

11 The Context of Plant Invasions in New Zealand: Evolutionary History and Novel Niches

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“The annals of Tutira can be read in its weeds. Each phase ... has been marked by the arrival and establishment of aliens particularly fitted for the particular condition”

Herbert Guthrie-Smith in 1921

11.1 Introduction

With the large environmental and economic costs of species invasions, predicting the invasion potential of non-native species and managing them post-establishment is an important component of New Zealand's biosecurity. Current efforts to assess the invasion potential of plant species utilize phenomenological approaches where the invasion probabilities of species are identified based on their invasion history in other regions, or climatic matching of the distribution of the non-native species with local environments (Pheloung et al. 1999). These phenomenological approaches are easily applied to numerous species, and may aid in recognizing new and latent invaders, but they are likely to be a coarse filter that is not calibrated to the uniqueness of New Zealand's habitats and flora. Consequently, the weed potential of many species will be overestimated, whereas others that may aggressively spread will be overlooked. Phenomenological approaches are likely to fall short in identifying invasive species, are also unable to help manage existing non-native species' expansions, and can not identify vulnerable communities.

In contrast to phenomenological approaches, a mechanistic, predictive invasion theory identifies the processes by which one species invades a habitat and/or the factors that allow an assemblage to resist invasion (Wiser et al. 1998; Kolar and Lodge 2001). Long recognized as a major challenge for ecologists (Elton 1958), a mechanistic invasion theory requires knowledge of the potentially numerous plant traits that are critical for plants to both establish

and dominate (Mooney and Drake 1986; Williamson 1999; Olden and Poff 2003). The mechanisms of establishment also need to be coupled with the mechanisms by which assemblages resist invasion (Lodge 1993).

Our knowledge of the relationship between the structuring of assemblages and the traits of individuals is still rudimentary, but generalizations are emerging along stress and disturbance gradients (Reich et al. 2003; Verheyen et al. 2004). The success of a plant species invading a habitat depends not only on the traits of the invasive species and the abiotic characteristics of the habitat, but also on the spectrum of traits represented in the habitat's biotic assemblage (Robinson et al. 1995; Hector et al. 2001; Miller et al. 2002). Plant invaders appear to be less successful where similar functional groups are present in the resident flora (Fargione et al. 2003), and when unutilized resource levels remain low (Davis and Pelsor 2001). Operationally, there are far too many plant species, traits, and environmental factors to reasonably incorporate into a mechanistic framework, and our knowledge of critical plant traits determining a species' stress and disturbance tolerance is always likely to be limited. Yet, understanding and predicting invasions can be made more efficient if phenomenological approaches are adjusted by mechanistic theory of invasions.

The habitats of New Zealand can be considered a collection of niches that differ in their similarity to niches elsewhere in the world. We consider a niche to be described by a series of environmental axes that define the way in which plants acquire, allocate, and maintain resources to be successful. Important factors that determine the niche include resource supplies, disturbance regime, biotic interactions, and abiotic stresses. Niches differ not only along these major axes, but also in their spatiotemporal extent and consistency over evolutionary timescales.

For a given set of niches that make up a habitat, the functional trait diversity of the extant assemblage is driven by evolutionary-scale patterns of species radiation, immigration and extirpation, and is constrained by the size and diversity of the regional species pool and characteristics of the dominant abiotic and biotic drivers. Applying theories of island biogeography (MacArthur and Wilson 1967), immigration increases functional diversity as propagules with novel functional characteristics come into contact with appropriate habitats. Extinction rates depend on the spatiotemporal extent and continuity of the habitat, the composition of the resident biota, the availability of refugia, and the temporal pattern of major environmental changes. The expansion of functional diversity reflects the spatiotemporal extent of a habitat and the trait diversity found in the regional species pool.

Understanding the evolutionary and ecological history of New Zealand plant assemblages can assist in identifying which assemblages are more likely to be invaded, and suggesting some approaches to managing established non-native plants. Although biogeographic processes may limit the size and variation of the regional species pool, the spatiotemporal extent and continuity of

ecosystems plays a large role in shaping the level of native functional diversity in an assemblage. When environmental conditions associated with a current habitat have been spatiotemporally rare and/or discontinuous, the assemblage that currently occupies the habitat is less likely to contain species or traits that will be competitively successful in the habitat, and therefore resist invaders. In novel habitats, the appropriate native functional diversity is likely to be lower than for donor assemblages, and the native assemblage therefore highly vulnerable to invasion. We propose that the large proportion of invasions in New Zealand are dependent on the presence of these novel niches, whereas core niches, which have been more continuously present for a longer period and/or over a larger spatial extent, are less likely to be invaded. The key to applying this approach to New Zealand begins with identifying the core and novel niches of the country.

