Ecology and consequences of invasion by non-native (wilding) conifers in New Zealand

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Abstract
Invasion by non-native woody species into largely treeless vegetation such as grasslands and shrublands is widespread, and has prompted both research and management in response. Here I review the current situation of invasions by non-native Pinaceae, better known as 'wilding conifers' in New Zealand, and how both research and management are working to better understand and manage these invaders. The success of wildings is explained by a combination of history (e.g., deforestation of previously woody vegetation), biological traits of the species (rapid growth and early reproduction), and propagule pressure (introduction effort). Wildings represent a major land use change affecting about 2 million ha, including many grasslands, rare ecosystems and subalpine habitats. Wilding invasions into grasslands have profound impacts on biological diversity, but also have important ecosystem impacts including legacy effects belowground by altering nutrient cycling and soil biota. Recent expanded efforts are underway to control and co-ordinate management to avoid or mitigate the negative impacts of wilding conifers. The long-term value of managing invasions, and whether additional management interventions are needed to restore grasslands or woody vegetation is in progress, but is urgently needed given recent moves to widely establish new woody vegetation at large scales in New Zealand.

Keywords: biological invasions, ecological impacts, ecosystem legacies, non-native tree species, *Pinus contorta*, plant-soil interactions, removal effects, wilding conifers

Introduction
Biological invasions by non-native species are an important component of global change, and are a major driver of changes in ecological communities and ecosystems (Vitousek *et al.* 1997; Early *et al.* 2017). Moreover, many of these drivers interact, for example, changing land use or climate can exacerbate the number or success of biological invaders in a system (Tylianakis *et al.* 2008). More specifically, New Zealand is one of the world's most invaded countries. This is highlighted through such national-scale efforts as predator-free New Zealand. For plants, about half of the New Zealand flora is comprised of non-native plant species, and many of these are considered environmental weeds. As a consequence, there are ongoing efforts to better understand and manage biological invasions at both regional and national scales.

Invasion by non-native tree species into non-forested areas is a global problem because tree invasions can drive declines in conservation values or biodiversity as well as altering land use suitability for agriculture or other primary industries (Richardson & Rejmánek 2011). Internationally, one of the best studied and most widespread group of invasive non-native trees are the pines (Pinaceae); this is unsurprising given their widespread deliberate introduction for timber, fibre and shelter (Richardson & Rejmánek 2004; Procheş *et al*. 2011). Invasive Pinaceae have become widely naturalised in the southern hemisphere (Richardson *et al*. 1994; Simberloff *et al*. 2010). Most literature refers to these species as invasive non-native Pinaceae or conifers; but the more succinct New Zealand term is "wilding conifers" (Froude 2011). Wildings represent about a dozen species including lodgepole and back pine (*Pinus contorta, P. nigra*), Douglas fir (*Pseudotsuga menziesii*) and larch (*Larix decidua*) (McGregor *et al.* 2012). Below, I briefly review why these species are so successful, why they are a problem, what is currently being done to manage wildings, and finish with some longer term or unresolved issues.

So why are wildings so successful?
Successful establishment, naturalisation and spread of introduced species is often attributed to their biological characteristics such as rapid growth, high reproductive output and tolerance of environmental conditions. For example, lodgepole pine (*Pinus contorta*) grows much faster in countries where it has been introduced compared to the home range in North America (Ledgard 2001; Taylor *et al.* 2016a). However, for pine species introduced to New Zealand the best predictors of naturalisation are introduction effort (forestry use, area planted, and date of introduction) and climate-matching; the main biological trait is early age to reproduction (McGregor *et al.* 2012). In addition, seed traits (terminal velocity, or the rate of seed fall vertically) and wind, interact to drive both short and long-distance dispersal of conifers, and in combination with high survivorship of seedlings, this allows pine invasions to rapidly establish in grasslands (Buckley *et*

ISSN 2463-2872 (Print) ISSN 2463-2880 (Online)

al. 2005; Caplat *et al*. 2012). Overall, this demonstrates that early, large-scale plantings overcome the lag times between when a species is introduced and when it becomes naturalised and invasive, but also suggests that some species that are not currently widespread invaders are able to spread, but are just taking longer to invade because of lower initial introduction effort.

