



Applying ecological research to improve long-term outcomes of wilding conifer management

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Abstract: Removing wilding conifers (invasive non-native trees in the Pinaceae) has become a major focus of conservation and land management in Aotearoa New Zealand. Management of wilding conifers has been supported by applied research on control methods, generally with a short-term focus of removing or containing invasions to prevent further spread. However, a focus on short-term management activities may not achieve desired longer-term outcomes of restoring economic and environmental values. Greater integration of ecological research on wilding conifer impacts and legacies with management can help to ensure long-term goals are achieved. We review how impacts and legacies of wilding conifers develop and persist over time. Several key thresholds or tipping points are identified, where prioritising management may avoid state-changes in ecosystems. We then review the potential of sites to support different land uses after wilding conifers have been controlled, including pasture, plantations and native restoration, and develop a decision support tree to guide successful transition to these land uses. We find that maintaining anthropogenic native tussock grasslands is unlikely to be a sustainable goal on most invaded sites without major sustained management interventions. Native woody cover is likely more sustainable, but often requires additional management of post-removal legacies of wilding conifers, including other invasive plants such as sward-forming non-native grasses. Shade tolerant wilding conifers, such as Douglas-fir, remain a pernicious problem in any effort to prevent reinvasion into woody vegetation. Although there are still questions about the causes and consequences of wilding conifer invasions, ecological research can provide helpful guidance to improve long-term outcomes following wilding conifer control.

Keywords: applying ecological knowledge, belowground processes, biological invasions, ecosystem restoration, legacies, non-native trees, research-management interface, species removal, tipping points, weed management

Introduction

Of the more than 2500 non-native plant species naturalised in New Zealand, “wilding conifers” (invasive trees in the family Pinaceae, particularly *Pinus contorta*, *P. nigra*, *P. radiata*, *P. mugo*, *Larix decidua* and *Pseudotsuga menziesii*) are amongst the most problematic (Brandt et al. 2021). In the absence of management, some estimates suggest that wilding conifers could spread to 7.46 million hectares over the next 15–30 year period, or approximately 28% of New Zealand’s land area, albeit at variable abundance (Wyatt 2018). Wilding conifer invasions particularly threaten tussock grasslands, frost flats, and alpine areas (Campbell 1984; Smale 1990), where the invasion of fast growing trees into treeless or low-statured vegetation causes fundamental shifts in almost every aspect of these ecosystems.

Wilding conifer management first began in the 1960s

(Fig. 1) (Ledgard 2001), but has accelerated over the past 15 yrs. Wilding conifer control operations attract a national investment of \$100 million over four years as of 2020 (<https://www.beehive.govt.nz/release/budget-2020-jobs-and-opportunities-primary-sector>), and substantial additional costs are borne by landowners, industry, and local community groups (Peltzer 2018; Wyatt 2018). While the expense of control is considerable, economic analyses suggest that this investment is highly worthwhile, achieving an outstanding benefit:cost ratio of 38:1 (Wyatt 2018). This reflects the relatively high potential cost of wilding conifer impacts on water resources and grazing land if invasions are not controlled. Biodiversity is also under a high level of threat from wilding conifers, but is more difficult to quantify in monetary terms (Wyatt 2018).

Given the relatively high economic costs and ecological effects of wilding invasion, it is not surprising that a substantial amount of research has been done on wilding conifers in



Figure 1. Illustrative examples of different invasions and how they progress through high-cost management strategies to post-control results, showing wilding conifer invasions in different habitats: (a) geothermal area in the Waikato, and (b) flats and slopes along Clarence river, Canterbury; (c) control methods using herbicide applied into holes drilled into tree trunks (“drill and fill”) and (d) aerial application of herbicide as foliar spray; and (e, f) post-control outcomes of the drill and fill and aerial foliar spray application methods. Photos by R Sprague (a–c, e, f) and N Ledgard (d).

New Zealand. Management-oriented research has included improved methods for detection (Dash et al. 2019), management techniques (Ledgard 2009), herbicide application (Gous et al. 2015; Scholten et al. 2019; Richardson et al. 2020), and potential for biocontrol (Hill et al. 2003; Brockerhoff et al. 2016). Based in part on this research, removal of wilding conifer via herbicides, cutting, and other techniques is now routine. This research has underpinned the New Zealand Wilding Conifer Management Strategy 2015–2030 (MPI 2014) which has a focus on removing wilding conifers at the landscape scale through control, containment, or eradication but does not consider rehabilitation or restoration.

Removal frequently fails to kill 100% of trees and may result in post-removal dominance by other non-native species, or reinvasion by wilding conifers (Dickie et al. 2014a; Peltzer 2018). From other plant invasions, we know that changes of ecosystem state driven by invasive species can result in long-term ecosystem legacies following eradication (Reynolds et al. 2017), and this appears to be the case with wilding conifer removal as well (Dickie et al. 2014b). These legacies may contribute to long-term challenges in management and contribute to undermining weed management objectives over time (Hulme 2020). Thus current control methods may help reduce spread, but fail to restore ecosystems. This is reflected in a national-scale focus on area treated and percent kill, rather than whether long-term desired land-use outcomes are achieved.

In parallel to control-oriented research, there has been extensive ecologically focussed research on wilding conifers in New Zealand, which is highly relevant to ecosystem restoration. Ecological research has investigated drivers and mechanisms of invasion, including seed production and

dispersal (Caplat et al. 2012; Coutts et al. 2012; Wyse et al. 2019; Wyse & Hulme 2021), plant traits versus introduction effort (Bellingham et al. 2004; McGregor et al., 2012), and fungal associations of wilding conifers (Davis & Smaill, 2009; Dickie et al. 2010; Moeller et al. 2015; Gundale et al. 2016) and their dispersal by mammals (Wood et al. 2015). Other ecological research has focussed on impacts on soil nutrients (Dickie et al. 2011), plant communities (Dickie et al. 2014b; Howell & McAlpine 2016; Davis et al. 2019), and fire risk (Taylor et al. 2017) in invaded areas. Lastly, a few studies have considered impacts of wilding conifer invasions on surrounding ecosystems, including stream biofilms (Thompson & Townsend 2004) and deep sea trenches (Leduc & Rowden 2018). Several recent studies consider societal dimensions of invasion including social values associated with wilding conifer invasions (Edwards et al. 2020; Gawith et al. 2020; Mason et al. 2021a; Yletyinen et al. 2021), including concerns over control methods (Edwards et al. 2020), and around ecosystem service trade-offs and social conflict (Dickie et al. 2014a; Mason et al. 2017).

While ecological research may have potential to improve outcomes, uptake into wilding conifer management remains limited. In part, this may be due to granularisation of research into scientific publications and a focus on international scientific novelty rather than local application. Here we seek to overcome this gap by gathering all New Zealand-relevant ecological research on wilding conifer legacies and applying this knowledge to improve long-term outcomes following wilding conifer removal. We review the abiotic and biotic impacts of wilding conifers at a local scale (or “within site”). We then consider temporal processes that span from invasion to

restoration: lag-phase, tipping points, ecosystem development, post-removal legacies, and the desired ultimate land-use outcomes. Based on the evidence gathered from reviewed literature, we develop a preliminary decision support tool to help improve chances of long-term desired land-use outcomes, and review knowledge gaps that remain to be addressed.

