.020	-45.78	95.6	1.74	No support	0.00
Latitude	2	-0.037	-45.88	95.8	1.93	No support	0.00

Table S5 Summary of statistical models predicting the presence of *Rosa rubiginosa* (briar) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
Rainfall	2	-0.005	-59.64	123.3	-86.39	V strong	1.00
MeanTopHeight	2	-0.392	-77.79	159.6	-50.10	V strong	0.00
MinTemp	2	-0.425	-94.65	193.3	-16.38	V strong	0.00
NationalPark	2	-17.26	-95.09	194.2	-15.50	V strong	0.00
DistNonNativeForest	2	-0.137	-97.15	198.3	-11.38	V strong	0.00
NULL	1	–	-103.84	209.7	0.00	–	0.00
Latitude	2	-0.113	-102.92	209.9	0.16	No support	0.00
Elevation	2	0.001	-103.05	210.1	0.42	No support	0.00
DistRoad	2	-0.031	-103.12	210.2	0.56	No support	0.00
DistPCLEdge	2	-0.060	-103.36	210.7	1.04	No support	0.00

Table S6 Summary of statistical models predicting the presence of *Ulex europaeus* (gorse) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
Elevation	2	-0.00535	-66.93	137.9	-25.47	V strong	0.50
MinTemp	2	0.46154	-66.95	137.9	-25.43	V strong	0.49
DistRoad	2	-0.35479	-71.84	147.7	-15.66	V strong	0.00
DistPCLEdge	2	-0.76814	-72.37	148.7	-14.60	V strong	0.00
DistNonNativeForest	2	-0.20438	-73.79	151.6	-11.76	V strong	0.00
MeanTopHeight	2	-0.14664	-73.79	151.6	-11.75	V strong	0.00
Latitude	2	0.31645	-74.19	152.4	-10.95	V strong	0.00
Rainfall	2	-0.00045	-78.73	161.5	-1.87	No support	0.00
NULL	1	–	-80.67	163.3	0.00	–	0.00
NationalPark	2	-0.74314	-79.91	163.8	0.48	No support	0.00

Table S7 Summary of statistical models predicting the presence of *Cytisus scoparius* (Scotch broom) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
MeanTopHeight	2	-0.17049	-53.77	111.6	-9.68	Strong	0.54
Rainfall	2	-0.00131	-54.04	112.1	-9.13	Strong	0.41
DistRoad	2	-0.11294	-57.59	119.2	-2.05	Weak	0.01
DistNonNativeForest	2	-0.07815	-57.64	119.3	-1.94	No support	0.01
DistPCLEdge	2	-0.21911	-57.96	119.9	-1.30	No support	0.01
NULL	1	–	-59.61	121.2	0.00	–	0.00
MinTemp	2	-0.16132	-58.78	121.6	0.34	No support	0.00
NationalPark	2	-0.77770	-59.04	122.1	0.87	No support	0.00
Elevation	2	-0.00052	-59.39	122.8	1.56	No support	0.00
Latitude	2	0.00084	-59.61	123.2	2.01	No support	0.00

Table S8 Summary of statistical models predicting the presence of *Hakea sericea* (prickly hakea) from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	delta AICc Null	Support	Weight
MinTemp	2	0.971	-22.92	49.9	-43.98	V strong	0.98
Latitude	2	0.983	-27.04	58.1	-35.73	V strong	0.02
Elevation	2	-0.008	-35.54	75.1	-18.74	V strong	0.00
DistPCLEdge	2	-1.180	-40.29	84.6	-9.25	Strong	0.00
DistRoad	2	-0.436	-40.70	85.4	-8.43	Strong	0.00
Rainfall	2	-0.001	-41.49	87.0	-6.84	Moderate	0.00
DistNonNativeForest	2	-0.242	-41.95	87.9	-5.91	Moderate	0.00
MeanTopHeight	2	-0.146	-42.49	89.0	-4.85	Moderate	0.00
NULL	1	–	-45.92	93.8	0.00	–	0.00
NationalPark	2	-1.220	-45.05	94.1	0.28	No support	0.00