Positive interactions can also occur among introduced species. For conifers, the most obvious is mutualisms involving mycorrhizas: beneficial fungi associated with plant roots that are needed for tree establishment and can improve the subsequent survival and growth of plants. For example, lodgepole pine co-invades with non-native mycorrhizal fungi rather than associating with native fungi (Dickie *et al*. 2010), and even a single mycorrhizal species can enable pine invasion (Hayward *et al*. 2015). Furthermore, few mycorrhizal fungal species are needed to facilitate pine invasion, including into grasslands that do not contain ectomycorrhizal tree species. This differs from native beech (nothofagus) tree species that are also ectomycorrhizal, but are notoriously slow at reinvading grasslands. In addition, non-native mycorrhizal fungi can be transported by non-native mammals such as deer and possums, but presumably other mammals can also disperse fungi (Wood *et al*. 2015). Positive interactions amongst wilding tree species, their co-invading mycorrhizal fungi and dispersal of these fungi by non-native mammals helps to explain the invasion success of wilding conifers into grasslands (Figure 1).

Why are wildlings a problem?

The invasion by trees into grassland has both obvious consequences and less obvious legacies. Although the invasion potential of conifers has been known for some time (e.g., Benecke 1967; Hunter & Douglas 1984; and references in Froude 2011), wildings are now broadly viewed as a serious threat to grassland biodiversity, pasture or primary production, and some ecosystem processes, through profoundly altering vegetation composition and resource availability (Dickie *et al*. 2011; Rundel *et al*. 2014; Taylor *et al*. 2016b). Different impacts of wildings occur at different stages of the invasion process. Grassland plant diversity can initially increase with invasion but then rapidly declines; carbon scales positively and linearly with increasing tree density; and water yield declines most rapidly with canopy closure because of rainfall interception (Fahey & Payne 2017). As a consequence, different impacts of wildings occur as invasion proceeds, and this can create trade-offs in net impacts, or conversely, the benefits of managing invasions for conservation or primary production (Mason *et al*. 2017). The less obvious legacies of wildings include belowground changes to nutrient cycling and the soil biota that can persist following the control of wildings (Dickie *et al*. 2014). This includes increases in both soil available nitrogen and phosphorus compared to native grasslands, and changes in plant-associated nematodes that can act as pathogens. What is surprising is how rapidly impacts and legacies can develop (<10 years) given the invasion is by tree species (Figure 1; Taylor *et al*. 2016a).

Figure 1 Invasion by non-native pines or 'wilding conifers'. Early invasion in the Mackenzie Basin (top panel), ongoing invasion near Hanmer Springs (middle panel), and a long-invaded site in the Kawekas (bottom panel).

The total area affected by wildings (defined as a minimum of one tree/ha) is thought to be around 2 million ha, or about the same area as is in plantation forestry in New Zealand (MPI 2014). The area invaded has by some estimates increased by about 5%/year over the past few decades. Because wildings can invade high-country grasslands, threaten rare ecosystems (many of which are treeless vegetation and have high conservation value), and can establish above the natural treeline, they are considered a national-scale weed issue (Froude 2011). The speed and scale of wilding invasion occurred despite ongoing management efforts by landowners, community trusts and government departments alike, and this prompted a call for increased management to contain or eradicate wildings. In response, the Ministry of Primary Industry spearheaded a national strategy to raise general awareness of this issue, and to co-ordinate management efforts amongst central and regional government, landowners and industry at a national scale (MPI 2014). More recently, this has prompted formation of the National Wilding Conifer Management Programme that organises and co-ordinates these renewed management efforts (www.wildingconifers.org.nz).

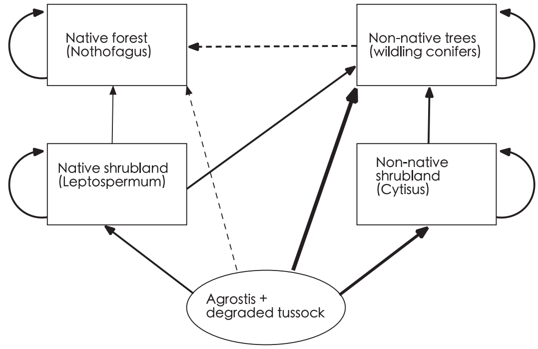

Figure 2 Illustrative state and transition model for grasslands modified and simplified from Standish *et al.* (2009). Arrows show vegetation changes from tussock grassland towards dominance by either native (left side) or non-native weeds (right side). Depending on propagule pressure (seed sources) and environment, most trajectories tend towards dominance by non-native trees or wilding conifers, but in some cases states can persist through self-replacement (shown by loops for a vegetation-type).

