

Effect of artificial canopy gaps on native regeneration in mature *Pinus radiata* forest in New Zealand

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Bachelor of Forestry Science

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Abstract

Gap creation is what drives succession in natural forests. This research explored the effect of artificial canopy gaps in a mature single-aged *Pinus radiata* forest on understorey native regeneration, and what potential role artificial canopy gaps could have in transitioning a pine forest to a native forest. Species and abundance by cover class was recorded at 22 plots beneath a 22-year-old *P. radiata* forest, in the Marlborough Sounds. The plots included three treatments comprising (1) a closed canopy control, (2) a small gap with trees within a 2.3 m radius felled, and (3) a large gap with trees within a 5.6 m radius felled. The gaps were established in 2014, allowing six years for species to regenerate before they were measured.

The effect of treatment and gap ratio on native species importance value was found to be highly significant ($p < 0.01$). Whereas only the effect of gap ratio, and not treatment, was found to be significant on native species richness ($p < 0.05$). Native species importance value was found to be significantly different between the small gap and the control, and the large gap and the control. However, there was no significant difference between the small and large gap treatments. The composition of understorey species was also found to be significantly different between treatments ($p < 0.05$).

The growth and abundance of regenerating understorey species was strongly influenced by the creation of canopy gaps. Gap creation also caused an increase in species richness; however, this effect was not as strong as the effect on growth and abundance. The presence of gaps was found to be more important than the size of the individual gap as there were only minor differences in understorey regeneration between small and large canopy gaps. This suggests that artificial canopy gap creation can be used to facilitate native regeneration beneath a mature pine canopy.

There was a distinct lack of later successional species in the forest understorey. This is likely due to both a lack of nearby mature forest to act as a seed source and effective seed dispersal mechanisms. Enrichment planting is likely to be necessary in many restorations to bring later successional species into ecosystems from which they have been lost. Herbivore exclusion and control of other mammalian pests is also likely to be necessary to allow for species to regenerate freely in the understorey without browsing pressure. Artificial canopy gap creation in single-aged plantation monocultures creates light environments and structural heterogeneity which can accelerate succession to a natural indigenous forest. However, long-term management and monitoring will be essential for successful ecosystem restoration.

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1. Introduction

1.1 Background

The New Zealand forestry industry relies on the harvesting of timber from large areas of planted single-age exotic monocultures. *Pinus radiata* is the dominant species planted, contributing 90% of the 1,725,400 hectares of net stocked area of production forest. The forestry industry is the third largest export earner in New Zealand and contributes approximately \$3.55 billion to New Zealand's GDP annually (FOA, 2019). However, plantation forests provide much more than just revenue from logs. They provide a multitude of ecosystem services such as erosion mitigation, reduced long-term sedimentation, carbon sequestration, and enhanced biodiversity when compared to pastoral land uses (Maclaren, 1996). They also present unique opportunities for the regeneration of native forests and the restoration of ecosystems (Forbes et al., 2020; Norton & Forbes, 2013).

Monoculture production forests are often viewed as 'biological deserts', however, the reality is significantly different (Brockerhoff et al., 2008; Norton, 1998; Norton & Forbes, 2013; Pawson et al., 2008). Plantation forests form habitats for native biota, enhance landscape diversity, and improve connectivity between native remnants in the landscape matrix (Norton 1998; Norton & Forbes, 2013; Pawson et al., 2010). They have also been proven to be host to a wide range of indigenous understorey plants across many parts of New Zealand (Allen et al., 1995; Brockerhoff et al., 2003; Forbes et al., 2019; Ogden et al., 1997;). This suggests that plantation forests could be used as a nurse crop for regenerating indigenous forest plant species.

