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REVIEW

International use of exotic plantations for native forest restoration and implications for Aotearoa New Zealand

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Abstract: The desire for ecosystem restoration and native forest expansion is growing internationally. Transitional forestry, where an exotic plantation forest is transitioned to a native forest, is a potential method of native forest restoration and carbon sequestration that is gaining interest in Aotearoa New Zealand. However, it is currently unknown whether this approach can produce a permanent native forest ecosystem and how representative of remnant native forest it could be. This article explores international research into the use of exotic plantations to facilitate native forest restoration, specifically the ecological processes affecting restoration, and management interventions which could be applied to improve the forest transition. We found that the composition of the landscape matrix is highly influential on native regeneration. Increasing native vegetation cover to at least 25% has a strong positive effect on native regeneration within exotic forests. Increased native vegetation cover also improves effective seed dispersal as there are more sources of seed, shorter distances for the seed to travel, and improved habitat size and connectivity for avian seed dispersers. Further research into which seeds are entering plantation forests, by what method, and the distance from the seed source would be highly useful in understanding the potential for exotic plantation forests to transition to a native forest, and what barriers may be preventing this from occurring. Canopy manipulation was also found to be a key tool in stimulating establishment and growth of native species within an exotic plantation, especially those later-successional species which rely on small-scale disturbance in their natural succession. Practical methods of gradual canopy removal while minimising disturbance is an area which requires further research. We found that pest management is likely to be critical for transitioning exotic plantation to native forest. Herbivores present a significant barrier to succession as they can prevent growth and survival of susceptible species of regenerating plants and have significant effects on species composition and forest structure due to preferential browsing. Rodents which consume seeds prevent plants from establishing, further limiting regeneration. Mammals which predate native birds also disrupt the forest ecosystem due to the importance of avian seed dispersal for many tree species. This review highlighted the need for further research into transitional forestry and the potential to revert an exotic plantation to a native forest. Research conducted must occur across a variety of macroclimates, forest types, soils, and landforms throughout Aotearoa to ensure advice represents regional differences and is as comprehensive as possible.

Keywords: landscape matrix, native forest restoration, plantation biodiversity, transitional forestry

Introduction

The over-exploitation of natural resources and large-scale ecosystem degradation occurring globally has led to the point of crisis. In recognition of this the United Nations have begun the UN Decade on Ecosystem Restoration with the intention of ending ecosystem degradation, and restoring ecosystems to improve livelihoods, offset climate change, and stop a global collapse of biodiversity (United Nations 2021). Several countries, including Aotearoa New Zealand (hereafter Aotearoa), are directing more resources into producing strategies, goals, and objectives to improve biodiversity outcomes and expand ecological restoration.

Many countries use exotic species for plantation forestry to produce a sustainable source of fast-growing timber and fibre. Common species for exotic plantation forestry belong to the genera *Pinus* (Pinaceae) and *Eucalyptus* (Myrtaceae). There has been much debate over the impact of exotic plantation forestry on biodiversity, with some studies finding it to be neutral or beneficial (Tomasevic & Estades 2008; Pawson et al. 2010), while others find it to be detrimental (Pawson et al. 2011; Braun et al. 2017). Plantation forests tend to improve the landscape matrix in highly modified environments by enhancing forest habitat connectivity and providing a buffer to edge effects on native forest remnants (Norton 1998; Denyer et al. 2006; Pawson et al. 2008). However, exotic plantation species, especially *Pinus* species, also can have a damaging effect on natural ecosystems through plant invasions (McAlpine et al. 2016; Bellingham et al. 2022). Clear-fell harvesting operations can have further negative impacts including destruction of

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the native understorey (Ogden et al. 1997), loss of habitat for native fauna, and increased suspended sediment yields in waterways during harvesting activities in the catchment (Fahey et al. 2003). Recently in Aotearoa there has been increasing interest in returning exotic plantations to historic natural forest cover for environmental, social, and economic reasons (Forbes & Norton 2021). This could be through a transition from exotic to native (Forbes et al. 2019), restoration on land following clear-fell harvest, or a combination of both (Forbes & Norton 2021).

In Aotearoa there is growing interest in the concept of transitional forestry, where a fast-growing exotic forest is managed to transition to a native forest. Transitional forestry may be applied to a forest that is not able to be harvested due to economic, social, or environmental reasons, or to a forest that has been established with the purpose of transitioning. The increasing price of carbon in the New Zealand Emissions Trading Scheme (NZ ETS) has driven the expansion of carbon farming whereby landowners plant permanent forest, usually *Pinus radiata*, with the intention of earning carbon credits from the carbon sequestered through the growth of the trees. Such forests are not intended to ever be harvested. Stakeholders, such as farmers and rural communities, are concerned that, following current trends, carbon forestry is at risk of displacing productive land uses such as sheep and beef farming, and production forestry (Orme et al. 2021). The New Zealand Government has recently released a discussion document that proposes restrictions to exotic forests being registered in the NZ ETS (Ministry for Primary Industries 2022). A potential outcome from this consultation is that permanent exotic forests may only be able to be registered in the NZ ETS if they are being actively transitioned to native forest (Ministry for Primary Industries 2022). Therefore, it is critical that practical means of achieving a successful transition are explored and tested for both future forests established for transitions, and for those permanent exotic forests that already exist.