What is currently being done to manage wildings?

In response to widespread invasion, there are many management programs internationally that are pursued to prevent or mitigate the spread and impacts of biological invaders (e.g., Hulme 2015; Nuñez *et al.* 2017). Usually, multiple management strategies are deployed in an attempt to reduce the abundance or distribution of invasive species, but with an ultimate goal of avoiding or mitigating negative impacts on native ecosystems (e.g., Zavaleta *et al.* 2001; Barney *et al.* 2015). For wilding conifers there are multiple methods used for controlling trees that are used depending on tree density, the species involved and site access. These include mechanical (grubbing, pulling, cutting, mulching) and chemical (ground and aerial basal bark herbicides, aerial boom spraying) methods as well as land management (mob stocking, pasture improvement). The selection and use of different management strategies is well-covered in work plans, user guides and vast previous experience (e.g., Ledgard 2009; Briden *et al.* 2014; Gous *et al.* 2014, 2015). Current total spending nationally wilding control is about $16 million/year, but this excludes ongoing management efforts on private land and by communities (MPI 2014).

Selection of different management strategies typically considers the effectiveness of control (e.g., proportion of trees killed) and cost, and in some cases, the response of native communities (Flory & Clay 2009). A few studies that consider the non-target impacts of wildings show that changes in plant communities caused by both wilding invasion and different management or removal strategies have contrasting outcomes for vegetation recovery. For example, early control of wilding seedling or saplings returned a tussock grassland community to resemble the uninvaded community, whereas later removal of trees drove the vegetation towards dominance by few non-native grasses (e.g., *Agrostis capillaris, Anthoxanthum odoratum*; Ledgard & Paul 2008; Paul & Ledgard 2009; Dickie *et al.* 2014). Overall, woody invasion into grasslands follows somewhat predictable state and transitions (Figure 2), but the rapid shift towards dominance of wilding conifers rather than native woody plant species is a major concern (Standish *et al.* 2009; Young *et al.* 2016). More specifically, management of wildings can have different outcomes depending on the methods used and the more rapid establishment of many non-native plants compared to native species (Wardle & Peltzer 2017). Other potential management tools including fire, biological control and the use of sterile trees in plantations, are all options for efficient longer-term management to prevent future wilding spread, but are not currently in use.

Many invasive plant management or eradication efforts in general either fail to meet their stated management goals or do not carry out rigorous evaluations of success (e.g., Maxwell *et al.* 2009; Wilson *et al.* 2014); those that do measure effectiveness as change in invasive species to management *per se* rather than wider values or benefits (Reid *et al.* 2009). However, an implicit goal of management, including of wildings, is often to generate benefits beyond immediate control of the invader itself. These benefits