11.2 New Zealand's Core and Novel Niches

Novel niches for a region can be defined a priori though an understanding of the region's evolutionary-scale history. Novel niches are more recent in origin, less extensive in space, and more discontinuous in space or time. Core niches, in contrast, are defined by having greater spatiotemporal extent and/or continuity through time. For simplicity, we refer to niche novelty categorically (i.e., core or novel), rather than trying to express the degree of novelty associated with niches. In core habitats, native diversity of functional traits in relation to stress and disturbance gradients should be higher and better adapted than is the case for native functional diversity in novel niches, especially when compared with similar niches in other parts of the world where the niche has been less extensive over space and time.

For most of the past 70 million years, New Zealand has been dominated by warm, wet, low-fertility habitats that lacked regular fire (Wardle 1991). The vegetation was largely forest, with a distinctive fauna of avian herbivores, lizards, and large insects. Novel niches have been produced by recent (i.e., less than 2.5 million years) geological and climatic changes as well as human alteration of habitats over the last millennia. Glacial activity, tectonism, a climate that has oscillated in temperature, herbivorous mammals, fire, and soil disturbance are the major factors that have created novel niches in the latter part of the Tertiary. Each has reduced the relative abundance of core niches, making a larger proportion of New Zealand more likely to be invaded by non-native species.

11.2.1 High Nutrient Supply

Throughout most of the Cenozoic, strongly weathered lateritic and infertile volcanic soils predominated, perhaps with local nutrient enrichment around coastal bird colonies. Relatively high phosphorus availability across much of the landscape was created only during the Pleistocene by sediment redistribution associated with mountain erosion and glacial activity (O'Connor 1980). European agricultural practices have also involved phosphate and nitrate fertilizer addition, especially in the lowlands, together with the widespread use of pasture legumes. The long-term absence of nutrient-rich soils in New Zealand has restricted the development of functional diversity for high-nutrient-supply environments, and limited the evolutionary capacity of plants to efficiently utilize or compete with introduced plants on resource-rich soils (Lloyd et al. 2002).

Native grasslands in New Zealand occupied cold or wet, low-nutrient-supply ecosystems and few of the grasses were well suited for growth at high nutrient supply. Craine and Lee (2003) analyzed the functional traits of roots and leaves of grasses from 30 grasslands across a broad altitudinal gradient on South Island. When compared at a common altitude, native New Zealand grasses have traits that are associated with low nutrient supply, whereas non-native species have traits associated with high nutrient supply. This reflects both the lack of native species that are adapted to high nutrient supplies, and that the non-native species that have been introduced are the ones that perform well in high-nutrient-supply sites. The agronomic species Europeans brought to New Zealand were either largely selected for their ability to grow in pastures that were fertilized and/or they were grown in association with non-native nitrogen-fixing *Trifolium* species. This is evident from their higher nutrient concentrations, superior morphology for light competition, and low structural investment into leaves and roots that confers short longevity, a trait associated with high nutrient supply. Over the past 100 years, areas where fertilization or clover growth has ceased have often reverted to native grasses and other low-N plants such as bracken fern.

Adaptations to low soil fertility also extend to native woody species. Few New Zealand trees have short leaf longevity and high rates of photosynthesis, traits associated with high nutrient supply, and deciduous species are sparse (McGlone et al. 2004). Nitrogen-fixing plants, which are dependent on high phosphorus levels, are uncommon in the native flora, being largely limited to a few shrubs (*Coriaria*, *Carmichaelia*, *Discaria*). Compared with the widespread introduced N₂-fixing woody species (*Cytisus* and *Ulex*), the natives are slow growing and far less competitive on the nutrient-rich soils associated with agricultural development and in natural alluvial systems.