Appendix 1 references

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Appendix 2 – Appendix material related to the areas under greatest pressure from non-native species on public conservation land

An aggregated *index of pressure* was constructed from seven attributes measured as part of Tier 1 monitoring: (1) percent of plant species that are non-native, (2) percentage of foliar cover from non-native plant species, (3) ungulate FPI, (4) lagomorph FPI, (5) possum TCI, (6) percentage of bird species that are non-native and (7) percentage of individual birds counted that are non-native.

An approach called Point of Truth Calibration (PoTCal; Barry & Lin 2010) was used whereby a range of experts score a subset of locations based on the seven attributes. A model is then fit to the expert scores to produce an *expert emulator*, which can be used to estimate a pressure index score for all locations where all seven attributes have been measured/surveyed.

Methods

The detailed methodology is covered in Barry & Lin (2010). In brief, a number of experts were asked to score a subset of sampling locations based on multiple attributes, thereby obtaining a *score* for each plot i from expert j . (Note that not all experts score each site, and not all sites are scored by each expert). This results in a general model of the general form:

$$Score_{ij} \sim \alpha + \beta_1 f(X_{1i}) + \beta_2 f(X_{2i}) + \beta_3 f(X_{3i}) + \dots + \gamma_j + \varepsilon_{ij}$$

Where X_1, X_2 etc are the attributes at each sampling location i , the β values are the coefficients to be estimated for those measured variables, γ_j is a random effect for expert j and ε_{ij} is an overall error term.

Experts scored a subset of sampling locations on a scale from 0 to 100 in steps of 5, where 0 indicated locations with zero pressure and 100 indicated location with maximum pressure. Scores were divided by 100 to obtain values on a 0 to 1 scale.

A variety of methods can be used to estimate the fit the model, including, but not limited to, generalised linear models and decision tree learning. We used a regression tree approach, an advantage of which is that it can easily cope with non-linear relationships between the measured variable and the expert score. Specifically, we used an ensemble regression tree method called random forests (Breiman 2001) implemented with the R package `randomForest` (Liaw & Wiener 2002). This approach alleviates some of the known issues associated with single regression trees that tend to over-fit the data.

The data from 126 locations were used for the model building phase. A total of 40 experts were contacted and each asked to score 16 locations based on seven variables from the Tier 1 data. The sampling locations were balanced so that each was to be scored by five experts. Each expert was given the same two reference sites to assist in calibration among experts: one with very low and one with very high values for all the attributes.

Results

Responses were obtained from 21 experts across 120 sampling locations. There was wide variation among experts in the scores for some sites (Figure S2).

The random forest approach generated a large number of trees, each with their own different scoring rules. For example, for the first tree, there were 72 final nodes. The first node of the first tree would score any locations where WeedProp <66.5 & Lagomorph >32 as a pressure index of 0.78. The second final node would score any locations that satisfy the criteria WeedCover <65.5 & WeedProp >66.5 & Lagomorph >32 as 0.92, etc.

Averaging across all the ‘trees’ in the ‘forest’, final pressure index scores for each location was obtained. The predicted scores from PoTCal fitted the mean expert score fairly well, but slightly under-predict when scores are high and over-predict when scores are low (Figure S2; lower panel).