There are still many questions to be answered regarding the use of exotic plantation transitions for native forest restoration. The desired result of much native forest restoration is to restore forest cover comparable to what would have existed prior to disturbance and land-use change, with a goal of restoring the ecosystem and its functions. There remains a considerable uncertainty as to in which circumstances any meaningful restoration can be achieved, and in circumstances where regeneration is possible, how representative of the historic forest cover, or old growth forest, any transitioned forest will be and the timeframes for those outcomes (Forbes & Norton 2021). The factors affecting transition potential relating to the location of a forest, such as macroclimate, composition of landscape matrix, and the ability of seed dispersal to penetrate exotic forests, are areas which need further research. The length of time a transition may take, the establishment, survival, and growth of native and exotic vegetation throughout the transition, and the level of native regeneration required to secure a transition are all matters which are yet to be determined. Additionally, the management interventions needed to achieve a transition, and the thresholds where these will be necessary requires further research and investigation (Forbes & Norton 2021).

Here we synthesise research and observations in the use of exotic species in the facilitation of native forest restoration from around the globe, as well as current knowledge from within Aotearoa. The aim of this review is to integrate the findings from both Aotearoa and internationally into the use of exotic plantations for native forest restoration, consider what methods could be applied in Aotearoa, and highlight the most important areas for further research. We ask:

(1) What are the key forest ecological processes affecting restoration of native forest from exotic plantations?

(2) What forest management interventions have been trialled to influence restoration of native forest from exotic plantations and how could these be implemented in Aotearoa?

(3) Where should further research focus to improve our understanding of transitional forestry, whether a transition may be possible, and under what circumstances?

Overview of forest transitions

Biodiversity strategies

Preservation, enhancement, and restoration of ecosystems is vital to the health of both people and the planet (United Nations 2021). There are many instances of biodiversity strategies both internationally and in Aotearoa. An example of a large-scale strategy is The EU Biodiversity Strategy for 2030 which aims to address significant drivers of biodiversity loss whilst implementing structures and policies for long-term commitment and action on ecosystem protection and restoration, and biodiversity enhancement (European Commission 2021). The Australian government has also issued a national biodiversity strategy entitled Australia's Strategy for Nature that provides a framework of goals and objectives with the intention of strengthening the nation's response to biodiversity decline and developing deeper connections between people and nature (Interjurisdictional Biodiversity Working Group 2019). Te Mana o te Taiao – Aotearoa New Zealand Biodiversity Strategy 2020 is the national biodiversity strategy for Aotearoa which works in conjunction with the National Policy Statement for Indigenous Biodiversity. The National Policy Statement implements seventeen specific policies to protect, preserve, and restore indigenous biodiversity in Aotearoa (DOC 2022). The broader national biodiversity strategy provides direction and guidance to all government and non-government groups, communities, and individuals who work with or influence biodiversity. Implementation plans from the strategy will be produced every five years to provide specific goals and objectives in working towards the vision of Te Mauri Hikahika o te Taiao – the life force of nature is vibrant and vigorous (DOC 2020).

Biodiversity enhancement and ecological restoration are becoming more important both at national and local levels. Further research and development of restoration methods as well as ecosystem management and monitoring are mentioned throughout biodiversity strategies. To achieve the aspirations and outcomes detailed in these strategies further research into methods of ecological restoration which are effective and economical is essential. Forest transitions are one such method of ecological restoration which is currently unproven but has the possibility of bringing a new process whereby positive biodiversity and economic outcomes are realised. As more research is undertaken into transitional forestry, this method will likely become more important in ecological restorations, provided that research finds the process viable.

Forest transitions

The term 'transitional forestry' describes the concept of converting an exotic plantation forest to a native forest over time, drawing on the exotic plantation species' ability to act as a nurse plant for the regenerating native species. The plantation trees tend to be fast growing, allowing for canopy closure to be achieved in a relatively short timeframe. Fast growth also allows for the rapid sequestration of large volumes of carbon, hence why the exotic plantation species may be chosen over native early successional nurse species. The plantation trees outcompete light-demanding weed species, allowing for shade-tolerant species to establish beneath the canopy (Forbes et al. 2015). While the ecological processes acting on native regeneration within plantations are understood (Brockerhoff et al. 2003), relatively little is known about the practical means to achieve a transition and what management interventions are required, and in what circumstances, to facilitate forest succession towards a native forest.

There are many reasons why an exotic to native forest transition may be desirable. Benefits include earning income from carbon sequestration through an emissions trading scheme, or for retiring areas of plantation forest established on highly sensitive land which is not suitable for clearcut harvest. However, the overarching goal should be one of ecological restoration where the forest is returned to an ecosystem that is similar in species assemblages to what would have existed prior to land conversion. In line with ecological restoration principles, the transitioned forest should be self-sustaining reproducing populations of native plant species. The restored ecosystem should be resilient to environmental stress and have the ability to remain as a native forest in perpetuity (Society for Ecological Restoration International Science & Policy Working Group 2004). The ideal outcome is to produce a functional ecosystem which is reminiscent of remnant native forest ecosystems in the vicinity.

Plantation biodiversity

The restoration of a native forest occurs following successional processes. However, the potential for a transition from exotic plantation to native forest will depend on multiple factors, such as effective seed dispersal, favourable macroclimate, and committed ongoing forest management (Forbes & Norton 2021). The diversity and density of species present should be managed throughout the transition to attempt to resemble a remnant native forest to ensure succession will effectively produce a transition to a mature-phase native forest (Fig. 1).

The presence of native regeneration, especially that of tree species, in exotic plantation understoreys indicates the potential of a transition from plantation to native forest. *Pinus taeda* plantations in Argentina contain an understorey of native regenerating vegetation dominant in creeping herbs, vines, and ferns, with some graminoids, light-demanding trees, shade tolerant trees, and shrubs (Trentini et al. 2017). Species richness, composition, and density of native regeneration increases as plantation age increases and when there is a lower plantation basal area in *P. taeda* plantation (Ritter et al. 2018). *Pinus radiata* plantations in Chile have also been found to harbour many species of native plants in their understorey (Heinrichs et al. 2018; Kremer et al. 2021a), as have *P. radiata* plantations in Australia (Lindenmayer & Hobbs 2004), Northern Spain (Onaindia et al. 2013), and Aotearoa (Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2003).