11.2.2 Low and High Temperature

Compared to Northern Hemisphere trees, indigenous tree species are remarkably cold-sensitive; no species tolerates temperatures below -30°C (Wardle 1991). This can be linked to the oceanic influences that ameliorated climatic extremes during successive Pleistocene glaciations. Geographic isolation and the limited regional species pool created by warm-temperate/subtropical antecedents also contributed to the weak frost tolerance amongst native plants. Extensive terrain above the upper limit of trees became available during the early Pleistocene when New Zealand was well isolated from cold-adapted woody species. The youthfulness of high-altitude cold habitats and the fluctuations in temperature have left open a zone of alpine grasslands above New Zealand's treeline that, based on climate data, would be occupied by trees in other parts of the world (Wardle 1985). Not surprisingly, Northern Hemisphere high-altitude trees such as *Pinus contorta* are quickly spreading from erosion control plantings throughout this zone, and displacing the native mixed shrubland and grassland communities.

Cold temperatures began relatively recently in the Pliocene in New Zealand, and extirpated at least 36 plant genera with strong subtropical affinities, which are now mostly confined to New Caledonia and Australia (Lee et al. 2001). The impact on the vegetation of cooling climates and of the extreme climate cycles during the Pleistocene was exacerbated by the absence of refugia at lower latitudes. These extinctions, and New Zealand's relative isolation, created a flora depauperate in warm-temperate and subtropical plants. Subsequent reintroduction by humans of many of the lost flora (e.g., *Eucalyptus*, *Acacia*, and many Proteaceae), and their demonstrable invasive ability in warmer climates, suggests numerous vacant niches in our current warm-temperate/subtropical communities.

11.2.3 Low Precipitation

Sub-humid environments characterized New Zealand for most of the Cenozoic, and strong continental climates probably developed only with the origin of the Southern Alps, which created summer-dry climates in eastern regions. Though there are areas where annual precipitation has averaged less than 500 mm in historical times, they are rarely consistently seasonally summer-dry and can receive ecologically significant rainfall at any time. Worldwide, annuals are a notable feature of these dryland habitats but are rare in the New Zealand flora, which has less than five summer-drought-adapted annual species (Rogers et al. 2002). Present in the native flora are xeromorphic features such as deep tap roots or leaves that roll during water stress and/or have waxy cuticles. Although these may have evolved in response to drying of the

climate, they are likely to be primary adaptations related to nutrient-poor ecosystems during the Cenozoic. Adaptations to low water availability may be similar in coexisting native and non-native shrubs in a semi-arid environment (Kissel et al. 1987); the range of functional types present is markedly less amongst the natives. Continental climates in New Zealand have experienced probably the greatest invasion of non-native plant species of any biome. Over the last 150 years, a great range of annual, biennial, and perennial plants, grasses and forbs from California and the Mediterranean have invaded low-rainfall areas (Walker and Lee 2000).

11.2.4 Mammalian Herbivory

New Zealand is highly unusual in having had a rich fauna of avian megaherbivores, with no terrestrial herbivorous mammals. Bird browsing was likely a strong selective force in the past, and a major component of many core niches in New Zealand. For example, a high proportion (~20%) of native plant species in New Zealand are represented in ephemeral turf communities that occupy less than 1% of the current landscape (Johnson and Rogers 2003). The turf species (<3 cm tall) are well adapted to seasonally dry wetlands, and the removal of aboveground biomass and local nutrient input that is likely to have occurred when numerous birds browsed in these habitats. Observations indicate that these functionally diverse communities maintain their native dominance under strong avian herbivory, nowadays largely by introduced waterfowl, and under these conditions are remarkably resistant to invasion by introduced plants.

In addition to turf communities that may have been browsed by birds, there are also a large number of medium-fertility woody plant species that are well defended against browsing birds, within 3 m of the ground (Bond et al. 2004). Adaptations to the distinctive modes of feeding by the large dinornid ratites are widespread amongst woody plants (Bond et al. 2004), and include strong narrow stems, small widely spaced leaves, and complex three-dimensional branching patterns. However, this architectural syndrome fails against mammals that can shear and manipulate woody shoots. The importation of diverse mammals by Europeans in the early 19th century found an ecologically naïve flora with few defenses against the feeding strategy of herbivorous mammals. Extensive grasslands comprised of tall (*Chionochloa*) and short (*Festuca*, *Poa*) caespitose species were similarly poorly adapted to foraging by grazing mammals, with elevated and exposed meristems, slow growth rates, and episodic flowering. For example, recovery rates in *Chionochloa pallens*, a fast-growing tall tussock species associated with nutrient-rich soils, are exceedingly slow, taking at least two decades to restore biomass removed after one clipping of lamina material (Lee et al. 2000). Low foliar nutrient concentrations may have initially deterred avian herbivores from eating these plants; however, cattle,

sheep and rabbits rapidly consumed juvenile plants and those on more fertile soils, and overstocking quickly depleted most montane grasslands.