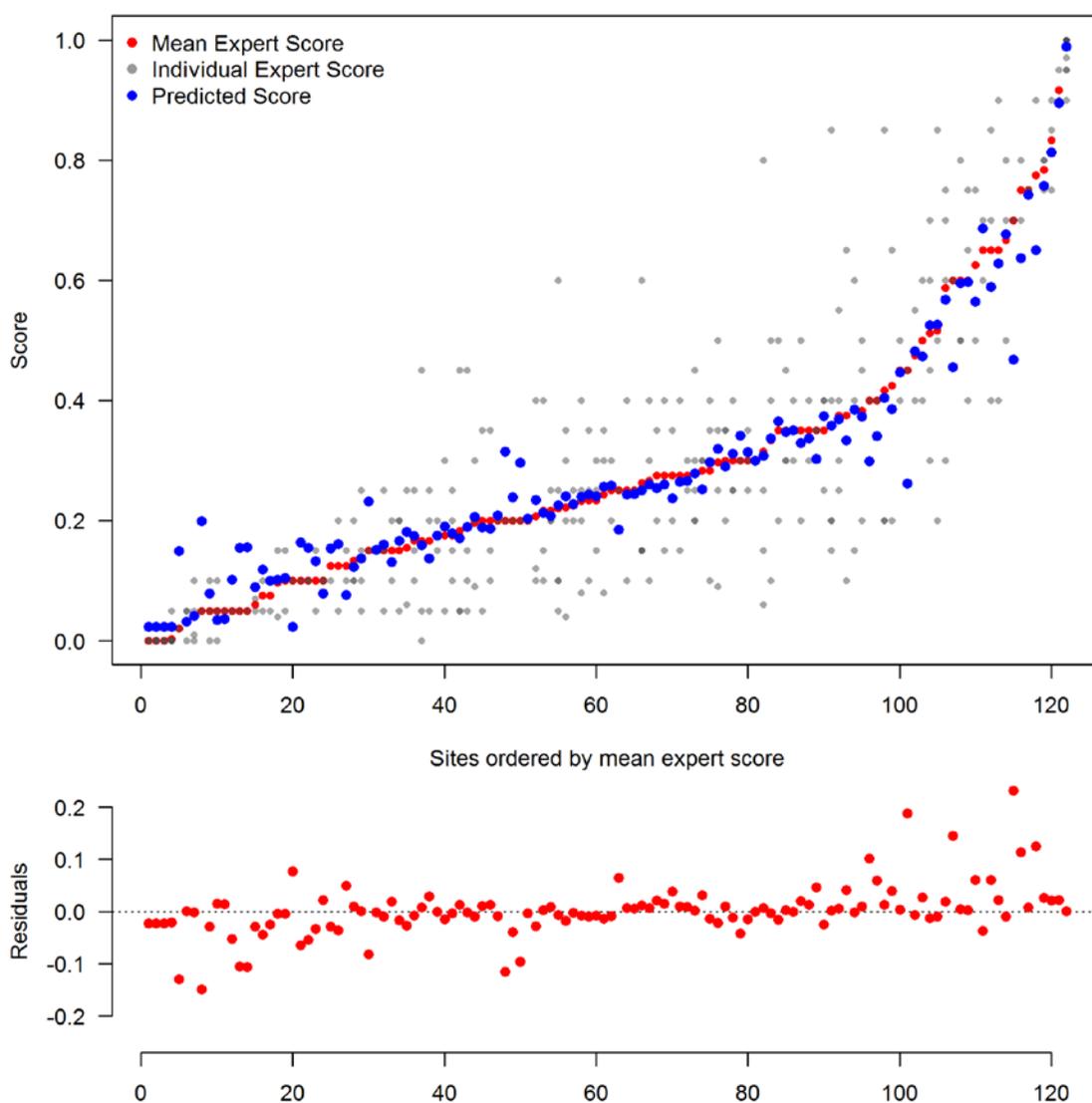


Figure S2: Predicted pressure index from PoTCal using random forests (blue dots), plotted against mean expert score (red dots) and individual expert score (grey dots), ordered by mean expert score (top panel); and residuals (bottom panel). Scores of pressure index are between 0 and 1.

The variable importance scores suggested that WeedProp and WeedCover were the two most important variables used by experts for scoring locations.