Comparisons of understorey of exotic plantation with that of native forest has found important similarities and differences. The native species composition in *P. radiata* plantations in Northern Spain was found to become more like native forests with plantation age (Onaindia et al. 2013). The important species of *Ulmus minor* and *Ulmus glabra* were noted to be absent from the plantations, however, these species are colonisers of old-growth forest and the plantation ages sampled were likely too young to create the conditions required for these species to establish (Onaindia et al. 2013). In *Pinus sylvestris* plantation forests, also in Northern Spain, whilst native regeneration did occur in the understorey, the species composition was distinctly different to that of the

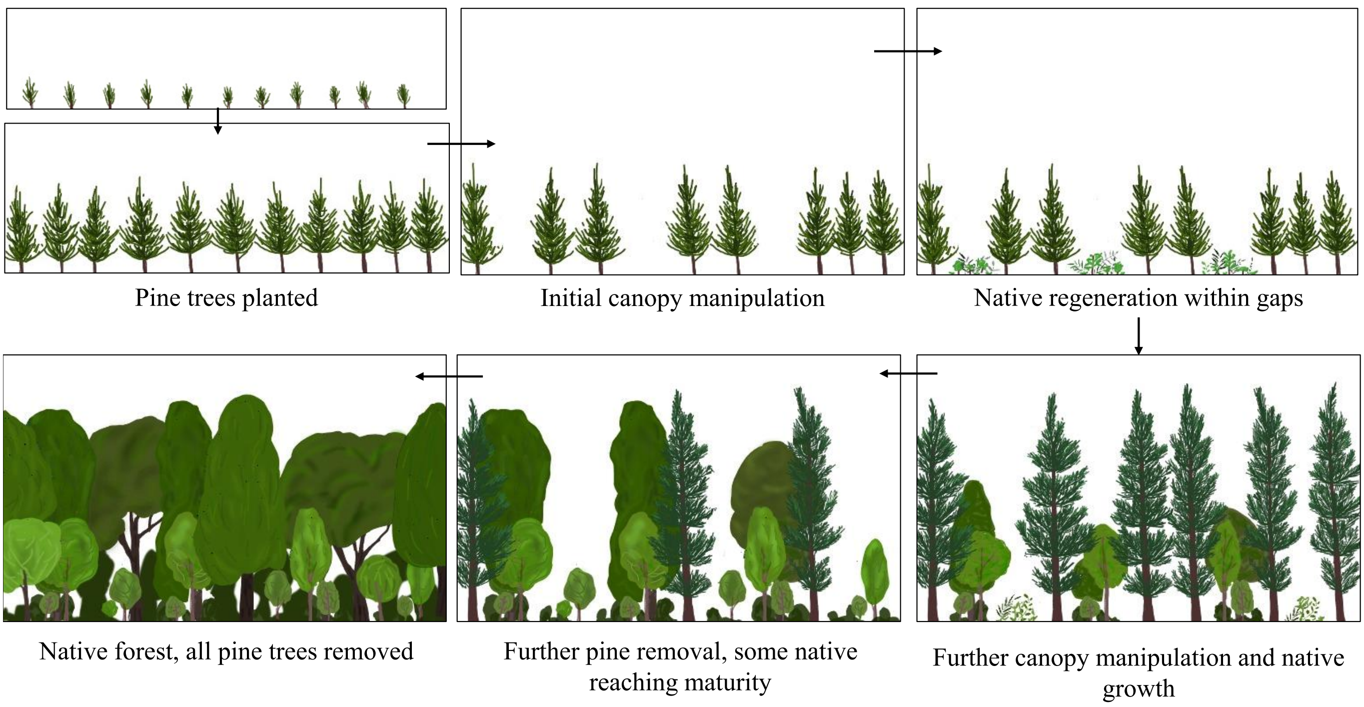

Figure 1. Exotic pine forest to native forest transition: Concept diagram.

native *Fagus* and *Quercus* forests. There was also a noticeable absence of the late-successional *Fagus* and *Quercus* seedlings in these exotic *P. sylvestris* forests (Tárrega et al. 2011). Lack of late-successional species and differences in density and diversity of native species between plantation and native forest were also observed in *P. radiata* plantations in Chile (Heinrichs et al. 2018; Kremer et al. 2021a). In Aotearoa *P. radiata* plantations, late-successional species are typically absent from the understorey (Forbes et al. 2019), although occasional records of these species in plantation understorey suggests that their establishment is possible (Brockerhoff et al. 2003). The widely observed absence of late-successional species from *P. radiata* plantations in Aotearoa may, therefore, be due to factors such as macroclimate, poor seed dispersal, lack of a seed source within a suitable range, or the plantation forest being too young for the late-successional plants to have established (Ogden et al. 1997; Brockerhoff et al. 2003).

Forest ecological processes

Seed dispersal

Effective seed dispersal is crucial for native forest establishment and succession on clear-felled sites as well as for exotic to native transitions. Understanding the mechanisms by which seeds are dispersed and the distances they can travel from their source will give an indication of the species that may more easily colonise and the balance between passive and active restoration activities that is required for successful native forest restoration (Forbes & Norton 2021).