Recently, the Climate Change Response (Emissions Trading Reform) Amendment Act 2020 has increased the carbon price cap on a New Zealand Unit (NZU) traded under the Emissions Trading Scheme (ETS) from \$25 to \$35/NZU, which will then be further increased to a cap of \$50/NZU in 2021 (Ministry for the Environment, 2020). A substantial increase in carbon price will have significant implications on the profitability of permanent forests and make their establishment a more economically viable alternative to the traditional rotational harvesting model. Landowners may desire to plant *P. radiata* plantations and reap the financial returns from the NZUs acquired through the ETS by the fast-growing trees. They may then wish to gradually convert this to an indigenous forest which would provide many ecosystem services as well as acting as a

permanent carbon sink and removing the liability of the reduction in carbon stock which will eventually occur as the pine trees senesce (Woollons & Manley, 2012).

Due to the geology of New Zealand, a large amount of the land is highly susceptible to erosion. Forests have historically been established on this erodible land to protect the soil by offering root reinforcement and regulating the volume and rate of water reaching the surface. However, when these forests reach maturity and are harvested there is a window of vulnerability where the soil is exposed again, and the risk of erosion increases dramatically (Maclaren, 1996). Poor environmental outcomes are often realised during this vulnerable period and there are increasing calls for highly erodible land to be retired from production forestry. The establishment of permanent pine forests is well-suited to such situations. The potential to then transition exotic pine forests to a natural indigenous forest provides an exciting opportunity to both enrich the landscape and provide a range of benefits to landowners.

1.2 Purpose of research

There is increasing interest in the potential of converting *P. radiata* plantations to native forest for both economic and environmental reasons. Permanent pine forests offer long-term erosion control, revenue from carbon sequestration, and increased biodiversity at both the forest and landscape level. There is a wide range of research on the diversity of species which are found in these exotic pine plantations, but very little into how to improve this diversity and effectively enhance the transition to native forests.

The use of artificial canopy gaps is widely regarded as a key tool in facilitating the regeneration of later successional, more shade tolerant tree species (Baret et al., 2008; Coates & Burton, 1997; Forbes et al., 2016, 2020; Rouvinen & Kouki, 2011; Tulod et al., 2018; Zhu et al., 2003). The fast growth and rapid canopy closure which can be achieved by *P. radiata* in New Zealand suggests that it could be a suitable nurse crop in facilitating and possibly accelerating ecosystem restoration (Forbes et al., 2019). The use of *P. radiata* as a nurse crop combined with the creation of artificial canopy gaps and the possibility of enrichment planting presents an exciting prospect for the restoration of New Zealand's unique indigenous forest ecosystems.

This research aims to provide further insight into the effect of artificial canopy gap creation in mature *P. radiata* forest on indigenous understorey species. Data on species richness, abundance and structural importance was gathered across plots with a variety of

gap treatments. Statistical analyses were undertaken to determine differences in the response variables between treatments. The outcomes of this research will help to fill knowledge gaps in the current development of strategies to transistion exotic pine forest to indigenous forest in New Zealand. This research should aid in helping landowners and/or forest managers to make informed decisions on managing the transisition of permanent exotic forest to an indigenous forest.

1.3 Research Questions

The purpose of this research is to gain a further understanding of the factors affecting the regeneration of indigenous species under a canopy of single-aged mature *P. radiata* forest. To do so, the research will be directed by the following questions:

- What effect do artificial canopy gaps have on native regeneration?
- Which treatment results in the most prolific regeneration?
- What guidance can be given to those wanting to use *P. radiata* forests to facilitate native regeneration?



Figure 1: Regenerating native species in a canopy gap in the understorey of the Kakapo Bay forest, Port Underwood, Marlborough Sounds

2. Literature Review

2.1 Plantation forest biodiversity

Plantation forests are usually intensively managed for timber products. The management strategies often involve the use of genetically improved seedlings, herbicides, fertilizers, thinning, pruning and eventual clear-felling after a relatively short rotation (Brockerhoff et al., 2003). The typical single-aged monoculture production forest is not generally synonymous with high biodiversity (Norton 1998; Brockerhoff et al., 2008; Pawson et al., 2008, 2010). Despite the increasing importance of environmental stewardship and conservation among forest managers, many stakeholders are still highly critical of plantation forests (Brockerhoff et al., 2008). Literature concerning plantation biodiversity is continually expanding. Increasingly, these forests are being found to have an important role in enhancing biodiversity and habitat at both the forest and landscape level (Norton 1998; Brockerhoff et al., 2003, 2008; Norton & Forbes, 2013; Pawson et al., 2008, 2010). Timber supply from plantation forests is a substitution for harvesting indigenous forests and cannot be overlooked in a biodiversity context. Harvesting of plantations instead of natural forests is a key factor in the retention of the complex and diverse ecosystems that indigenous forests form (Pawson et al., 2010).