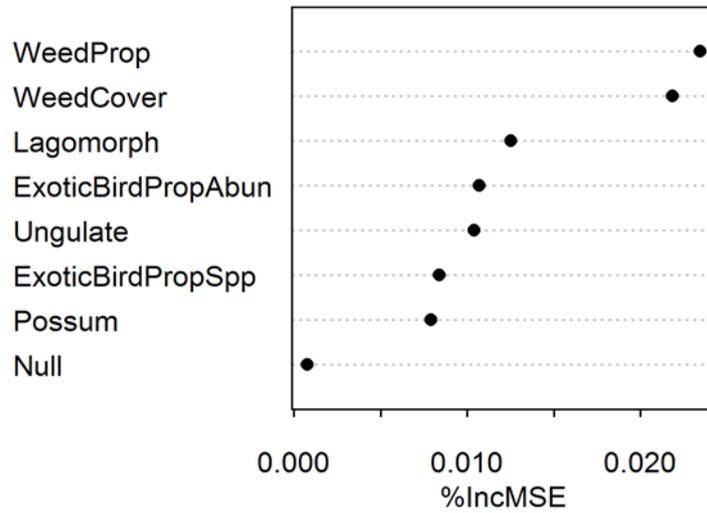


Figure S3 Plot of variable importance for the random forest.

All seven attributes showed a positive relationship between their values and the pressure index (Figure S4).

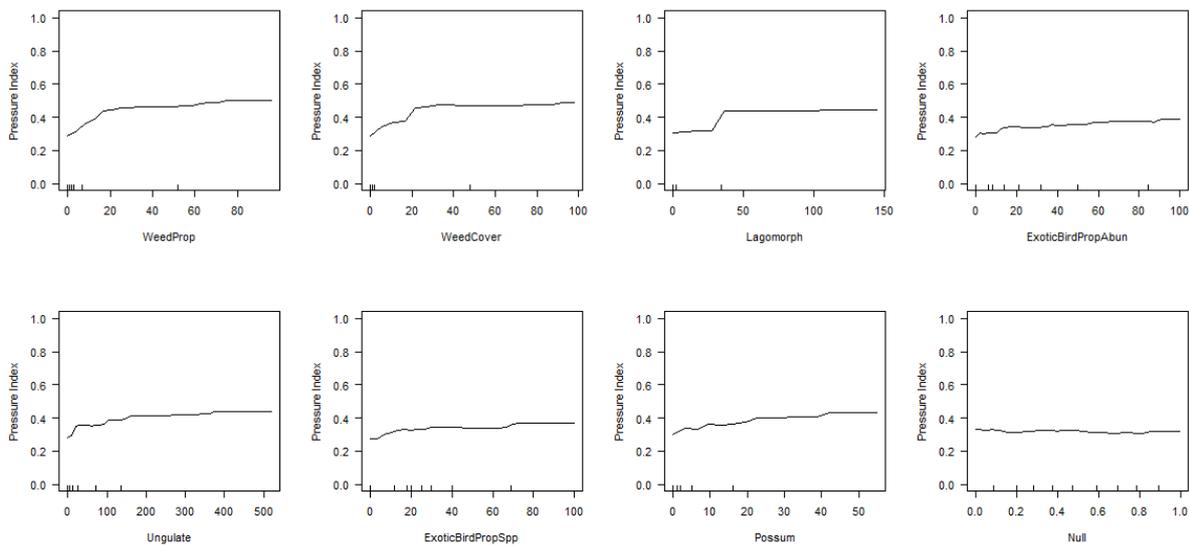


Figure S4 Marginal effect (i.e. partial dependence) of each attribute on the pressure index.

Separate random forests were also constructed using the responses from each the five types of experts separately (Figure S5): Crown Research Institutes (CRI) ($n = 5$), DOC staff ($n = 4$), independent researchers ($n = 4$), regional government staff ($n = 3$), and university researchers ($n = 5$).