When planning a forest restoration, assessing the level of contrast between the native forest that is acting as a seed source and the target site may give an indication of the species that will more readily establish, and those that may need some assistance. Seeds that are dispersed by wind may spread with ease to sites that are structurally very different from the native forest. However, seeds that are dispersed by vertebrates such as birds may more easily arrive in sites which are more structurally similar to the native forest, such as an exotic plantation (Vespa et al. 2014).

It is evident that the success of native forest regeneration is highly dependent on a nearby seed source and effective dispersal (Onaindia & Mitxelena 2009; Alday et al. 2015; Torroba-Balmori et al. 2015; Norton et al. 2018). In Aotearoa, many native tree species rely on birds to disperse their seeds, with 33% of native species utilising the dispersal mechanism of endozoochory (dispersal by animal consumption) (Thorsen et al. 2009). Vegetation structure is a highly important factor in the distribution of bird-dispersed seeds, with significantly higher diversity and density of seed rain found in areas of native forest compared with that of nearby grassland (Ferguson & Drake 1999). Seed rain of bird-dispersed seeds should, therefore, be greater within an exotic plantation forest compared with an open site. However, frugivorous birds are less likely to use exotic plantations as habitat compared with native forest, thereby reducing opportunities for large-fruited canopy species to penetrate an exotic forest (Clout & Gaze 1984). Kererū (*Hemiphaga novaeseelandiae*) are crucial for the dispersal of large-fruited canopy species such as *Beilschmiedia tawa* and *Pectinopitys ferruginea*, as all other dispersers capable of consuming the large seed are either extinct or extremely rare (Norton 2009). Avian dispersers often require large areas of habitat to maintain a sustainable population (Norton et al. 2018) and thus remnant patches of native forest in the landscape are critical to provide sources of propagules, as well as maintaining species and habitat diversity, improving landscape connectivity, and restoring ecosystem functions (Clout & Gaze 1984; Heinrichs et al. 2018; Norton et al. 2018).

Landscape matrix

The presence of native forest patches nearby to a plantation forest, or target site, is highly important for diverse and abundant seedling establishment (Vespa et al. 2014; Ritter et al. 2018). In addition, the quantity of native forest cover in the landscape matrix is also influential on native regeneration. In Argentina, a significant positive effect on the species richness and composition of seedlings regenerating within a *P. taeda* plantation was found when the landscape matrix contained at least 25–30% native vegetation cover (Ritter et al. 2018).

Land use history of a site appears to be a significant prohibitive factor in both passive regeneration and direct planting of seedlings in Australia (Standish et al. 2007; Kasel 2008; Kasel et al. 2015). Plantation forest established on what was previously agricultural land and in a predominantly agricultural landscape matrix is likely to be readily invaded by exotic weed species. The vigorous exotic vegetation can outcompete native species and prevent establishment and growth of native regeneration following plantation harvest (Kasel et al. 2015). Exotic weed species invading from the surrounding landscape are also an issue in Aotearoa (Norton 2009) and in Argentina (Tecco et al. 2006). The presence and cover of exotic weed species in the landscape matrix, as well as the history of the site will provide insight into the level of weed control that may be required for establishment, survival, and growth of native species that have either arrived passively or have been planted.

The composition of a landscape matrix is influential on the biodiversity that exists within it. Exotic plantation forest biodiversity can be enhanced by ensuring that vegetation patches are physically connected to improve the dispersal of fauna in the landscape (Lindenmayer & Hobbs 2004; Pawson et al. 2011) as well as reducing edge effects on forests. Preserving and maintaining native forest patches will improve passive regeneration by reducing distances to seed sources and increasing habitat area and connectivity for seed-dispersing vertebrates.

Facilitating regeneration

Exotic plantation forests have the potential to encourage succession towards native forest regeneration due to their ability to facilitate native seedling establishment, growth, and survival. This is known as a nurse effect where nearby adult plants have a positive influence on the establishment and growth of seedlings. The nurse effect occurs due to the fundamental processes of improved microclimate, shelter from herbivores, and increased availability of water and nutrients (Padilla & Pugnaire 2006). In Chile, open sites where invasive *P. radiata* individuals had established facilitated the natural regeneration of native shade-tolerant and intermediate tree species (Becerra & Montenegro 2013). However, patches of native trees had a greater positive effect on native regeneration than the *P. radiata* individuals. Whilst it may be preferable to use only native species when actively restoring an indigenous forest, existing exotic species on the site should be viewed for their facilitative potential before planning their removal (Becerra & Montenegro 2013). Provided the invading *Pinus* trees do not establish in a dense stand with little understorey light, they may be beneficial for facilitating native regeneration (Fig. 2), as well as improving landscape connectivity and habitat availability. However, it is desirable that the exotic trees can be either removed or naturally replaced in the native ecosystem, so they do not continue to spread and regenerate (Norton & Forbes 2013).

Afforestation with exotic pine trees will likely have below-ground impacts which could potentially influence the regeneration of native flora. *Pinus radiata* established on pasture can lower the pH of the soil at all levels. It can also reduce topsoil mixing through a reduction in earthworm activity. However, afforestation has been found to increase carbon: nitrogen ratio as well as plant-available phosphorus (Yeates et al. 2000). The diversity and density of Protura, a hexapod of the Class Insecta, has been found to be significantly greater in soils beneath *P. radiata* forest compared with those beneath native forest, with native beech forests having the next greatest diversity and density (Minor 2008). Old-growth kauri (*Agathis australis*) forest and plantation *P. radiata* forest were found to have no significant differences in soil pH. However, there were significant differences in bacterial and fungal communities within the soil, with the *P. radiata* forest exhibiting significantly greater fungal diversity (Byers et al. 2020). The implications of the below-ground changes which occur due to pine afforestation and how this may influence native regeneration are not yet fully understood.