Methods

We surveyed the literature on wilding conifers in New Zealand, using the search string “TITLE-ABS-KEY(wilding OR invasi* OR exotic OR alien OR weed OR contorta) AND TITLE-ABS-KEY(pine OR pinus OR conifer OR pinaceae OR pseudotsuga OR larix) AND AFFILCOUNTRY (zealand)” on the Scopus (Elsevier) database. This yielded 368 potential papers, which were then evaluated for relevance. Further *ad hoc*, heuristic searching was used to address specific topics. Research from outside New Zealand was incorporated where it was relevant, but not systematically surveyed.

More research has been done on conifers in plantations than on wilding conifers, and in some cases results from plantations may be relevant to understanding invasions. Nonetheless, plantations differ from invasions in species composition and stand structure of both trees and other vegetation, species composition of co-introduced or co-invading ectomycorrhizal fungi (Walbert et al. 2010) and microbiota, exogenous inputs of fertilizer and herbicide, disturbance associated with clearing of vegetation, planting and harvesting, and in underlying site properties. Data from plantations was therefore included with caution where relevant, but primarily when comparable data from wilding conifers was not available.

We consider impacts and legacies from the perspective of changes in ecosystem properties from comparable uninvaded ecosystems. In most cases, the comparison ecosystems are uninvaded grasslands that are primarily anthropogenic in origin, and that have themselves been considered “novel ecosystems” (Hobbs et al., 2006). Thus some of the changes that are attributed to “wilding conifers” could equally apply to any encroachment of woody vegetation (native or invasive) into grasslands (Dehlin et al. 2008; Dickie et al. 2011). In identifying and quantifying changes to ecosystem properties, we do not assume that change is necessarily “bad” or “good”, noting that invasive species such as wilding conifers can provide valued ecosystem services (Dickie et al. 2014a; Mason et al. 2017). Instead we focus on those changes that are likely to affect the success or failure of wilding conifer control efforts and longer-term ecosystem outcomes.

Results

Understanding local scale impacts of wilding conifers is key to managing for enduring desired outcomes. The ecosystem modifications of invasive trees can initiate longer-term legacies, which can, in turn, drive reinvasion and failure of ecosystem restoration. We focus on abiotic and biotic impacts, followed by discussion of how abiotic and biotic impacts vary with time.

Abiotic impacts

A driving motivation for the initial establishment of non-native conifers in New Zealand was to reduce soil erosion. Erosion prevention can be a positive ecosystem service provided by wilding conifers (Mason et al. 2017), based on the assumption

that any species of woody vegetation is equivalent in terms of erosion reduction. This assumption is supported by evidence that *Pinus radiata* plantations can provide erosion control similar to that provided by native woody vegetation, with more positive effects in older stands (Hicks 1991; Ekanayake et al. 1997). Grassland soils have 2.5 times higher root density in surface layers of soil than planted pine stands, but pine stands have larger roots and greater root mass in deeper soil layers (Chen et al. 2000). Logically, wilding conifers probably provide similar benefits in terms of reduced soil erosion as plantations, but there appear to be no direct measurements of the impact of wilding conifers on soil erosion in New Zealand.

The impacts of wilding conifers on hydrology are critically important to their estimated economic impact (Wyatt 2018), but remain poorly documented in New Zealand. However, there is substantial literature on pine plantation impacts on hydrology that is likely indicative of wilding conifer impacts (Mark & Dickinson 2008). Soils under pine plantations are consistently drier than adjacent pasture due to higher canopy interception and transpiration (Giddens et al. 1997). In comparison with pasture, planted pines reduced water flows by up to 80% in a Nelson catchment study (Duncan 1995), by 30–50% in the western Waikato (Hughes et al. 2020), and by 40% in the Southern Alps (Mark & Dickinson 2008). The hydrological impacts of planted conifers vary with soil, rainfall, slope, extent of conifer area, and original ecosystem state (e.g. pasture, gorse) (Duncan 1995; Hughes et al. 2020). Overseas, research from south-west Australia has shown invasive *P. pinaster* has reduced an aquifer which serves as a major water source for the city of Perth (Stock et al. 2012; van Etten et al. 2020).

In addition to hydrological impacts, wilding conifers cause substantial changes in soil chemistry and function. Most notably, wilding conifer invasions are associated with a loss of around 20% of soil carbon in soil surface horizons (0–100 mm depth) and increases in soil P availability (Dickie et al. 2011; Dickie et al. 2014b). Soil pH tends to drop with increasing wilding conifer density, whereas nitrate-N, and total N and P responses vary across studies. These chemical changes are similar to some observations of planted pine in New Zealand (Davis & Lang 1991; Davis 1998; Chen et al. 2000; Scott et al. 2006) and elsewhere (Chapela et al. 2001), with a loss of soil carbon being particularly consistent.

Leaf area index of wilding conifers, and hence shading, increases rapidly with tree density and can be maximised at intermediate densities due to crown shape (Dickie et al. 2011). Soil respiration is better correlated with wilding conifer leaf area index than density, possibly reflecting total carbon input into soil (Dickie et al. 2011). A major controller of soil carbon dynamics and ecological processes is temperature. High shading by wilding conifers can moderate soil temperatures, particularly summer high temperatures. In a comparison of dense *P. nigra* invasion vs adjacent uninvaded grassland, mean annual soil temperatures at 50 mm depth were reduced 15% under pine invasion (from 10.1 to 8.6 °C), while maximum temperatures were reduced 41% from 29.3 to 17.2 °C and minimum temperatures remained unchanged (0.1 °C, unpublished data from Dickie et al. 2011).

Biotic impacts

While biological invasions are often predicted to cause a loss of biodiversity, wilding conifers do not have universally negative effects on native plant diversity (Sapsford et al. 2020). Howell and McAlpine (2016) found that the understory of *Pinus contorta* can support a high diversity of native species, and

Dickie et al. (2011) found that low to intermediate densities of *Pinus nigra* had little or even positive impacts on other plant species richness, although plant diversity decreased at higher pine densities. Negative impacts of dense trees may be driven by shade, competition for water, and changes to soil properties (Dehlin et al. 2008). The reported impact of wilding conifer invasions on plant diversity may depend on scale of measurement, as smaller plots are more likely to show a linear decrease in plant diversity with tree density, while larger plots show an initial increase in plant diversity followed by decline at high wilding conifer density (Sapsford et al. 2020). An initial increase in plant diversity in larger scale plots is likely driven by increased habitat heterogeneity at low to moderate tree densities (Sapsford et al. 2020).

Similar to the effects of wilding conifer density on plant diversity, aboveground insect diversity may also be robust to low and moderate density wilding conifer invasions. For example, *Pinus nigra* planted at densities up to 800 trees ha⁻¹ had relatively small negative effects on invertebrate diversity (Pawson et al. 2010), while other studies have shown that conifer plantations can support an equal diversity of native detritivores as native forests (Parker & Minor 2015). Similarly, generalist aboveground invertebrates are more abundant in *Pseudotsuga menziesii* plantations compared to adjacent native *Nothofagus cliffortioides* forest, whereas specialist taxa are more abundant and diverse in *Nothofagus* forest (Evans et al. 2021).