There were some differences in the scores from different groups of experts, with CRI researchers and independent researchers scoring sites lower on average than the other groups (i.e. less pressure), whilst university researchers tended to score sites higher on average (i.e. more pressure). However, the very small numbers of experts in each group means that differences among groups should be interpreted with care as the experts may not be representative of their group.

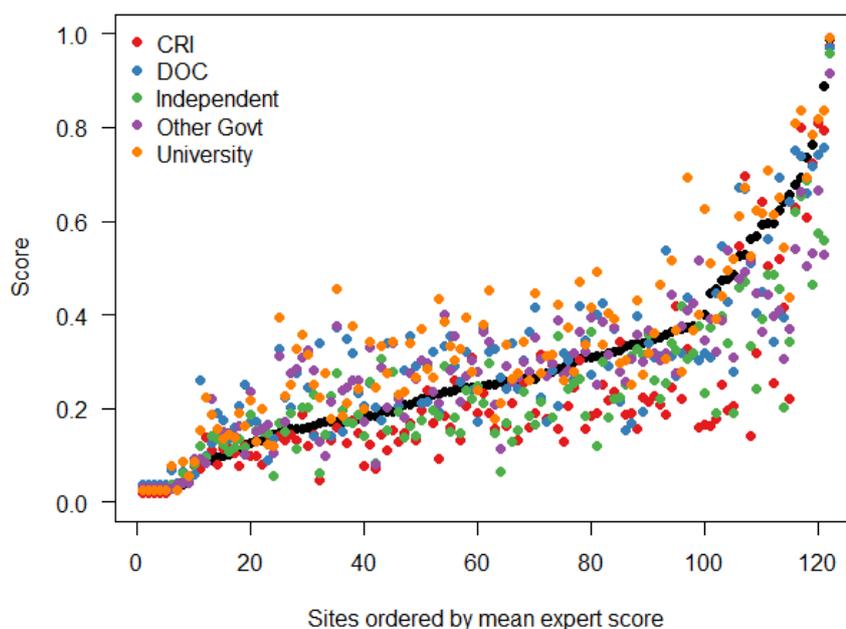


Figure S5 Predicted score from PoTCal using random forests from five groups of experts separately, ordered by predicted score from full mode of all experts (black dots).

Application to Tier 1 data

The resulting model was used to predict the pressure index scores for all 534 locations where all seven attributes have been measured to date (Figure S6). The predicted scores ranged from 0.02 to 0.85. That no location was predicted to score near 1 was likely due to no locations in the Tier 1 data set being near the extreme of the *very high* reference location used for model fitting. Similarly, four locations with no invasive or non-native species recorded were given predicted scores close to, but not equal to 0. This reflects the model fitting shown above where the model slightly over predicted when expert scores were very low.