Figure 2. Early successional indigenous species regenerate beneath the canopy of an 18-year-old *Pinus radiata* forest in the Marlborough Sounds, Aotearoa.

The facilitative effects of native shrubs (Raffaele & Veblen 1998; Kitzberger et al. 2000; Nuñez et al. 2009) and exotic shrubs (Tecco et al. 2006; Svriz et al. 2013) on native regeneration have been widely recognised in Argentina. Native shrubs have also been recognised as facilitators for native regeneration in Spain (Alday et al. 2015; Torroba-Balmori et al. 2015). In Aotearoa, the invasive woody weed *Ulex europaeus* (gorse) is a common early-successional species across the country. Despite being an invasive weed, *U. europaeus* has been found to facilitate the establishment of native forest regeneration (Lee et al. 1986; Sullivan et al. 2007). *Ulex europaeus* also creates habitat for some native bird species, resulting in the dispersal of native seeds into the stands. The canopy of *U. europaeus* tends to become senescent earlier and increase in canopy openness sooner than that of the native early-successional shrub *Kunzea ericoides* s.l. (kānuka) which may further promote seedling establishment and survival by creating more favourable light conditions (Williams & Karl 2002). However, when comparing similar successional stages of stands of *U. europaeus* and *K. ericoides*, the *K. ericoides* stands had greater species richness (Sullivan et al. 2007). Therefore, although the exotic weed *U. europeaus* can facilitate native regeneration it is not an exact substitute for native pioneering shrubs and may result in a novel community in the regenerating forest.

Management interventions

Canopy manipulation

The way a plantation forest is managed can influence the level of biodiversity within it. Stand management that prioritises structural heterogeneity through the preservation of understorey vegetation and structural elements such as fallen trees will enhance habitat diversity (Lindenmayer & Hobbs 2004). Managing an exotic plantation forest transition to native forest will likely apply these principles at a higher intensity, with less focus on preserving economic timber production. The establishment and thinning treatments applied to a stand could be used to keep plantation basal area lower to improve understorey microclimate for native plant establishment and growth. Trials of two thinning treatments in *Pinus taeda* plantation in Argentina found that the most severe treatment of removing 50% of trees had the most significant effect on increasing understorey establishment and growth (Trentini et al. 2017). The thinned *P. taeda* logs could be recovered to provide a source of income if the site allows for cost-effective and low disturbance extraction, which would further improve this method of increasing native understorey biomass.

Strip cutting is another form of canopy manipulation that allows for merchantable wood to be removed from the forest, whilst also improving light conditions for native regeneration, growth, and establishment. A trial undertaken in mature *Pinus radiata* forest in Chile produced promising results, as the native species planted into the felled strips performed significantly better than those under the undisturbed canopy and those in the open clear-cut (Kremer et al. 2021b). These findings are highly significant as strip-cutting provides a way of removing timber for financial gain whilst also providing a favourable environment for native regeneration and removing exotic biomass to help transition the forest to native dominance. However, canopy manipulation, especially the removal of strips, may increase the forest's susceptibility to wind damage depending on the size, orientation, and location of the strip/gap. The prevailing wind direction and exposure of the site should be considered when planning a canopy manipulation intervention.

Any method of canopy manipulation will reduce the volume of carbon sequestered in the stand at the time of tree removal which may result in liabilities if the stand is part of an emissions trading scheme. The native plants which benefit from the removal of some exotic canopy trees will also take many years to grow to a point where they have replaced the carbon sequestered by the removed canopy trees. Therefore, it is important to understand the effects canopy manipulation will have on the carbon profile of a stand or forest and that these interventions are managed to reduce their impact and potential for liabilities.

Natural disturbances in forests create light conditions that are required for many late-successional seedlings to grow into canopy trees (Wyse et al. 2018; Forbes et al. 2019). Canopy manipulation in the form of gap creation makes an exotic plantation forest more structurally diverse and is likely to improve growth of understorey plants, especially canopy species (Forbes et al. 2016), provided that browsing pressure in the forest is low and that canopy gaps do not result in increased animal activity within the gaps. Canopy gaps created in a mid-rotation *P. radiata* stand in Marlborough, Aotearoa were found to improve the growth of native seedlings planted within the gaps (Forbes et al. 2016), as well as the abundance and richness of native plants naturally regenerating, when compared to the undisturbed canopy (Marshall 2020). Gap creation in a dense stand of native early successional *Kunzea robusta* (*Kunzea ericoides* s. l. prior to taxonomic revision; de Lange 2014), also in Aotearoa, produced similar results with increased growth of planted *Podocarpus totara* (Tulod et al. 2019), as well as improved diversity, density, growth, and survival of naturally regenerating species (Tulod & Norton 2020). In a coastal forest of *Pinus thunbergii* in Japan, canopy gap creation was found to significantly increase the establishment and growth of regenerating seedlings, with the largest gap size yielding the highest rate of seedling growth and establishment (Zhu et al. 2003). Gradual canopy removal may be required in exotic plantation forest to create the structural heterogeneity and small-scale disturbance required for the establishment and growth of later-successional canopy species (Forbes et al. 2016; Heinrichs et al. 2018; Kremer et al. 2021a).

Open site restoration

There may be circumstances where a return to native forest is desired following the clear-fell of an exotic plantation. The process of forest restoration is likely to require a mixture of both active and passive restoration, the balance of which will be determined by factors such as macroclimate, distance to seed source, landform, and land-use history (Holl & Aide 2011; Forbes et al. 2021). Exotic weed species are likely to rapidly colonise a site following the harvest of a plantation, creating competition for native species to passively regenerate, and are likely to require ongoing control throughout the early years of establishment and growth of the native species (Partridge 1989; Norton 2009; Forbes et al. 2021).