In contrast to the more gradual effects of wilding conifer density on plant and insect diversity in the above studies, even low densities of wilding conifers have been linked to substantial changes in soil biology and function. Dickie et al. (2011) found rapid losses of oribatid mite and plant-feeding and plant-associated nematode richness with increasing *P. nigra* density. A further analysis of this data showed that increased *P. nigra* density caused nematode communities to lose structural complexity and showed an increased dominance of stress tolerant species (Peralta et al. 2019). Similarly, even low levels of *P. contorta* invasion have been shown to result in a reduction of nematode diversity, and an increase in nematodes with short life cycles (Peralta et al. 2020).

Fungal communities are highly sensitive to wilding conifer invasion. Wilding conifer invasion is associated with a successional accumulation of a relatively small number of species of non-native ectomycorrhizal fungi, along with a few native, generalist species (Dickie et al. 2010; Sapsford et al. 2021), although diversity of both co-invasive and native fungi is somewhat higher on *Pseudotsuga menziesii* (Moeller et al. 2015). This relatively small increase in ectomycorrhizal fungal diversity occurs at the same time as a loss of around 50% of saprotrophic fungal diversity and a concomitant homogenisation of fungal communities and loss of overall fungal diversity (Sapsford et al. 2021). Ectomycorrhizal fungi have enzymatic capabilities for organic nutrient uptake that may represent fundamental shifts in soil function (Nunez & Dickie 2014). Wilding conifers also support a diverse community of fungal pathogens, which have the potential to spill over into native vegetation or plantation forests (Steel et al. 2022). Comparative analyses of fungal endophytes associated with *Pinus contorta* roots showed that pathogenic taxa are more abundant, about 4-fold more diverse and compositionally distinct on plants from New Zealand compared to northern hemisphere plants or native *Nothofagus* (Gundale et al. 2016). It has been suggested that soil from pine plantations can support *Phytophthora agathidicida*, the causative agent of kauri dieback, with potential to spill over into kauri (*Agathis*

australis) forest (Lewis et al. 2019).

The simplification of soil fungal and invertebrate communities following wilding conifer invasion coincides with an increased dominance of the bacterial energy channel. As bacteria are primarily top-down regulated by predators, this shift is reflected largely in increased bacterial feeding nematodes (Dickie et al. 2011; Dickie et al. 2014b). This shift is also supported by data from pine plantations showing a moderately high diversity of bacteria, but low diversity of fungi under plantations compared with other land-uses (including native forest, low-producing grasslands, and agriculture) (Wood et al. 2017). Increased bacterial energy channel dominance is often indicative of faster nutrient cycling rates (Wardle et al. 2004), which combined with potentially novel enzymatic capabilities of ectomycorrhizal fungi (Nunez & Dickie 2014), may contribute to the observed increase in availability of phosphorus and loss of soil carbon. Increased nutrient availability, in turn, is likely to contribute to the invasion of other plant species, including high phosphorus demanding species such as invasive legumes.

The element of time

The abiotic and biotic changes driven by wilding conifers vary with time, with some impacts accumulating rapidly and others developing more slowly following initial invasion. For management, explicit consideration of time may therefore be important. Here we consider several critical time-dependent processes: lag phases in invasion, tipping points in impacts, ecosystem development, legacies of wilding conifers following control, and restoration vs re-invasion. These are shown conceptually in Fig. 2, and relevant literature reviewed below.

Lag phase

At a national or regional scale, plant invasions commonly show an extended “lag phase” of slow initial establishment and spread followed by rapid increase (Aikio et al. 2010). Of the more than 25 000 introduced plants in New Zealand, only around 10% have naturalised and many of those remain limited in population or range size (Brandt et al. 2021). It is likely that some of these, including some not-yet-invasive conifer species, may currently be in a lag phase with future increases in population or range likely (Howell 2019). Predicting which species are in lag phase and which will never become invasive remains elusive. Therefore, while removing low-abundance non-native plants would be relatively low cost per naturalised species, managing potential weeds during the lag phase requires a high investment in surveillance (Harris et al. 2001), and a willingness to invest in removal of non-natives that might never become invasive. Lag phases also occur at local scales, where initial establishment and growth may be slow. Initial establishment may depend on infrequent long-distance dispersal, with individual wilding conifer seeds being dispersed 40 km or more (Ledgard 2001), and suitable microsites being available (Tomiolo et al. 2016). Rare, long-distance dispersal is critical to species spread but difficult to predict (Nathan 2006), and may be driven by a few individual seed trees on suitable take-off sites such as hill tops and ridges (Ledgard 2001). Initial growth of wilding conifers may be strongly limited by grazing, but as seedlings become woody with age, grazing becomes less effective as a control method (Ledgard & Norton 2008). Once established, wilding conifers produce viable seed from as young as five years of age, and an individual tree can initiate an invasive population within

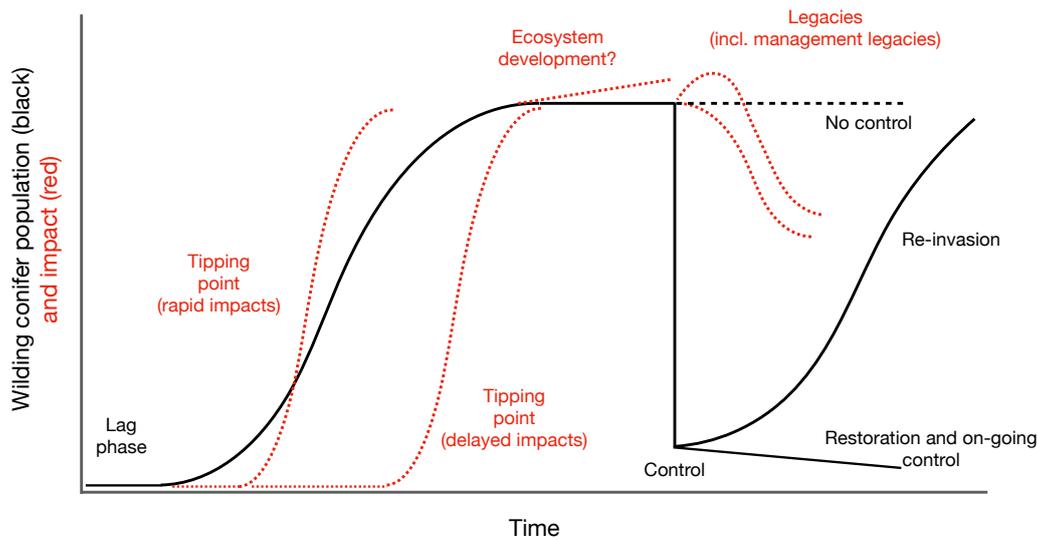


Figure 2. Conceptual figure of dynamics of wilding conifer populations (black lines and text) and impacts (red lines and text) over time. Impacts are shown where nonlinearities with density occur and are otherwise assumed to overlap with the black population line. Shown are early and late tipping points, ecosystem development over longer-term occupancy, and legacies that persist following wilding conifer control.

15 years of arrival (Ledgard 2001).