2.1.1 Plant and animal diversity

Research conducted in several countries has found that plantation forests do offer habitat to plants, animals, and fungi; including populations of rare and/or threatened species (Norton 1998; Brockerhoff et al., 2008; Pawson et al., 2008, 2010). However, natural indigenous forests are likely to support superior biodiversity due to greater habitat diversity and higher habitat complexity (Brockerhoff et al., 2008). Research in south-western Nigeria compared a natural forest, a degraded forest, and a plantation forest of *Gmelina arborea* (Onyekwelu & Olabiwonnu, 2016). It was found that, while the overstorey of the natural and degraded forests had a much greater species richness, the understorey of all three forest types had a species richness which was statistically comparable (Onyekwelu & Olabiwonnu, 2016). In a study on the populations of birds and small mammals occurring in *Populus spp.* plantation forests in North America compared with other land uses, *Populus spp.* plantation forest was found to be at least as favourable for native bird and mammal species as agricultural cropland by assessments of species richness, diversity and overall density (Christian et al., 1998). However, the plantation forests were found to be less favourable by the same indicators when compared to natural

forests (Christian et al., 1998). Similar research explored populations of beetle taxa inhabiting a variety of land-use types. It was found that a mature plantation production forest of *P. radiata* contained the most similar composition of beetle species to a native forest (Pawson et al., 2008). This research further demonstrates the preference of plantation forest as habitat for many forest species over other intensive land uses such as pasture and cropland.

The presence of native plant species in the understorey of a plantation forest is important for its potential to be transitioned to a native forest. The abundance, diversity and life-history traits will also give an indication of the level of human intervention which will be required for ecological restoration. The high variability in understorey diversity of *P. radiata* stands in New Zealand has been emphasised in several studies (Allen et al., 1995; Brockhoff et al., 2003; Forbes et al., 2019; and Ogden et al., 1997). Although there is currently no clear understanding for this variability, it has been suggested that geographic location and changes in canopy structure over time could be strongly influential (Brockhoff et al., 2003). Brockhoff et al., (2003) suggest that where soil moisture is not a limiting factor, succession of understorey species will be driven by variations in light availability due to changes in canopy structure. However, in dry areas understorey vegetation may be limited by slow litter decomposition and may result in very low abundance and diversity of understorey plants, resulting in much slower succession (Brockhoff et al., 2003).

2.1.2 Facilitation of regeneration

Research suggests that plantation forests could be used to facilitate ecological restoration by increasing the speed of succession and creating a more favourable habitat for regeneration (Lamb, 1998). In lowland Costa Rica, it was observed that both pure and mixed native species plantations facilitated the regeneration of other native tree species in the understorey (Carnevale & Montagnini, 2002). Tree regeneration was found to be more abundant and diverse than in areas where there were no trees. Plantations of mixed species were also found to produce the greatest diversity of regenerating species (Carnevale & Montagnini, 2002). It has also been suggested that plantation forests could facilitate regeneration on previously grazed or degraded land (Brockhoff et al., 2003).

The fast growth of *P. radiata* in New Zealand allows for fast canopy closure, creating a desirable understorey microclimate and light environment for native tree species to regenerate (Brockhoff et al., 2003; Ogden et al., 1997). Research on the understories of

P. radiata stands in the Central North Island of New Zealand found a variety of indigenous plants inhabiting the plantation forest understorey, with older stands tending to have the greatest species richness (Allen et al., 1995; Ogden et al., 1997). More recent research on the understorey vegetation in plantation *P. radiata* forests also observed similar trends of the increasing of species richness and structural complexity with stand age (Forbes et al., 2019). This study noted that the success of *P. radiata* in facilitating native regeneration and ecosystem restoration in New Zealand will, however, depend on the presence of nearby seed sources and an effective means of seed dispersal. Climatic constraints, the light levels within the forest, and the ability to control or remove exotic conifers once native species become self-sustaining are also important issues (Norton & Forbes, 2013).