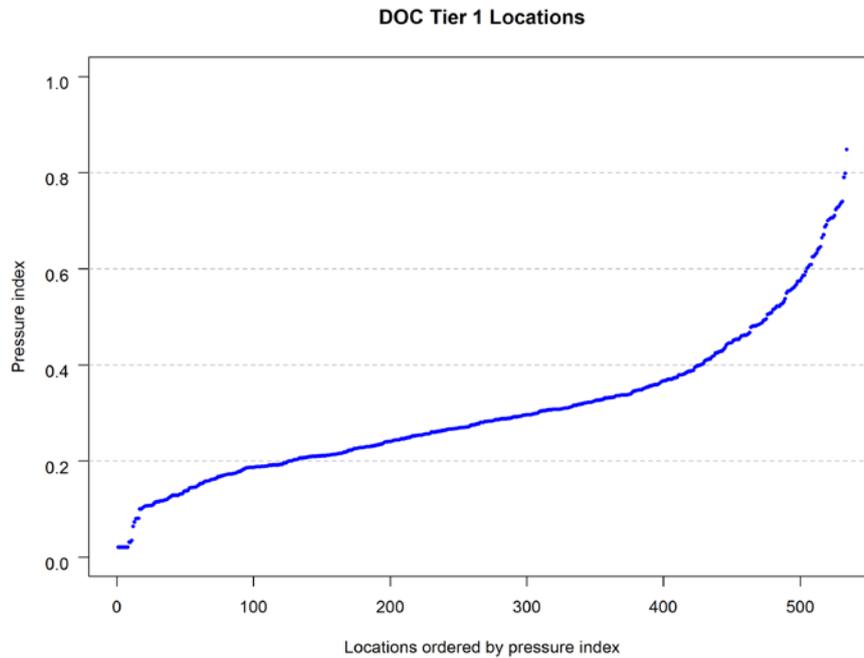


Figure S6 Pressure index from PoTCal using random forests for all 534 locations using all experts.

Finally, we undertook an exploratory analysis to examine the relationship between the predicted pressure index values and nine environmental and ecological covariates (Table S9). Single-term linear regression models were all fitted separately for each covariate in R using the `glm()` function with a Gaussian error distribution. We tested how well each of the nine variables accounted for variation in the presence or abundance of each species or species group, with the goal to assess the strength of support for each covariate relative to the null model. We ran ten models, one each for each covariate and a null (intercept-only) model, and calculated the difference in AICc between the null model, and each fitted model (termed '**delta AICc Null**'). Models with a delta AICc Null > -2 are equivalent to the null model and have no support; models with a delta AICc Null of -2 to -4 have weak support; models with a delta AICc Null of -4 to -7 have moderate support; models with a delta AICc Null of -7 to -10 have strong support; and models with a delta AICc Null of -10 or more have very strong support.

Six of the covariates had a very strong level of support relative to the null model, indicating a general relationship between the pressure index and the covariate value. However it is worth pointing out that the magnitude of the relationship (i.e. slope) was often small (Figure S7).

Table S9 Summary of statistical models predicting the predicted pressure index from nine environmental and ecological predictors. For each model, we present the number of fitted parameters (k), the fitted coefficient (slope), the log-likelihood (LL), the AICc and the difference in AICc between the fitted model and the null model (delta AICc Null). Models are ranked according to delta AICc Null, with the lowest value being the model with greatest support. Support is based on the delta AICc Null. Model weights were calculated using the AICc values. The null model was an intercept-only model. We emphasise that the variables are not additive: each model was fitted separately.

Predictor	k	Slope	LL	AICc	deltaAICc Null	Support	Weight
Rainfall	2	-8.48E-04	-1289.2	2584.5	-99.4	V strong	1.00E+00
Mean Top Height	2	-7.96E-02	-1306.6	2619.3	-64.6	V strong	2.79E-08
Dist. To Exotic Forest	2	-5.14E-05	-1307.9	2621.8	-62.1	V strong	8.04E-09
National Park	2	-1.78E+00	-1318.3	2642.6	-41.3	V strong	2.45E-13
Dist. to Road	2	-5.01E-05	-1331.4	2668.9	-15	V strong	4.78E-19
Dist. To PCL	2	-1.31E-04	-1331.5	2669.1	-14.8	V strong	4.27E-19
Latitude	2	1.25E-01	-1336.5	2679.2	-4.7	Moderate	2.86E-21
NULL	1	NA	-1339.9	2683.9	0	-	2.70E-22
Elevation	2	-1.99E-04	-1339.7	2685.5	1.6	None	1.19E-22
Min. Temperature	2	-2.70E-03	-1339.8	2685.6	1.7	None	1.14E-22