Lag phases can be driven by factors intrinsic to a species or by external drivers. Intrinsically, natural selection and adaptation, whether through genetic or epigenetic mechanisms (Zenni et al. 2016) may contribute to increasing invasiveness of species over time. It has also been suggested that wilding conifers in Europe may evolve increased resistance to native herbivores, and hence become more invasive through time (Moreira et al. 2013). Epigenetic changes may also drive rapid changes in species traits and have been shown to be important in other invasive species in New Zealand (Hawes et al. 2019). Slowly expanding populations may increase local genetic diversity, reducing inbreeding as has been observed in small natural populations of *Pinus* (Robledo-Arnuncio et al. 2004).

Infrequent and largely unpredictable events, such as fires or unusual weather patterns, can also result in sudden rapid increases in invasion following slow establishment. Disturbance events provide windows of opportunity where weeds (including wilding conifers) can rapidly expand. Wilding conifers include many fire-adapted species that are particularly well suited to rapid seeding following episodic fire. Climatic variability may contribute to fire risk and can also result in periods either particularly favourable or antagonistic to wilding conifer invasion. As one example, Tomiolo et al. (2016) suggested that climate prevented high elevation spread of *Pinus contorta* from planted stands for around 12 years, although the effect of climate subsequently diminished.

A number of extrinsic biotic factors play key roles in lag phases. Invasions of wilding conifers can be initially limited or slowed by intensive grazing and by dense vegetation, and then increase when those pressures are removed (Ledgard 2001; Ledgard & Norton 2008). Ledgard (2001) suggests that a reduction in grazing both from rabbits and sheep, combined with restrictions on high frequency burning contributed to a rapid increase in wilding conifers since the 1950s. Initial establishment of wilding conifers in New Zealand and elsewhere in the southern hemisphere was limited by a lack of compatible ectomycorrhizal fungi (Rundel et al. 2014). Deliberate and inadvertent introduction of non-native fungi

(Dickie et al. 2016), combined with subsequent dispersal by introduced mammals (Wood et al. 2015) has largely overcome this limitation (Dickie et al. 2010). At a local scale, initial, low-density wilding conifer invasions may increase mycorrhizal inoculum and allow a greater diversity of ectomycorrhizal fungi to establish (Sapsford et al. 2021). This may benefit multiple wilding conifer species, as an initial co-invasion of *P. contorta* and mycorrhizal fungi was shown to increase mycorrhization of *Pseudotsuga menzeisii* seedlings (Dickie et al. 2014b).

Tipping points

The term tipping points refers to the concept that a small change in one parameter can drive large changes in ecosystems, including driving systems into alternative stable states (Lenton 2013). Conceptually this can have some similarities to lag phases, but lag phases refer to the population and distribution of the invasive species, whereas tipping points apply more generally to impacts. Tipping points are also related to the concepts of ecological thresholds and alternative stable states (Norton et al. 2018).

Increasing tree density can cause both rapid and delayed impacts, which could correspond to tipping points. While few research papers have explicitly linked the theory of tipping points to actual wilding conifer invasion stages, we suggest that a few tipping points are well supported. These are:

- (1) Initial establishment of the first wilding conifer. This is an important tipping point because a single established tree can initiate the establishment of ectomycorrhizal fungi, greatly reducing the barrier to subsequent invasion (Fig. 3a).
- (2) First production of viable seed, resulting in rapid increase in invasion rate and density (Fig. 3b).
- (3) Shifts in belowground function. Biotic impacts of wilding conifers on many aspects of soil appear to be driven largely by the presence of any wilding conifer, rather than density. Tree roots (in general) have been shown to influence soils at distances of 2–3 times the height of the tree that they originate from (Baylis 1980; Dickie & Reich 2005). This suggests that for soil function and diversity, there is an important tipping



Figure 3. Development of wilding conifer invasions over time, showing (a) initial establishment, where no wilding conifers are visible, but establishment occurs between tussock grasses, allowing ectomycorrhizal fungal communities to build up populations, (b) initial seeding, (c-d) increasing below-ground occupancy, such that all areas are within 2–3 tree heights of established wilding conifers, (e) closed canopy forest, and (f) post-control legacies, showing high levels of wilding conifer necromass, invasive sward-forming grasses, and reinvasion by wilding conifers. Photo locations are (in order), Mt Bruce, Canterbury (a, b), Tekapo area with Aoraki Mt Cook in the background, Otago (c), Mt Isobel, Canterbury (d), Ngahere Experimental Basin, Kaweka Range, Hawke’s Bay (e) and Craigieburn Forest, Canterbury (f).

point when tree roots reach all microsites within the area (e.g. Dickie et al. 2005). This could be quantified based on tree height and spatial distribution (Sprague et al. 2019), or pragmatically assessed as the proportion of area within 3 tree heights of an established wilding conifer (Fig. 3c, d).

(4) Canopy closure and loss of native plant diversity. Wilding conifers most commonly invade into grassland ecosystems, largely comprising plants with limited shade tolerance. Thus, while initial impacts on native plant diversity may be slow to develop, canopy closure can drive a rapid change later in the invasion process, with a subsequent loss of native plant diversity and seed sources (Fig. 3e).

Other tipping points may occur, and further research on the application of tipping point theory to the density and age of wilding conifer invasions is needed.

Ecosystem development

Ecosystem development refers to the gradual change in ecosystem properties over time, including the accumulated effects of vegetation. In New Zealand, most wilding conifer invasions remain relatively young, while the majority of planted conifer stands are managed on fairly short rotation. This makes it challenging to predict the longer-term ecosystem changes that would occur if wilding conifer populations are allowed to persist. Thinning of pine plantations can result in increased native diversity in the understorey (McQueen 1973), but whether self-thinning in older wilding conifer stands would follow similar patterns remains unknown. Furthermore, there is evidence that wilding conifer populations exhibit ecosystem effects that differ from mature conifer stands in their native range. For example, in a comparison of *Pinus contorta* as an invasive in Chile vs as a native in a North American site,

Taylor and colleagues (2016) found that biodiversity impacts with increasing tree density were greater in the invasive range, while litter depth increased more rapidly with increasing tree density in the native range. Wilding conifers are associated with increased bacterial dominance, whereas conifer stands in their native range are generally assumed to be fungal dominated. This may suggest that the increased bacterial dominance of wilding conifer stands is a transitional state that will eventually reverse to fungal dominance (Dickie et al. 2014b). However, there is also some evidence that the importance of the bacterial energy channel in conifer stands in their native range has been previously underestimated (Pollierer et al. 2012).

Legacies

The impacts of invasive plants on soils and on biotic communities are not immediately reversed following control efforts but may persist for some time (Corbin & D'Antonio 2012). While killing and, in some cases, removing wilding conifers aboveground is fairly straightforward, removing the effects of those wilding conifers on soils or belowground communities is not generally possible. A common outcome following wilding conifer control is invasion of other non-native species, particularly grasses (Fig. 3f), and soil bioassay results suggest at least part of this effect is driven by soil legacies (Dickie et al. 2014b). The dominance of grasses following wilding conifer removal may decline over time, with one study showing lower grass dominance ten years after wilding conifer removal, although this did not coincide with recovery of native vegetation (Paul & Ledgard 2009).