Restoration of native forest in abandoned wheat fields in Western Australia reveals obstacles that are likely to be faced in native forest restoration on plantation cutover. Agricultural land use can result in highly limited seed dispersal and a depleted soil seed bank (Zimmerman et al. 2000; Standish et al. 2007; Holl & Aide 2011). The highly controlled environment of the wheat field has lacked natural disturbance to trigger revegetation. These obstacles are a common experience in native forest restoration across Australia (Standish et al. 2007; Kasel 2008; Kasel et al. 2015; Dudley et al. 2021). Improving seed dispersal, supplementary planting, and simulating natural disturbance to encourage regeneration are all methods that could be employed across a range of sites and forest types to promote successful forest restoration.

Native and exotic shrub species have been found to have positive effects on the establishment and survival of native species regenerating in open disturbed landscapes (Raffaele & Veblen 1998; Tecco et al. 2006; Svriz et al. 2013; Torroba-Balmori et al. 2015). Exotic shrubs may, however, also encourage a high density of other exotic species to establish (Tecco et al. 2006) indicating a potential need for weed control in the early stages of ecosystem restoration to reduce competition with regenerating native species. The strong facilitation of shrubs is largely due to the reduction in solar radiation and increased soil moisture in the microsites they create (Kitzberger et al. 2000; Nuñez et al. 2009; Svriz et al. 2013; Alday et al. 2015). The shrubs may also increase seedling survival and growth by offering some protection from browsing mammals (Tecco et al. 2006; Svriz et al. 2013; Torroba-Balmori et al. 2015). The positive effects of pioneering shrubs have also been found to increase as environmental stress increases (Alday et al. 2015). Pioneering shrub species can quickly create environmental heterogeneity and favourable microsites for plant establishment and growth in open disturbed sites and could be planted in open restoration sites to improve forest restoration success. The shrub species act as a nurse similarly to the exotic plantation species by improving conditions for species establishment and growth. However, some woody weed species can persist indefinitely so the suitability of the pioneering species for the purpose of open site restoration would need to be assessed on a case-by-case basis depending on factors such as the species, the surrounding landscape, and the level of observed native and exotic regeneration beneath the woody weed (McAlpine et al. 2021).

Pest Control

Browsing mammals pose a significant threat to native forest restoration. Browsing has been widely recorded as prohibiting growth and survival of palatable regenerating seedlings (Tecco et al. 2006; Standish et al. 2007; Torroba-Balmori et al. 2015; Forbes et al. 2016). In Aotearoa, introduced mammalian browsers such as *Cervus elaphus scoticus* (red deer) are invasive in native forests throughout the country. The deer are prolific browsers and will consume a substantial portion of palatable regenerating seedlings resulting in slowed regeneration (Norton 2009) and long-term impacts on species composition, depending on the structure of the forest and its original abundance of palatable species. *Capra hircus* (feral goats) also have significant impacts on indigenous vegetation. Feral goats are generalist browsers and will switch their diet when preferred species are not available. Like deer, feral goats can have long term effects on the structure of forests as their intense browsing prevents the regeneration of palatable species (Parkes 1993). Invasive mammals exert negative influences on ecosystems in a variety of ways that constrain forest restoration success. Herbivorous browsers limit plant growth and survival. Rodents such as *Mus musculus* (house mouse) consume seeds, restricting seedling establishment. *Quercus* seeds are often predated by rodents, even after the seed has germinated. Mesh protection to prevent seed predation significantly improved emergence rates of *Quercus* seeds on an open site in Northern Spain (Torroba-Balmori et al. 2015). In Aotearoa, non-native carnivores that predate native birds have a significant impact on the ecosystem as they are required for dispersing the seed of many later successional tree species (Norton et al. 2018). Controlling pest impacts is critical for native forest restoration. Reducing the influence of pests will improve restoration success as well as benefit the biodiversity of any remnant forest patches captured by the pest control measures.

Negative effects on native plant regeneration can also be exerted by native animals. Damage to seedlings from trampling and digging from ungulates and wild boar (*Sus scrofa*) has been observed to negatively impact survival and growth of *Quercus* seedlings, in Northern Spain (Alday et al. 2015). Kangaroos (*Macropus spp.*) were observed to be browsing regenerating vegetation, alongside European rabbits (*Oryctolagus cuniculus*) on open site restoration in Western Australia. The kangaroos exhibited preferential browsing of more palatable species, potentially impacting the composition of the regenerating vegetation (Standish et al. 2007).

Canopy manipulation treatments in exotic plantation forest could increase the incidence of browsing from mammals on native understorey regeneration (Forbes et al. 2016; Tulod et al. 2019). In mid-rotation *Pinus radiata* plantation forest in Aotearoa, artificial canopy gap creation was found to increase the incidence of browsing on planted native seedlings, especially in the larger canopy gap size trialled (Forbes et al. 2016). In regenerating *Kunzea robusta* forest, also in Aotearoa, mammalian browse on planted seedlings was observed to increase in both created canopy gaps and at the edge of the forest, thus reducing survival and increasing variability in seedling growth (Tulod et al. 2019). Suggested strategies to mitigate browsing include planting of less palatable species and reducing the size of canopy gaps created to increase light availability without creating large clearings preferred by ungulates (Forbes et al. 2016; Tulod et al. 2019), which may also reduce the potential for windthrow among the surrounding canopy trees. Exclusion of ungulates would offer the most significant improvement for seedling growth and survival; however, this is a costly option and may not be viable, especially at large scales (Forbes & Norton 2021). Poisoning, trapping, and sustained hunting pressure are also strategies which can be effective in controlling pest numbers.