Multiple mammalian herbivores are now virtually ubiquitous on the mainland, and are strongly filtering plant assemblages. In this selection process, non-native species with a long evolutionary history of mammalian herbivory are increasingly displacing native species – most dramatically in non-forest communities with the highest loadings of mammals. The reduction of palatable and susceptible native species increased resource availability for species that are better adapted to grazing and browsing, due either to chemical defenses (*Hieracium*, *Anthoxanthum*) or physical defenses (spines in *Ulex europaeus*, *Hakea* species), or having a grazing-tolerant growth form (*Agrostis*).

11.2.5 Fire

Natural ignition events have a long history in New Zealand, associated mainly with volcanic eruptions and lightning strikes, but these have never been sufficiently frequent or widespread in a dissected landscape to result in strong selection for fire-adapted traits in the flora. For example, serotiny is limited to populations of the myrtaceous shrub *Leptospermum* and is extremely low, and most native woody and herbaceous species are extremely fire-sensitive. Burning by Maori led to an expansion in range of some native species such as bracken, *Leptospermum*, and *Chionochloa rigida* grasslands (McGlone 2001), but during the pre-European era there was a low diversity of non-native plants available to exploit the reduction in forest. European burning, however, enhanced the spread of an imported pool of fire-adapted non-natives with serotinous or heavily protected capsules (e.g., *Hakea*) and/or large seed banks (e.g., *Ulex europaeus*, *Calluna vulgaris*). Fire also enhances the opportunity for the expansion of numerous ruderal non-native species with prolific seed production (e.g., *Melilotus* spp., *Medicago* spp.).

11.2.6 Soil Disturbance

Soil disturbance in New Zealand is largely created by windthrow, landslides, and a range of erosional and depositional processes associated with colluvial and alluvial systems. Native ruderal plants are rare, and are easily outcompeted by a large number of non-native herbaceous and woody plant species from regions of the world with a long history of human disturbance, and coexistence with burrowing mammals. Native burrowing animals in New Zealand soils are limited to earthworms and although some species reach over 1,000 mm in length, these are generally subsoil specialists (Lee 1959). Terrestrial birds and sea birds such as petrels may have been significant soil-

forming and burrowing agents before their widespread demise over a century ago on the mainland by introduced mammalian predators, but evidence for their role in enhancing ecosystem processes remains unclear. Annual and biennial life-forms are well represented amongst non-native plant species, together with fecund, small-seeded, wind-dispersed perennials that effectively colonize disturbed areas created by large-mammal grazing, and a range of human activities associated with settlement and agriculture that maintain open ground.

11.2.7 Interactions Among Factors

Human activities and the template of novel niches that existed when humans arrived overlap to create niches that were even more divergent from what was present over evolutionary timescales in New Zealand. For example, nutrient-rich sites on valley floors that were previously burnt are heavily browsed or grazed by mammalian herbivores and represent a combination of novel niches for native plants, and would be highly susceptible sites for invasion because each factor has generally been rare or absent in New Zealand until recently. This is confirmed for grasslands associated with alluvial systems in eastern South Island, where non-native species richness increases with grazing pressure, flooding frequency, and soil fertility (Walker and Lee 2000).

The large-scale fertilization of tussock grasslands was coupled with a rise in the abundance of European pasture grasses. Native grasses were unable to successfully compete against non-native grasses and legumes under the dual conditions of high nutrient availability and mammalian grazing. The native grasses are unlikely to have experienced equivalent herbivory pressures from the avian fauna because these grasses characteristically inhabited low-nutrient-supply habitats, and the nutritional quality of the grass would seldom be above the minimum level required to support herbivores. Consequently, it is likely that ratite browsers would rarely have removed leaf biomass from these grasses. Native shrubs do invade these systems, but they are either spinescent (*Discaria*), unpalatable (*Ozothamnus*, *Leptospermum*), or prostrate (*Coprosma petriei*).