The mechanisms driving legacies include the residual biomass of wilding conifers, persistence of biotic changes (e.g., other invasive species), or lasting changes to the abiotic environment (Reynolds et al. 2017; Wardle & Peltzer 2017). Killing of wilding conifers results in a major input of carbon and nutrients in the form of leaf and root litter and deadwood, but the degree to which this occurs is dependent on the methods used (clearcut, mulching, herbicide; Fig. 4a). Dead trees left on site can provide shelter for seedlings of both invasive and native species (Paul & Ledgard 2008). Biotic legacies include the persistence of ectomycorrhizal fungi, which may facilitate re-invasion by wilding conifers (Dickie et al. 2014b).

Management activities (e.g. herbicide, roading) during wilding conifer removal can create another mechanism for legacies, and these legacies can be highly method-dependent. For example, aerial foliar herbicide application can result in mortality of remaining native vegetation. Further, herbicides and their break-down products have been shown to persist in soils for up to two years, and longer in forest floor litter (Paul 2020). Contrary to some prior suggestions, this residual herbicide does not appear to directly suppress ectomycorrhizal fungi (SS, ID, CA Rolando, T Paul, unpubl. data), but does affect germination and growth of both wilding conifer seedlings and other vegetation for at least 16 months, including inducing severe root and shoot deformities (Fig. 4b). Direct application of herbicide through drilling and filling may greatly reduce non-target impacts (Paul & Ledgard 2009).

There are two largely unresolved questions around the timing of wilding conifer legacies. First, how rapidly do legacies develop following initial invasion? Most studies of wilding conifer legacies have compared well established stands to uninvaded sites, and we were unable to find any studies of stands younger than 20 years. Second, how long do legacies persist following removal? We found no published data on the persistence of wilding conifer legacies over time since

removal. However, soil legacies of native conifers in New Zealand have been shown to persist over 40 years (Wardle et al. 2008). Further, overseas data suggests that at least some mycorrhizal fungi associated with wilding conifers have high spore longevity in soil, with inoculum potential of some species increasing with time over a period of at least a few years (Bruns et al. 2009).

Long-term outcomes: Pasture, Plantation, Restoration or Reinvasion?

Pasture

In some cases, the goal of wilding conifer removal is to restore or establish pasture. Non-native grasses may have increased growth following wilding conifer removal (Davis 1998; Paul & Ledgard 2009; Dickie et al. 2014b), which in the case of pasture is advantageous. Once established, non-native grasses may successfully resist wilding conifer invasion, with fertilization increasing this ability (Ledgard 2006). Benecke (1967) found that fertilised and over-sown grasslands successfully resisted *P. contorta* establishment through competitive exclusion of seedlings, regardless of the level of grazing.

Heavy grazing by ungulates has been shown to effectively prevent *P. contorta* invasion in South America, but only at > 4 times the recommended sheep stocking rate for the area (Nasca et al. 2018). Interpreting this in the New Zealand

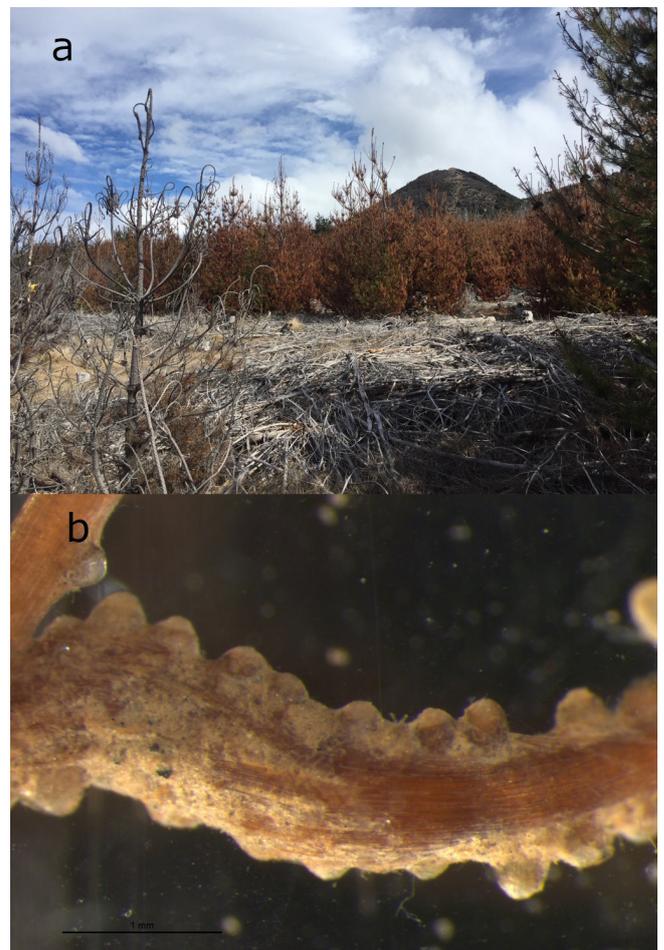


Figure 4. Legacies of management include (a) residual biomass left on site, providing shelter and nutrients, and (b) residual herbicide effects on other plants, in this case root deformities on *Pinus contorta* grown in post-spray soils.

context is challenging, as stocking rates are often much higher. Nonetheless, wilding conifers vary in palatability to sheep, but in general a sufficiently high stocking rate to suppress wilding conifers would likely also suppress most native regeneration and may exceed optimal stocking rates for pasture productivity or other environmental outcomes. Benecke (1967) suggests that unimproved grasslands with carrying capacities of 1 stock unit per 4 acres or less (equivalent to 1 female sheep 1.6 ha^{-1}) are susceptible to invasion; under these conditions conifers survived, but did not grow, for at least 27 months in unimproved grasslands. The importance of stocking rate is supported by further anecdotal evidence from New Zealand that reduced stocking and cessation of fertilizer can increase wilding conifer invasion (Ledgard & Norton 2008).

Plantation

A second possible outcome after wilding conifer removal is the establishment of plantations of other, less-invasive, non-native trees.

With any non-native planting, the risk of that species becoming invasive needs to be carefully considered. Obtaining fast-growing forestry species that present low risk of invasion remains a challenge. Conifers with greater seed mass are widely thought to have shorter dispersal distances, but recent work has demonstrated that seed dispersal is driven more by the ratio of mass to wing size in conifers rather than mass per se; furthermore, the ratio of mass to wing size trait varies considerably within species (Wyse & Hulme 2021). Serotiny, where seeds are retained in cones and only released after fire, is also of limited value in preventing invasion, as solar warming can cause cones to open (Wyse et al. 2019). There has been research into producing sterile pines, and into using species currently perceived to be lower invasion risk, such as *Pinus radiata x attenuata* hybrids (Froude 2011). Sterility has generally involved male sterility, rather than elimination of cone and seed production (Fritsche et al. 2018). Conifers produce copious wind-dispersed pollen, and hence male sterility may only limit invasion in situations where complete removal of surrounding pollen sources is possible. The perception that hybrids are lower invasion risk based on seed size and serotiny also needs to be rigorously tested, which has not yet occurred (Dungey et al. 2013). Previous failure to invade may not indicate future trends, as many species show extended lag phases (see above) before becoming invasive.

Replanting following timber harvesting in plantations is routine, and it is likely that planting non-native trees following wilding control may largely follow similar patterns. Nonetheless, some of the legacies of either wilding conifers or their management may affect planting success, such as persistence of pathogens or residual herbicide. The risk of reinvasion by wilding conifers under a planted forest requires consideration, including the possibility that wilding conifers may be challenging to detect when growing among plantation trees (Perroy et al. 2017).