2.2 Native forest restoration motives and challenges

Global trends show that the worldwide area of natural and semi-natural forest has decreased by 420 million hectares since 1990. However, the area of planted forest has increased by 123 million hectares in the same time period (FAO & UNEP, 2020). Forest ecosystems are estimated to be habitat for over half of known terrestrial plant and animal species. Loss and degradation of natural forests is, therefore, a major source of concern for declining biodiversity (Brockerhoff et al., 2008). It has been broadly acknowledged that the revival of biodiversity and functioning ecosystems necessitates large-scale ecological restoration (Pejchar et al., 2018).

Political commitments such as the United Nation's 'New York Declaration on Forests' and the New Zealand government's 'One Billion Trees Programme' have been used to gather support for ecological restoration. However, significant knowledge gaps exist regarding effective methods of restoration which can be implemented across a variety of ecosystems and socio-political environments to meet these lofty targets (Lu et al., 2017). The high cost of indigenous seedlings is a substantial obstacle to ecological restoration in New Zealand. Norton et al., (2018) suggest that investment in new technologies such as direct seeding could help to reduce the cost of revegetation and increase the accessibility of restoration on private land.

A significant barrier to effective ecological restoration is the selection of appropriate species for planting (Lu et al., 2017). Choosing species and provenances which are suited to site and region requires ecological data which is often lacking, especially in developing nations. Another challenge facing ecological restoration is the effective restoration of

habitat in the presence of exotic species which cannot be eradicated due to financial and/or ecological reasons (Pejchar et al., 2018). In circumstances such as these it will be important to understand how a novel ecosystem can be created which replicates its historic counterpart whilst incorporating both exotic and native species. Norton (2009) also addresses this challenge in a New Zealand context, expressing the improbable nature of complete eradication of invasive species and the need for ongoing human intervention throughout the ecological restoration process to control both mammalian and plant pests. The costs associated with pest control, site preparation, planting and ongoing maintenance can often be prohibitive and will require some form of financial assistance (Christian et al., 1998; Norton, 2009; Pejchar et al., 2018).

2.3 Gap creation effects

The succession of a forest is highly dependent on its disturbance regime. The most frequent form of small-scale disturbance in a forest is the natural falling of senescent trees, resulting in the formation of canopy gaps (Baret et al., 2008). The amount of light which reaches the forest floor is influenced heavily by the presence of canopy gaps. They also impact patterns of moisture and nutrients, creating a variety of microenvironments throughout the forest which provide niches for species with a diversity of life-history traits (Schneider & Larson, 2017). The creation of artificial canopy gaps mimics this small-scale disturbance regime.

In a study which investigated the changes in light environments and tree regeneration induced by gap creation in *Tsuga heterophylla* (western hemlock) dominated forest, in north-western British Columbia, Canada, Coates & Burton (1997) found that forests which contained a broad range of gap sizes have the greatest diversity of microclimates and habitats. This is due to the variation in habitat among gaps, within gaps, at the gap edge, and within the forest matrix. The increased heterogeneity of forest structure caused by the creation of canopy gaps is essential in the development of a diverse and structurally complex forest ecosystem (Coates & Burton, 1997).

The importance of canopy gap creation has been reiterated through many studies. For example, a study in coastal *Pinus thunbergia* (Japanese black pine) forest measured the response of seedling regeneration and change in microsite conditions to a variety of artificial canopy gap treatments. It was found that seedling density and growth increased as the size of the gap treatment increased (Zhu et al., 2003). This is likely due to the combined effects of increased light and water availability, reduced litter accumulation on

the forest floor, and reduced competition with adjacent mature trees allowing for a more favourable environment for regenerating seedlings (Zhu et al., 2003). This study further emphasises the importance of small-scale disturbance for the natural regeneration of trees across many different forest types.