Phosphorus enrichment in non-forest communities favors herbivore-resistant N_2 -fixing plants. The few native N_2 -fixers are mainly shrubs, but many of these appear to have little defense against mammalian herbivores and are generally rare. Only when mammals are locally removed, and nutrient levels maintained, do native N_2 -fixing woody species increase greatly in abundance (Walker et al. 2003). It is the combination of mammalian grazing and phosphorus addition that consolidates the presence of non-native woody and herbaceous N_2 -fixers in many montane grasslands. In the absence of mammals, native shrubs would be much more abundant and more likely to have resisted invasion by shrubs such as gorse and broom.

11.3 Core and Novel Niches: a Predictive, Useful Framework?

Current efforts to address invasive species can be sharpened by understanding the distinctive ecological and evolutionary history of New Zealand. We suggest that the niches that have been present in New Zealand with the least disruption, for the longest time, and over the greatest space should have relatively high relevant functional diversity, and therefore be the least likely to be invaded by plants not native to New Zealand. By implication, identification of factors that create novel niches should be useful not only in predicting invasions, but also in managing plants that have already invaded New Zealand.

The novel-niche theory predicts that the native assemblages of recent niches are more likely to be invaded than those in core or ancient niches. For example, low-fertility, warm, sub-humid, forested sites that lack a recent history of herbivorous mammals and frequent fire should have a higher proportion of native species as structural dominants, and fewer non-native species than those habitats characterized with novel niches. There have been few studies in New Zealand to directly test novel-niche theory, but plot data are gradually becoming available across the country to assess invasions in different environments (Wiser et al. 2001). One problem is that very few unmodified core habitats remain anywhere on the mainland, although the success of invasive species into intact, warm-temperate, infertile, forest systems appears to be relatively low compared with other habitats in New Zealand.

Anthropogenic niches can be managed to decrease the impact of invaders by reducing the impact of the novel factors associated with human activity. Dominance of native plant species is more probable when fire can be eliminated, mammals removed, and exogenous nutrient supply reduced. Introducing surrogate species, especially birds, for native species that have gone extinct should also help reestablish the core-niche factors, and increase community resistance to invasion. Few floras worldwide have evolved solely in the presence of avian herbivores, and it is likely that many introduced plant species would be at a disadvantage under this type of selection pressure. Some anthropogenic disturbances that mimic long-term natural disturbances may also facilitate the success of native plants and decrease invisibility. For example, actions such as mowing and maintaining grazing by small mammals may foster native turf plants while decreasing invasive, sward-forming introduced grasses.

Novel niches that are independent of humans will be the most difficult to maintain free of non-native species. This will be especially true when other areas with similar niches outside of New Zealand have had a greater evolutionary extent, and have greater native diversity than the New Zealand assemblages. For example, even in the absence of mammalian herbivores, alpine and southern beech forests have low native diversity relative to similar habitats in other parts of the world. It is probable that these habitats have not been

invaded yet due to low propagule pressure, not because of high long-term resistance to invasion. If these habitats are also subjected to additional novel-niche factors, such as increased fertility that comes with fertilization or nitrogen deposition, we hypothesize that invasions would become ever more likely at the same propagule pressure.

A complete theory of plant invasions will be a union of the mechanisms of invasion within the constraints imposed by evolution and dispersal associated with varying environmental conditions. A predictive theory will include plant traits that are associated with resource acquisition and maintenance, but will extend to other factors that are important in a plant's life cycle: predator escape, propagule availability, dispersers and pollinators abundance, stresses, and disturbances. These mechanistic, important details about the invasion process need to be contextualized to the evolutionary history of the niche as well as the native assemblage and non-native species. These broader analyses are helpful in structuring our questions regarding invaders, and determining where to focus scarce human resources. Operationally, incorporating our understanding of the history of habitats and their assemblages in New Zealand with mechanistic understanding of the invasion processes is the best way to proceed to manage invasions in the country.