Restoration

Wilding conifers frequently occur on land where the objective of wilding conifer removal is to restore native vegetation. Large areas of wilding conifer invasion occur in tussock grass and shrub dominated grasslands. Although dominated by native species, many of these ecosystems are the result of historical anthropogenic burning and grazing (Hobbs et al. 2006), but have come to have a high cultural value as an iconic landscape (Page et al. 2015). Wilding conifers are

able to establish between tussock spaces in these grasslands, particularly where tussock density is low (Allen & Lee 1989). It has been argued that wilding conifers represent a somewhat inevitable reversion to woody vegetation in these ecosystems, albeit comprising non-native rather than native trees (Hall et al. 2019). As such, restoring and maintaining grassland presents a higher reinvasion risk than taller-statured woody vegetation (Taylor et al. 2016).

McAlpine and colleagues (2016) found that native regeneration under *P. contorta* was limited by a lack of seed sources, while in other sites seed rain under wilding conifers can be dominated by native species (Moles & Drake 1999). Nonetheless, even where native species dominate seed rain, non-native weedy species may dominate dormant seed banks in the soil and are therefore likely to dominate if large scale disturbance occurs (Moles & Drake 1999). The method of wilding conifer removal may have a large effect on restoration success, with poisoning (resulting in gradual tree death) being more effective than clear felling, as this maintains partial shading and reduces weed growth (Paul & Ledgard 2009; McAlpine et al. 2016). Paul and Ledgard (2008) also suggest that dead conifers left in place can increase native shrub growth and reduce exotic dominance, but with some loss of plant diversity due to increased grass growth.

Opening gaps in wilding conifer canopies can increase native seed germination, but this is species dependent (McAlpine & Drake 2003). While some native species respond well to gaps, gaps also greatly increase germination of some weeds, including *Cytisus scoparius* (McAlpine & Drake 2003). Underplanting wilding conifers with native conifers has been successful in degraded pine plantations (Forbes et al. 2015), and may allow more rapid development of native, later-successional forest than would be achieved by clear-felling.

Although a few New Zealand native plant species are ectomycorrhizal (*Nothofagus*, *Kunzea*, *Leptospermum*, *Pomaderris*), there is very limited sharing of fungal partners between most wilding conifer species and native plants (Dickie et al. 2010; Moeller et al. 2015). The partial exception is *Pseudotsuga menziesii*, which may be more prone to forming associations with native fungi than other introduced conifers; but even for *P. menziesii*, non-native fungi predominate once *P. menziesii* is the dominant vegetation (Moeller et al. 2015). Sites where established native ectomycorrhizal vegetation is absent may require mycorrhizal inoculum of native plants during restoration, either by planting already mycorrhized seedlings, or through direct inoculation.

If successfully established, native vegetation could reduce subsequent wilding conifer reinvasion, as increasing vegetation cover is negatively correlated with *Pinus contorta* invasion (Taylor et al. 2016). Taylor and colleagues also found that tall shrub and woody vegetation had lower levels of invasion than either grasslands or short shrubland. The ability of tall woody vegetation to resist invasion has some limitations as edges of plantings, gaps, and disturbed areas may provide higher light environments where wilding conifers can establish. Further, *P. menziesii* has been shown to invade into native forest in Argentina (Orellana & Raffaele 2010), suggesting that restoration of native vegetation in New Zealand may not prevent invasion by shade tolerant species.

The ability of native vegetation to suppress reinvasion can depend on site factors. Wilding conifers can invade into favourable microsites well above native treeline (Tomiole et al. 2016). On these more extreme sites, competition from tussock grasses and shrubs may help suppress early

establishment of wilding conifers compared with bare soil or alpine mats (Tomuolo et al. 2016), but those wilding conifers that do establish in alpine sites are unlikely to be subsequently suppressed by relatively short stature native vegetation.

Reinvasion

Reinvasion by wilding conifers is common following wilding conifer control (Buckley et al 2007; Banks et al. 2018). Such reinvasion can differ from initial invasions as the legacies of the initial invasion and control method change the biotic and abiotic environment compared to the initial invasion.

A substantial seed bank may persist following wilding conifer death. For example, *Pinus contorta* seeds in direct contact with soil can retain viability for four years (Ledgard 2001) and may persist longer where partially open or closed cones are buried in soil (Teste et al. 2011). Any remaining trees either in or near a removal site will continue to produce fresh seed rain, while trees with surviving branches within managed sites can show rapid regrowth (Paul & Ledgard 2009). Choice of method may have a substantial impact on reinvasion. Harvesting wilding conifers can remove the trees, but it disturbs the soil and leaves it more vulnerable to reinvasion from the seed bank and from surrounding seed sources, while mulching, for example, fails to kill branches low on trunks, resulting in substantial reinvasion by resprouting (Paul & Ledgard 2009).

Wilding conifer removal creates a highly disturbed environment, and wilding conifers are adapted to establish well following disturbance. This has been termed a “weed-shaped hole” (Buckley et al. 2007), which either wilding conifers or other invasive species are likely to refill. Wilding conifers are also well adapted to fire disturbance, which is a major risk post-removal, driven by dead standing or felled trees and by increased grass biomass (Clifford et al. 2013). Early successional shrublands are fire prone, which is further promoted by non-native plant invasions, potentially preventing return to native vegetation dominance (Perry et al. 2015). Where there is an opportunity for selection of species used in restoration, consideration of flammability (Wyse et al. 2016) or ability to resprout following a fire (Teixeira et al. 2020) may increase resilience. Climate change may further increase the risk of reinvasion, particularly through increases in disturbance (e.g. fire).

The impacts of wilding conifers on mycorrhizal fungi, herbivores, and other biota can also contribute to reinvasion. Reinvading trees are unlikely to be limited by a lack of mycorrhizal fungi. Conversely, increased populations of wilding-conifer adapted pathogens may reduce wilding conifer growth and density, as has been observed in other weeds (Diez et al. 2010). Non-native herbivores also appear to have a larger negative effect on wilding conifer density than on total native plant abundance in one study (McAlpine et al. 2016).

Discussion

Despite much research on the management of wilding conifers in New Zealand, these invasive tree species remain a pernicious problem. Management of invasive species has been said to suffer from a “knowing-doing gap” where ecological research has little impact on management activities (Matzek et al. 2014). Management practitioners identify research on improved methods of killing invasive species as a key priority, along with further research on invasive species impacts, while longer-term outcomes are often seen as lower priorities (Matzek et al. 2014).

A focus on killing wilding conifers may be sufficient where the primary objective is reducing spread (Buckley et al. 2005), rather than restoring or otherwise rehabilitating the invaded site. Reducing spread protects uninvaded areas and thereby reduces overall long-term management costs. Nonetheless, as wilding conifers become increasingly common, and an increasing proportion of the landscape is impacted, it is logical to shift the focus toward mitigating impacts, increasing resistance to reinvasion, and restoring or transitioning ecosystems to new, presumably more desirable, states.