Artificial canopy gap creation has also been found to aid in ecosystem restoration. For example, a variety of treatments were applied to a *Pinus sylvestris* (Scots pine) forest in eastern Finland to explore the effects of gap creation and forest floor disturbance on the regeneration of both broadleaf and pine species (Rouvinen & Kouki, 2011). It was found that seedling regeneration was significantly more prolific where the soil had been disturbed. Although the study found regeneration of pine seedlings to be successful across a range of treatments, regeneration of *Betula pendula* (silver birch) seedlings was sparse throughout. Rouvinen and Kouki (2011) theorised that this was likely due to the shade-intolerance of *B. pendula* as well as the lack of mature *B. pendula* trees within the vicinity of the forest to provide a seed source. The study emphasises the importance of viable seed sources as well as the possibility of human intervention in the form of site preparation to create favourable microclimates for less dominant species to regenerate successfully (Rouvinen & Kouki, 2011).

Research on different strategies for aiding establishment of *Podocarpus totora* (tōtora) under a canopy of regenerating *Kunzea robusta* (kānuka) on abandoned pasture found that the creation of artificial canopy gaps had the greatest effect on *P. totora* growth, as this treatment had the largest increase in total light transmission and, therefore, created a suitable micro-climate for *P. totora* to grow (Tulod et al., 2018). Gap creation has shown to have a similar effect on the growth of planted *P. totora* and *Beilschmiedia tawa* beneath a mature pine canopy (Forbes et al., 2016). Both species of seedlings responded with an increase in growth rate in both small and large gaps when compared to control plots with no canopy gap creation. This research further strengthens the theory that artificial canopy gap creation is a necessary tool in facilitating the regeneration of later-successional indigenous forest species.

A recent review of literature concerning the restoration of later successional canopy species in New Zealand forests emphasises the necessity of enrichment planting and subsequent gap creation to form suitable micro-climates for successful growth and establishment (Forbes, et al., 2020). Much of New Zealand has been deforested and there

is now a severe lack of pollinators, dispersal mechanisms, and seed sources of later successional species. This ecosystem degradation has led to the stagnation of regeneration in many secondary forests across the country and emphasises the need for human intervention to restore a structurally complex and functional ecosystem. Forbes et al., (2020) suggest that successful restoration will require a considered balance between the choice of later successional species planted in terms of growth rate, shade tolerance and palatability to herbivores, and the frequency and size of artificial canopy gaps. Further research, such as this study, into the potential of exotic canopy trees to act as a nurse crop to later successional forest species will increase the understanding of how successful ecosystem restoration can be achieved in New Zealand's degraded landscapes (Forbes, et al., 2020).



Figure 2: Regenerating native species and some planted species from Forbes et al., (2016) in a canopy gap in the Kakapo Bay forest, Port Underwood, Marlborough Sounds

3. Methodology

The literature indicated that artificial gap creation will likely cause an increase in the growth and abundance of understorey plants within the gap. The size of the gap determines how much light reaches the forest floor and may influence the diversity and abundance of species. Variables which may indicate the effect of gap size on native regeneration in the understorey are native species importance value and native species richness. These response variables are likely to be influenced by the explanatory variables: extended gap diameter ratio, mesoscale topographical index, distance to nearest native seed source, slope, aspect, and landform unit. This section describes the study area, the methodology used to collect the data, and the statistical analyses performed.

3.1 Study area

The *P. radiata* forest from which the measurements were taken is located on the coast in Port Underwood, in the Marlborough Sounds, in the northeast of the South Island of New Zealand. The study area is subject to a mild humid climate (Laffan & Daly, 1985). It experiences high annual sunshine hours (1980-2019 average = 2,472 hours) and has a mean monthly temperature which ranges from 8.0°C in July to 18.2°C in January. The annual rainfall is an average of 1,411 mm and monthly rainfall varies from 84 mm in February to 146 mm in July. In the summer months the study area can experience soil moisture deficits (Forbes, Norton, & Carswell, 2016). The forest has a north-facing aspect and is situated on steeply sloping hill country with an elevation range of 40-120 m above sea level.