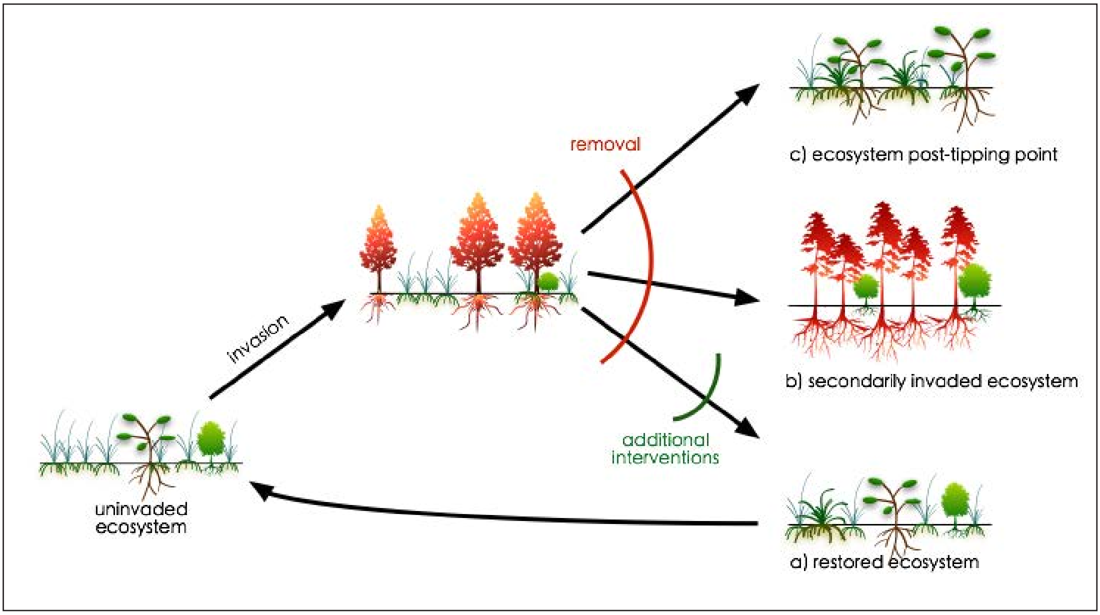

Figure 3 General trajectories of changes driven by invasion, invader removal or restoration. Management ('removal') of invaders can involve creating a new system (top right), reinvasion by wildings or secondary invasion by other weeds (middle right), or with sufficient seed sources or additional management, restoration towards an uninvaded system (bottom left) (modified from Wardle & Peltzer 2017).

span conservation of sites and native species, sustained water yield in catchments, and maintaining landscape values (MPI 2014; Nuñez *et al*. 2017).

Looking ahead

Non-native conifers in New Zealand are an interesting issue globally because they both underpin the plantation forest industry, but at the same time most species are also considered environmental weeds. The two issues are not directly comparable, however, because both the tree species involved and locations can differ between plantation forestry and wilding invasion. Overall, wildings are currently a widespread weed problem of non-native trees invading largely into grasslands and other non-forest vegetation-types, but new progress in management to contain or eradicate wildings is now being made through greater co-ordination and operational funding at a national scale (http://wildingconifers.org.nz/about-us/programme-2/). However, there remain several opportunities or gaps in understanding that remain to be filled, and that closely linking management and research can help to resolve including:

1. There is no one-off management method that can eliminate wildings in perpetuity, but rather follow-up or repeated management is typically needed (Ledgard 2009; Nuñez *et al*. 2017). Determining how long management must endure to control or contain wildlings is needed, but planning for a decade or longer is often essential.
2. If eradication or elimination of wilding conifers is not possible for a site, then what is the minimal wilding abundance that management should achieve to ensure benefits within a site (Barney *et al.* 2015)? In other words, can sustaining a low abundance of wildings provide nearly all of the benefits of management?
3. Taking a longer-term view, are additional management interventions needed to establish grassland or native woody species (e.g., McAlpine *et al*. 2016), or to prevent undesirable 'secondary invasions' by other non-native species (Figure 3; see also Firn *et al.* 2010)? The long-term options for wilding invaded sites converge on active management towards grassland (either native tussock or pasture), or woody vegetation (most likely mixtures of native and non-native woody species); making the end-point explicit is necessary to know when and what additional management efforts are needed.
4. What is the future risk of wilding invasion given changes in land use, climate and management? This is particularly pressing given that ongoing, large-scale changes in land use are likely (e.g., driven by the billion trees Government initiative), and the prediction that future climates might alter both plant performance (growth, height and reproductive effort) and extreme events (e.g., storms), thus potentially increasing spread risk (Caplat *et al*. 2013).

Controlling invasive non-native species such as wilding conifers is at the same time both simple (i.e., killing unwanted trees) and complex because it involves manipulation of complex systems across all stages of the invasion process from preventing new invasions, to managing established populations, and in a few cases, sorting out long-invaded areas. Because the outcomes of invasive species removal, in terms of conservation values and ecosystem impacts, are often variable (Kettenring & Adams 2011), it is essential to evaluate the performance of different management strategies. The renewed efforts and co-ordination of wilding management and research give new hope that effective control of wilding conifers will prevent or mitigate their negative effects at the landscape-scale.

ACKNOWLEDGEMENTS

I thank the numerous colleagues and collaborators who have helped to develop these ideas, brought into particular focus recently through the National Wilding Conifer Control Programme for wilding conifer management, and the Winning Against Wildings research programme funded by the New Zealand Ministry of Business, Innovation and Employment.

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