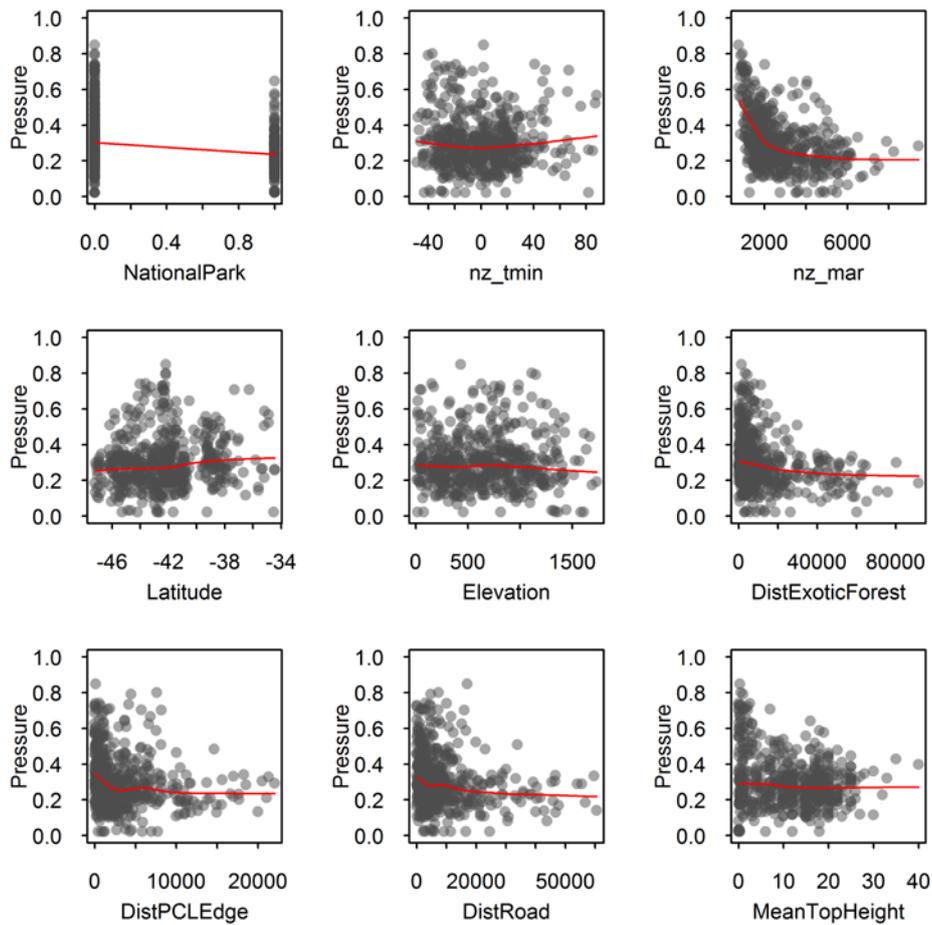


Figure S7 Relationship between the predicted index score and nine potential predictors. A non-linear relationship (lowess) is shown in red.

Future work

There are some issues that potentially require further research and development

Lack of agreement among respondents

For some locations, the respondents varied widely in their scores, with some very large observed differences. We attempted to calibrate the responses to some degree by providing the same ‘high’ and ‘low’ scored sites to each respondent. These were scored consistently by all respondents, but intermediate locations were where much of the disagreement arose. It is unclear whether this reflects real differences in opinion among experts or is just a random effect of the experts (i.e. tended to score all locations high or low).

It should be noted that lack of agreement could indicate that it may not be suitable to aggregate the measures because there is too much variation.

Interpretation of the index

Although the scores from both approaches are between 0 and 1, they are not probabilities, but are qualitative scores of invasiveness. They are unitless and could therefore be scaled to any range, such as 0–20. It is not apparent what ranges of scores constitutes subjectively *good* and *bad* locations. It may have been possible for subjective thresholds to be determined by eliciting cut-offs from each respondent to help scale their individual scores.

However, like any unitless index, such as a consumer price index, the real value is in tracking changes over time. Future work is required to determine whether the index can reliably respond to changes. An index is of little use if it is either invariant to changes or alternatively if it fluctuates widely.