Prior to European settlement the site would have been forested, however, most of this forest was cleared in the nineteenth century for pastoral farming. Some land has remained in pasture whilst many exotic plantations of *P. radiata* have been established on hilly sites in eastern parts of the Marlborough Sounds. The historic forest would have been coastal broadleaved with dominant angiosperm tree species of *B. tawa*, *Elaeocarpus dentatus*, and *Dysoxylum spectabile* with fewer *Weinmannia racemosa* and *Fuscospora fusca* (Forbes et al., 2016). The indigenous conifer, *P. totara*, would have existed as an emergent canopy tree, dispersed throughout the forest (Walls & Laffan, 1986).

The study area is populated by numerous introduced mammals. These include *Dama dama* (fallow deer), some *Cervus elaphus scoticus* (red deer), *Sus scrofa* (feral pig),

Trichosurus vulpecula (brushtail possum), and few *Lepus eruropoeus occidentalis* (brown hare) (Forbes et al., 2016).

3.2 Data collection

This site was selected as it had been used by Forbes et al., (2016) for a study on the effect of artificial canopy gap creation on the growth of planted *P. totora* and *B. tawa* seedlings. The original study design involved selecting 22 plot locations randomly using the geographic information system (GIS) ArcMap 10.1. The plots were contained within a 22-ha area of the forest (Fig.3.) and were located to not be within 20 m of any forest edge, to avoid edge effects. Plot centres were also to have at least 22 m of separation to prevent interference between treatments. Plot centres were marked with a peg and their GPS coordinates recorded which were used to locate the plots for the measurements recorded for this research.