Herbivory from mammals can have significant negative effects on the composition and structure of a forest through preferential and prolific browsing of seedlings (Coomes et al. 2003). In Aotearoa, browsing from mammalian herbivores can be so extensive that it will inhibit the regeneration of native seedlings and arrest successional development (Forbes & Norton 2021). Succession in forests post-fire has been found to entirely stagnate as canopy species fail to recruit due to herbivory from ungulates, possums (*Trichosurus vulpecula*), and seed predation by rodents (Richardson et al. 2014). This profound effect of browsers may require full exclusion to allow forest regeneration to occur. If exclusion is not an option, other pest control methods will still be necessary and will need to be continued long-term to effectively control populations to allow successful forest restoration and succession to occur (Forbes & Norton 2021). Even with the application of effective long-term pest control, the previous impact of browsing mammals may not be able to be reversed. In such cases, ongoing management will be necessary to reach a desired restoration outcome, and to maintain its success and prevent it from becoming degraded by pests (Norton 2009).

Prospects for Aotearoa

Exotic plantations throughout the world often contain a diverse understorey of native plants. The composition and density of the understorey, however, is often lacking in some key species, especially those that are late-successional and will eventually become dominant canopy species. The international experience is similar to the understanding in Aotearoa that exotic plantations do contain native biodiversity, however, they are often dissimilar to the natural forest in plant species composition, structure, and density.

Management interventions can be undertaken to encourage the regeneration and succession of native vegetation. It is important to consider what forest type would have existed prior to human intervention on a site, given that the goal of forest transitions is often to produce a native forest reminiscent of historic vegetation cover (Table 1 lists common canopy species found in a variety of forest types throughout Aotearoa). The canopy species are often bird dispersed and shade tolerant, however, this is not always the case. Unique forest types and canopy trees will respond to management interventions in different ways, finding some more beneficial than others. The summary in Table 1 gives an indication of how forest types may vary in their response to management interventions by outlining their regeneration requirements. Especially important factors to consider are the shade tolerance of the species, as this will dictate how well they respond to canopy manipulation and what size of canopy gap may be most beneficial. Assessing the ecology of the forest type which the transition is aiming towards will provide an improved understanding of how management interventions should be applied to have the greatest effect on the forest transition.

An exotic plantation forest may require canopy manipulation to stimulate succession towards establishment and growth of canopy species. Gradual removal of the exotic canopy trees will also assist in transitioning the dominant biomass of the forest from exotic to native. Research in Chile into strip-cutting an exotic plantation and planting native species in the strips is an exciting step towards discovering practical and economical methods of exotic to native forest transitions (Kremer et al. 2021b). Further research on the practicalities of gradual canopy removal and the retention of native regeneration in this process would be extremely useful for landowners and forest managers wishing to attempt a transition. Examination of the costs and potential income

Table 1. Summary of common native canopy species, their dispersal mechanism, shade tolerance, and regeneration requirements (Wardle & MacRae 1966; Wardle 1967, 1969, 1971; Ecroyd 1982; Knowles & Beveridge 1982; Knightbridge & Ogden 1998; Wyse et al. 2018).

Species	Method of dispersal	Shade tolerance	Regeneration requirements
Agathis australis (kauri)	Wind & gravity	Light-demanding	Seedlings can establish & persist in low light levels but require increased light availability to reach maturity.
Beilschmiedia tawa (tawa)	Bird	Shade tolerant	Seedlings susceptible to frost, wind, drought, and sun. Do not easily establish in large canopy gaps.
Dacrycarpus dacrydioides (kahikatea)	Bird	Light-demanding	Prefers alluvial soils, regenerates post-flood events.
Dacrydium cupressinum (rimu)	Bird & gravity	Partial shade	Will not establish where there is high root competition and low light intensities. Prefer disturbed soils and sites beneath light-crowned trees.
Didymocheton spectabile (kohekohe)	Bird & gravity	Shade tolerant	Requires leaf litter covering to germinate. Regenerates in full shade and small canopy gaps.
Fuscospora spp.	Wind & gravity	Partial shade	Suppressed seedlings under canopy respond strongly to increased light availability. Can establish on open sites.
Knightia excelsa (rewarewa)	Wind & gravity	Light-demanding	Pioneering canopy species. Can establish on open sites post disturbance.
Libocedrus bidwillii (kaikawaka)	Wind & gravity	Light-demanding	Regenerates in canopy gaps following disturbances such as windthrow or landslides.
Lophozonia menziesii (silver beech)	Wind & gravity	Partial shade	Suppressed seedlings under canopy respond strongly to increased light availability.
Metrosideros excelsa (pōhutukawa)	Wind & gravity	Light-demanding	Early successional species, establishes on open sites following disturbance.
Metrosideros robusta (northern rātā)	Wind & gravity	Light-demanding	Establishes as a hemi-epiphyte in host canopies, often on species in the Podocarpaceae. Occasional terrestrial establishment in canopy gaps.
Metrosideros umbellata (southern rātā)	Wind & gravity	Light-demanding	Often confined to less-favourable sites. Regenerates in the open or in canopy gaps with high light levels.
Pectinopitys ferruginea (miro)	Bird	Shade tolerant	Late-successional long-lived species. Regenerates in full shade, reaching canopy dominance through small scale disturbances to the canopy.
Podocarpus totara (tōtara)	Bird	Light-demanding	Hardy early successional species which readily establishes on open sites.
Prumnopitys taxifolia (mataī)	Bird	Shade tolerant	Regenerates in full shade under closed canopy. Small-scale disturbances allow for growth to canopy dominance.
Pterophylla racemosa (kāmahi)	Wind & gravity	Partial shade	Do not often establish on fully exposed sites, prefer light canopy or small canopy gaps.

involved in gradual canopy manipulation would also be valuable in understanding the cost-benefit of forest transitions with canopy manipulation.