References

- Bond WJ, Lee WG, Craine JM (2004) Plant structural defences against browsing birds: a legacy of New Zealand's extinct moas. *Oikos* 104:500–508
- Craine JM, Lee WG (2003) Covariation in leaf and root traits for native and non-native grasses during an altitudinal gradient in New Zealand. *Oecologia* 134:471–478
- Davis MA, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecol Lett* 4:421–428
- Elton CS (1958) *The ecology of invasions by animals and plants*. Methuen, London
- Fargione J, Brown CS, Tilman D (2003) Community assembly and invasion: An experimental test of neutral versus niche processes. *Proc Natl Acad Sci USA* 100:8916–8920
- Guthrie-Smith H (1921) *Tutira: the story of a New Zealand sheep station*. Blackwood, London
- Hector A, Dobson K, Minns A, Bazeley-White E, Lawton JH (2001) Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecol Res* 16:819–831
- Johnson PN, Rogers GM (2003). *Ephemeral wetlands and their turfs in New Zealand*. Department of Conservation, Wellington, New Zealand
- Kissel RM, Wilson JB, Bannister P, Mark AF (1987) Water relations of some native and exotic shrubs of New Zealand. *New Phytol* 107:29–37
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16:199–204
- Lee KE (1959) *The earthworm fauna of New Zealand*. DSIR Bull 130. Wellington, New Zealand
- Lee WG, Fenner M, Loughnan A, Lloyd KM (2000) Long-term effects of defoliation: incomplete recovery of a New Zealand alpine tussock grass, *Chionochloa pallens*, after 20 years. *J Appl Ecol* 37:348–355

- Lee DE, Lee WG, Mortimer N (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Aust J Bot* 49:341–356
- Lloyd KM, Lee WG, Wilson JB (2002) Competitive abilities of rare and common plants: comparisons using *Acaena* (Rosaceae) and *Chionochoa* (Poaceae) from New Zealand. *Conserv Biol* 16:975–985
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends Ecol Evol* 8:133–137
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton Univ Press, Princeton, NJ
- McGlone MS (2001) The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. *NZ J Ecol* 25(1):1–15
- McGlone MS, Dungan RJ, Hall GMJ, Allen RB (2004) Winter leaf loss in the New Zealand woody flora. *NZ J Bot* 42:1–19
- Miller TE, Kneitel JM, Burns JH (2002) Effect of community structure on invasion success and rate. *Ecology* 83:898–905
- Mooney HA, Drake JA (1986) Ecology of biological invasions of North America and Hawaii. *Ecological Studies Analysis and Synthesis*, vol 58. Springer, Berlin Heidelberg New York
- O'Connor KF (1980) The use of mountains: a review of New Zealand experience. In: Anderson AG (ed) *The land our future: essays on land use and conservation in New Zealand in honour of Kenneth Cumberland*. Longman Paul/New Zealand Geographical Society, Auckland, New Zealand, pp 193–222
- Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *Am Nat* 162:442–460
- Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *J Environ Manage* 57:239–252
- Reich PB, Buschena C, Tjoelker MG, Wrage K, Knops J, Tilman D, Machado JL (2003) Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. *New Phytol* 157:617–631
- Robinson GR, Quinn JF, Stanton ML (1995) Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76:786–794
- Rogers G, Walker S, Tubbs M, Henderson J (2002) Ecology and conservation status of three “spring annual” herbs in dryland ecosystems of New Zealand. *NZ J Bot* 40:649–669
- Verheyen K, Vellend M, van Calster H, Peterken G, Hermy M (2004) Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. *Ecology* 85:3302–3312
- Walker S, Lee WG (2000) Alluvial grasslands in south-eastern New Zealand: vegetation patterns, long-term and post-pastoral change. *J R Soc NZ* 30:69–103
- Walker S, Wilson JB, Lee WG (2003) Recovery of short tussock and woody species guilds in ungrazed *Festuca novae-zelandiae* short tussock grassland with fertiliser or irrigation. *NZ J Ecol* 27:179–189
- Wardle P (1985) New Zealand timberlines. 3. A synthesis. *NZ J Bot* 23:263–271
- Wardle P (1991) *Vegetation of New Zealand*. Cambridge Univ Press, Cambridge
- Williamson M (1999) Invasions. *Ecography* 22:5–12
- Wiser SK, Allen RB, Clinton PW, Platt KH (1998) Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79:2071–2081
- Wiser SK, Bellingham PJ, Burrows LE (2001) Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *NZ J Ecol* 25(2):1–17