Here we have reviewed ecological research on wilding conifers in New Zealand, with a goal of improving long term management outcomes. In broad strokes, the lessons gleaned from published ecological research can be summarised as follows:

- (1) Wilding conifers fundamentally change soils and other aspects of ecosystems, and these impacts are not easily reversed;
- (2) Altered soils and other site conditions, combined with increased invasion pressure, make re-invasion and invasion by other non-native species highly likely;
- (3) Impacts and legacies are non-linear with wilding conifer density and over time, showing tipping points where impacts rapidly increase;
- (4) Restoration and maintenance of tussock grasslands is problematic when wilding conifers are present, with ongoing intensive management in perpetuity likely necessary; and,
- (5) Viable long-term outcomes not requiring a high investment in ongoing management are:
 - (a) improved pasture,
 - (b) replanting to non-native trees of less-invasive species,
 - (c) tall woody native vegetation (large shrubs, trees).

These findings have direct implications for management, suggesting that a greater focus on desired land-use outcomes is critical, and that legacies of wilding conifers should be considered both during management (e.g. avoiding critical tipping points) and in restoration to ensure the objectives or goals of management are achieved.

An outcome-focussed decision tree to support management

Based on our consideration of tipping points, legacies, and restoration, and incorporating these ecological processes with management practices, we have developed a decision tree to achieve different desired land-use outcomes (Fig. 5).

The first step is perhaps the most critical in the decision tree: consideration of long-term desired land-use outcomes. The choice of land-use outcomes sits within the broader context of the site, including both biophysical constraints (soils, climate), invasion risk into the site, budget and timeframe, and social, cultural, and legal constraints. A critical consideration is the potential of the site to drive further spread, and whether avoiding this requires more rapid management.

Non-native vegetation

Where the goal is improved pasture (e.g. fertilised, non-native grasses with intensive grazing), wilding conifers can be removed using the most cost effective strategies (Ledgard 2009). Subsequent land uses that include fertilisation, over-sowing and heavy grazing or ploughing of soil should be sufficient to deplete seed banks and prevent reinvasion within a site (Crozier & Ledgard 1990; Nasca et al. 2018). The stocking densities sufficient to prevent wilding conifer reinvasion, particularly of lower-palatability conifer species,

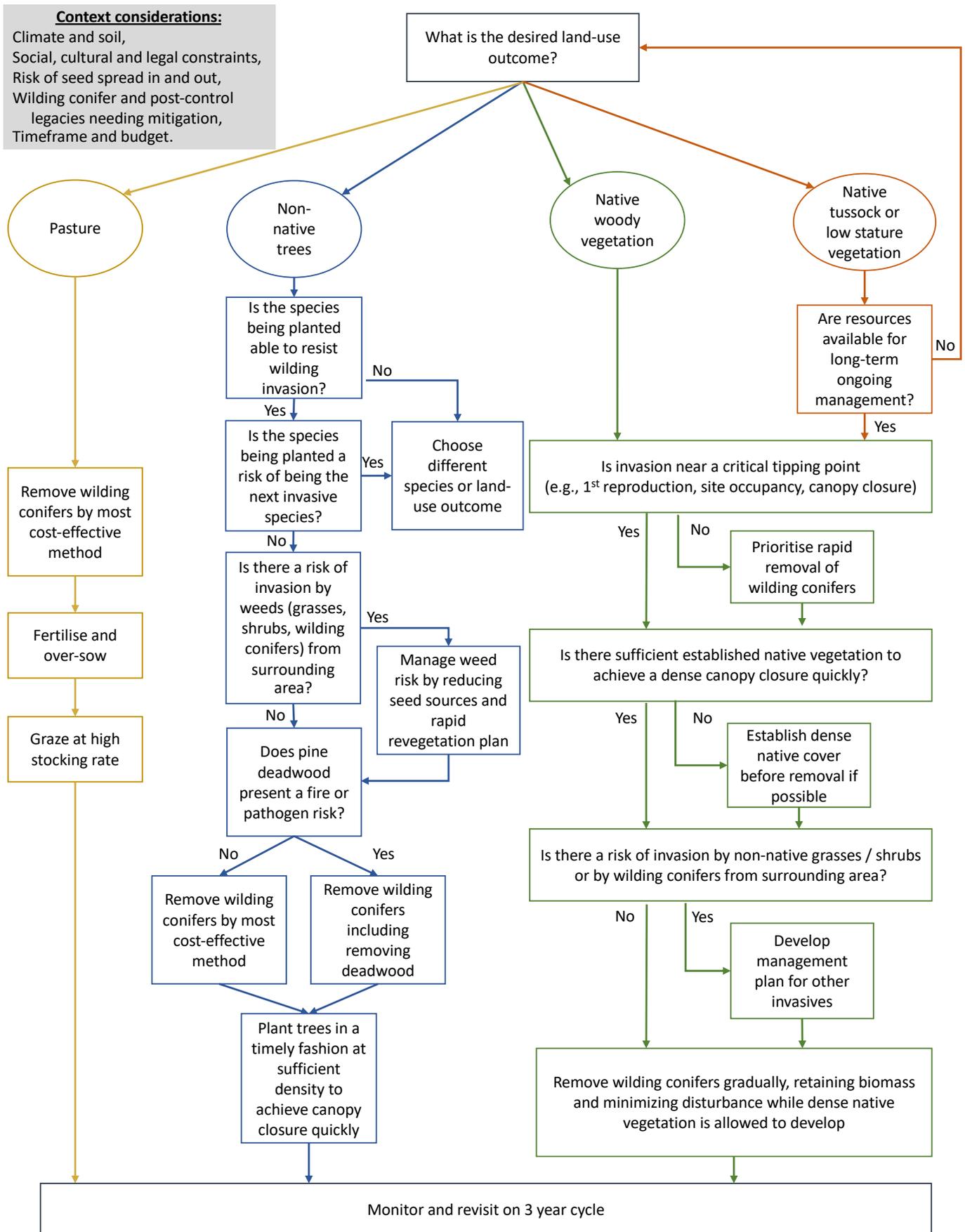


Figure 5. A preliminary decision support tool for long-term management of wilding conifer invasions, with a focus on desired long-term outcome.

may be higher than optimal for maximizing yield (Nasca et al. 2018). Ditches and fence lines or other sites inaccessible to stock present a risk of reinvasion and may require active ongoing management. Notwithstanding these issues, improved pasture remains the most straightforward land-use to achieve (Ledgard 2009).

A second option is to replace wilding conifers with another non-native tree or trees (typically fast-growing species with economic value). Any replacement tree species must simultaneously be able to resist wilding conifer invasion and not, itself, pose a risk of being the next invasive tree (Howell 2019). The latter problem is illustrated by Douglas-fir, which has possibly become much more invasive over time as compatible mycorrhizal fungi have spread (Moeller et al. 2015). It has been suggested that hybrid *Pinus attenuata x radiata* may be less invasive than some other conifers based on seed size and serotiny (Dungey et al. 2013), but evidence that hybrids will not become invasive remains lacking. Many traits desirable from a forestry perspective (e.g. fast growth rate, ability to tolerate high elevation climates) are also likely to promote invasive risk (McGregor et al. 2012).

Once a suitable tree species is identified, potential risk factors need to be considered. Wilding conifer legacies and disturbance associated with control elevate the risk of further species invasion. Management strategies for non-native grass, shrub (e.g. Scotch broom), and wilding conifer invasions post-wilding conifer removal need to be considered, including removing adjacent seed sources and ensuring that revegetation occurs rapidly following wilding conifer removal. Further risks affect the choice of removal method, including fire risk if deadwood is left on site, risk of disease organisms establishing in deadwood, residual effects of herbicides (if used) on seedling growth, and risk of reinvasion by wilding conifers into windrows or edges of plantations.