The landscape matrix in which a restoration site resides will be strongly influential on the success of the forest restoration regarding seed dispersal, pest plant and animal invasions, disturbance regimes, and native fauna populations and movement (Clout & Gaze 1984; Ritter et al. 2018). Seed dispersal from native *Eucalyptus salmonophloia*, *Acacia acuminata*, and *Melaleuca uncinata* woodlands was rare beyond 20 m from the edge of the forest in Western Australia (Standish et al. 2007). It would be beneficial to be able to quantify the effect of distance from seed source and percentage cover of native forest on the success of native forest restoration in Aotearoa. Research would need to be undertaken across various native forest types as different species assemblages rely on different seed dispersal mechanisms. This knowledge would be extremely useful when undertaking a restoration project as the landscape context will give a good early indication of how successful passive restoration may be and the level of active management that may be required for a full assemblage of native species to establish.

Effective seed dispersal is a key component of passive restoration and is often absent in forest restoration projects. This can be due to the landscape being highly modified where seed sources are few and distant, and also due to the mechanisms of seed dispersal being disrupted. It is important to preserve and enhance native forest patches in the landscape to provide a source of propagules for passive restoration. Native forest patches also increase landscape connectivity and habitat size for fauna that enhance biodiversity and often play a key role in seed dispersal. The role of avian fauna for seed dispersal in Aotearoa is widely recognised. Restoration of forest and preservation of remnants will increase habitat size and enhance connectivity to sustain a viable population of birds which will disperse seeds and enhance ecosystem biodiversity (Norton et al. 2018).

Shrubs were found to act as strong facilitators for native regeneration growth and establishment on open sites in Northern Spain and Argentina (Svriz et al. 2013; Alday et al. 2015). When attempting a native forest restoration on plantation cutover, early successional shrubs could be sown or planted to quickly increase structural heterogeneity and create favourable microsites for less light-demanding later-successional species to establish (Torroba-Balmori et al. 2015). Individual *Pinus* trees invading open sites may also create favourable microsites to facilitate native regeneration (Becerra & Montenegro 2013). However, they must be kept under control so that they do not create too much shade, spread beyond the forest, and can still be removed once the forest restoration reaches a point where the nurse effects of the exotic trees are no longer required.

Pest mammals can have a significant impact on a forest ecosystem. Both seed predators and herbivores can prevent seedling growth and survival and can inhibit succession of native plants, acting as barriers to forest restoration (Torroba-Balmori et al. 2015; Forbes et al. 2016). Preferential browsing from herbivores in Aotearoa is having profound effects on the species composition of regenerating plants (Coomes et al. 2003). To allow a full range of species to establish and grow either beneath an exotic canopy or on a cutover site herbivory must be limited as much as practicable. Pest control should continue throughout the restoration process to allow unconstrained succession to occur, and to prevent the new forest ecosystem from becoming degraded (Norton 2009). Pest mammals that predate native birds further disrupt the forest ecosystem as many bird species are highly important for seed dispersal (Norton et al. 2018). Effective pest control in Aotearoa is a critical component of forest restoration due to the evolution of the flora and fauna in the absence of ungulates and carnivores. Controlling pest populations allows the forest ecosystem to restore functions such as seed dispersal and succession. This is essential in exotic to native transitions as seeds of all species need to be able to arrive, establish, and survive without browsing pressure for a native forest to develop with a similar composition and structure as a natural forest.

Conclusions

Among the literature examined here, it is evident that exotic plantation forests do contain native biodiversity, and that the species composition and structure will become more like a native forest as plantation age increases. However, late-successional canopy species were often found to be absent or only present in very low numbers in the understorey. Native forest remnants are critical as a source of propagules, as well as for increasing landscape connectivity and habitat area for wildlife, especially those that act as seed dispersers. An absence of effective seed dispersal inhibits passive restoration, as disrupted dispersal mechanisms prevent a full range of species from arriving and establishing at restoration sites.

Further research should be targeted to improve knowledge and provide practical guidance for landowners or forest managers wishing to attempt an exotic to native forest transition over the range of forest types in Aotearoa. We suggest research should be undertaken in the following areas:

- Quantifying the effect of native forest cover percentage in the landscape matrix on native regeneration – in transitional forestry and in post-harvest native restoration.
- Quantifying the distance from a seed source where passive regeneration will most readily occur, and at what distance active restoration may be required.
- Investigate what seeds are entering plantations forests, the pathway of their arrival, and the effects of the surrounding landscape matrix on seed rain.
- Further trials on canopy manipulation targeting gradual removal of the exotic plantation species – how to remove the merchantable timber whilst minimising damage to regenerating native vegetation and soil disturbance.
- Research into the potential use of pioneering shrubs to facilitate native restoration in post-harvest open sites.

Further research should be conducted across a range of macroclimates and native forest types in Aotearoa, as advice needs to be applicable across the country. Transitional forestry is a relatively new concept and due to the time scales involved, it is not yet certain whether an exotic to native transition is viable. However, given the current appetite for transitional forestry, and the volume of exotic forests which have already been established as “carbon farms” it is essential that we find a way to make them work.

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Data and Code Availability

There are no data or code associated with this article.

Author Contributions

GRM, ASF, BRM, and SVW conceived the ideas. GRM undertook the literature review and led the writing of the manuscript, with contributions from ASF, BRM, and SVW.

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