Restoring native vegetation

Where the goal is to restore native woody vegetation, an important decision point is whether a critical tipping point has been reached that will make restoration more difficult. Management should be prioritised to remove wilding conifers as quickly as possible where tipping points have not yet been crossed; these include first reproduction, site occupancy (i.e. all areas within 2–3 tree heights of a wilding conifer), and canopy closure.

In some invasive conifer stands, native vegetation can be relatively abundant in the understory (Howell & McAlpine 2016), while in other sites a lack of seed can severely limit native regeneration (McAlpine et al. 2016). In areas without any native regeneration source, it should be considered whether native plants can be established before starting wilding conifer removal.

In most post-removal wilding conifer sites, there is a considerable risk of aggressive non-native weeds dominating. In particular, scotch broom and non-native grasses respond very vigorously to belowground legacies of wilding conifers and can dominate subsequent plant communities. Where advanced native regeneration is present and aggressive non-native weeds are absent, we suggest that removal can proceed either quickly or gradually, with monitoring and management of secondary invasion. If, however, aggressive weeds are present, then removal of wilding conifers may be best achieved using gradual removal strategies to try to reduce the release of these weeds. Gradual removal is also recommended to prevent wilding conifer reinvasion (McAlpine et al. 2016).

Restoring and maintaining native low-stature vegetation (e.g. small shrubs and tussock grasses) is the most challenging land-use outcome to achieve. Wilding conifers can easily invade even well-established native grasslands, as evidenced by the current wilding conifer problem. Before restoring native grassland, the capacity for ongoing management, likely in perpetuity, needs to be considered. For high value sites (rare ecosystems, alpine sites), biodiversity benefits may be sufficient to justify such long-term investment (Smale et al. 2011; Wisser et al. 2013; Tomiolo et al. 2016). Preventing tipping points is a key priority in these high value ecosystems, ideally stopping any invasion before it gets started. Otherwise, alternative land-use outcomes need to be considered. Tall woody native vegetation is more likely to resist wilding conifer reinvasion than low-stature vegetation, provided a high density can be achieved.

Ongoing management

Regardless of the desired land-use outcome, management of wilding conifers is not a single event, but rather requires ongoing monitoring and management. For *Pinus contorta*, a 3-year management cycle has been recommended to completely eliminate reproductive individuals before they can produce viable seed. Managing invasive trees on a relatively frequent cycle may also help avoid critical tipping points (e.g. shifts in belowground function), even for species having greater age to reproductive maturity. Multiple weeds are likely to respond to both the soil legacies of wilding conifers, and the disturbance created by their removal. Management of other invasive species (e.g. non-native grasses, Scotch broom, other invasive trees) may be necessary to achieve desired land-use outcomes.

Over much longer timeframes, the most resilient landscape is likely to be one dominated by improved pasture, planted non-native trees, and/or native forest. Native forest remains susceptible to invasion by Douglas-fir, which will require ongoing management. Low stature vegetation is likely to be maintained only in high value sites with intensive management. Outside of these high value sites, landowners are understandably adverse to managing wilding conifers where they believe re-invasion is inevitable and ongoing management will be required in perpetuity (Yletyinen et al. 2021). Conversely, land-use conversion including restoration to native woody vegetation may face social opposition due to a loss of iconic tussock grassland landscapes. Social conflict is widespread in invasive tree management (Dickie et al. 2014), with a recent study suggesting social concerns are the most critical constraints on wilding conifer management in New Zealand (Mason et al. 2021b).

Limitations and further research needs

Most of the research on wilding conifer impacts and dynamics reviewed here is based on a limited number of species (particularly *Pinus contorta* and *P. nigra*) and a limited number of locations, and generally over short time periods. The impacts and legacies of wilding conifers can be context dependent (Sapsford et al. 2020), and management may need to be tailored to individual regions and even individual sites. Long-term changes in impacts under older wilding conifer stands, and long-term persistence of legacies once wilding conifers are removed remain largely unexplored. Further, the impacts and invasibility of wilding conifers is likely to change over time due to, for example, evolutionary adaptation, accumulation

Table 1. Research gaps and questions remaining to be addressed.

Research gap	What is known	Key questions
Quantification of tipping points	Ecological theory of tipping points is well explored in the literature, and some response curves suggest tipping points are present in wilding conifer impacts at specific stages of invasion.	Can we better predict when tipping points occur? Are tipping points context dependent?
Resistance to reinvasion through native plant communities	Most wilding conifer species are shade intolerant, with the exception of <i>Pseudotsuga menziesii</i> . Establishment is associated with gaps between tussocks and disturbance.	Are there optimal mixtures of native plants? Can tussock grassland ever resist invasion? Can any native vegetation resist <i>Pseudotsuga menziesii</i> invasion?
Interactions of wilding conifers with other invasive plant species	Legacies of wilding conifers can favour non-native grasses and legumes.	How important are secondary invasions to long-term outcomes? Can legacies be mitigated by modifying soil or site conditions?
Interactions of wilding conifers with invasive animals	Deer, possums, and feral pigs are known to disperse invasive ectomycorrhizal fungi. Declining rabbit and hare populations are suggested to have led to increased wilding conifer invasions.	Are there any areas where invasive ectomycorrhizal fungi have not already established, and can invasive mammal management protect these areas? What is the role of herbivory in reducing wilding conifer populations?
Biotic resistance through other biota	Native <i>Armillaria</i> fungi were implicated in initial conifer plantation failures.	Can native pathogens be harnessed to increase ecosystem resistance to wilding conifer invasion?
Duration and reversibility of legacies	Wilding conifers impact multiple aspects of soil abiotic and biotic properties, which contribute to legacies following removal at least over relatively short time frames.	Long-term persistence of legacies has not been quantified. Potential for mitigation and reversal of legacies remains largely unknown.
Consequences of removal method for long-term trajectories	Disturbance can favour reinvasion, residual herbicide affects plant growth, and wilding conifer slash can facilitate both native and non-native plant growth.	Which removal methods are best in particular contexts or to achieve particular outcomes?
How do the impacts of wilding conifers on ecosystem services differ from native woody succession?	Some of the effects of wilding conifers (positive and negative) on ecosystem services are similar to the effects of any woody vegetation.	How much variation in ecosystem service effects of woody vegetation is driven by species?

of pests, pathogens and mutualists, changes in populations of other invasive species, and global climate change (Zenni et al. 2016; Dickie et al. 2017).

Despite the wealth of research that has already been performed on wilding conifers, a number of key questions remain to be addressed. Many of these deal with multi-species interactions of wilding conifers with other invasive plant species, with invasive animals, and with other biota (particularly pathogens). We identify a number of these key research questions in Table 1. From a management point of view, these remaining questions and uncertainties do not invalidate the value of ecological research but do suggest that an adaptive approach may be needed.

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Author contributions

IAD conducted the research and wrote the first draft with input from JG and SS. RS facilitated engagement with the New Zealand Wilding Conifer Group. All authors contributed to extensive discussions, editing and improvements to the manuscript.

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