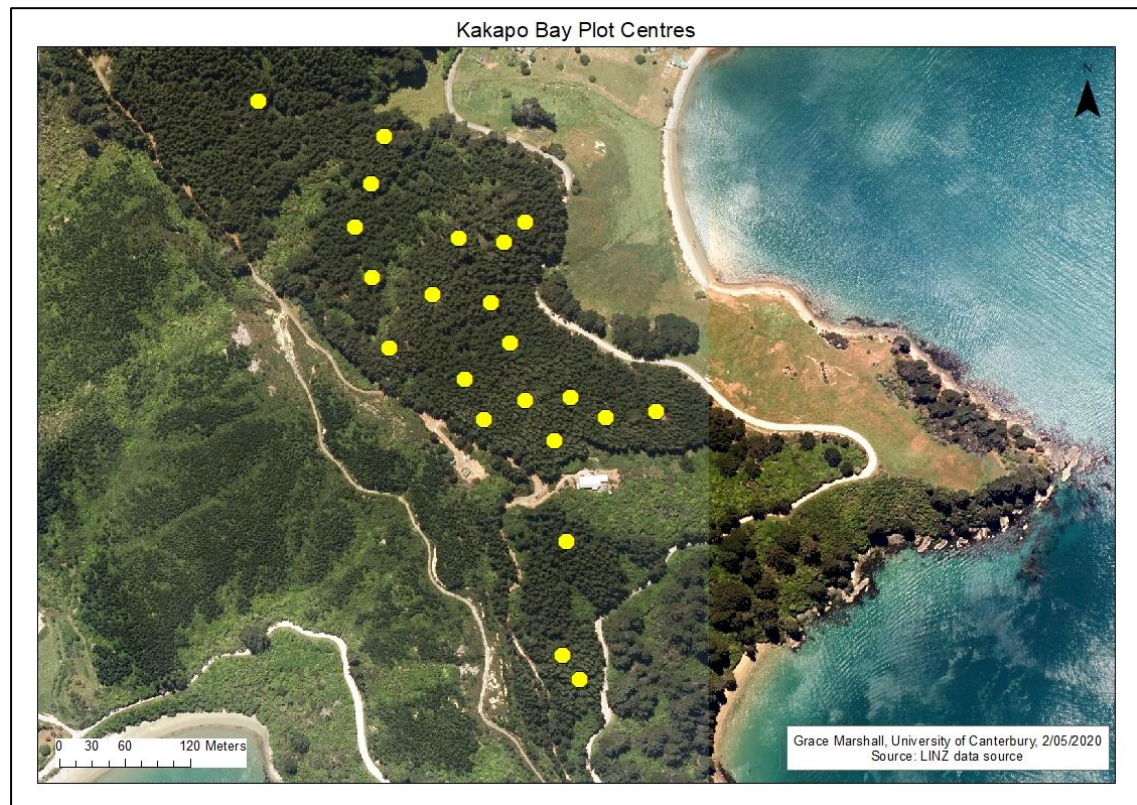


Figure 3: Plot centre locations in the Kakapo Bay forest, Port Underwood, New Zealand

Each plot was assigned a gap treatment of either control, small, or large gap. There were 8 control plots, 8 small gaps and 8 large gaps. The number of small gap plots was reduced in this study to 6 due to one plot needing to be excluded from the original experiment due to neighbouring livestock entering the plot and another plot being unable to be relocated

during the data collection for this research. In the control treatment no trees were felled, maintaining the closed canopy. For the small and large gap treatments, all *P. radiata* trees within a 2.3 m radius and 5.6 m radius of the plot centre for the two treatments respectively were felled. Felling occurred in 2014, six years prior to the data collection for this research.

3.3 Field methods

Once the plot was located, a 10 m x 10 m understorey vegetation plot was established using the pre-existing peg as the centre. A vegetation description of each plot was recorded using the Reconnaissance (RECCE) description method (Hurst & Allen, 2007) whereby the plot was divided into height tiers and the cover abundance of each species was recorded in each tier. Overall vegetation cover abundance was also recorded. The height tiers were: Tier 1 (>25 m), Tier 2 (12-25 m), Tier 3 (5-12 m), Tier 4 (2-5 m), Tier 5 (30 cm-2 m), Tier 6 (<30 cm). Each species in each tier was given a cover class number from 1-6 which represents the percentage cover of live foliage. The cover class numbers represent the following percentage foliage cover: 1 (<1%), 2 (1-5%), 3 (6-25%), 4 (26-50%), 5 (51-75%), 6 (76-100%). Slope, aspect, and landform unit were also recorded at each plot as part of the RECCE method (Hurst & Allen, 2007).

At each plot, the heights of four gap perimeter *P. radiata* trees were recorded using a Vertex III hypsometer. The tree heights were later used to calculate the extended gap diameter ratio for each plot by taking the mean of two orthogonal expanded gap diameters and dividing these by the average height of the four edge trees. The plot exposure was assessed by calculating the mesoscale topographic index which is the mean of eight equidistant slope to horizon measurements, taken from the plot centre (McNab, 1993).

The proximity to native seed source was measured by mapping all nearby areas of native vegetation using aerial imagery. The distance from each plot centre to the nearest area of native vegetation was calculated using ArcMap.

3.4 Statistical analysis

Statistical analyses were undertaken using R software (R Development Core Team, 2020). An initial scatterplot matrix was created to show possible relationships between all variables measured. These variables were:

- Treatment (gap size)
- Total exotic species importance value

- Total native species importance value
- Species richness
- Extended gap diameter to height ratio (gap ratio)
- Mesoscale topographic index
- Distance to nearest seed source
- Slope
- Aspect
- Landform unit (ridge, face, gully)

The scatterplot matrix (App. B) revealed relationships between some response and explanatory variables which was used to inform further statistical analysis. All statistical analyses conducted in this research look for a significance of $p < 0.05$.

The differences in the gap ratio among plots between treatments were modelled with a one-way analysis of variance (ANOVA).

One-way ANOVA was then used to determine the effects of treatment on native importance value, and again for native species richness. Post hoc pairwise comparisons were conducted to determine the effects of each treatment on both importance value and species richness.

A ‘best-fit’ ANOVA model for each of the response variables native importance value and species richness was selected using the Akaike Information Criterion (AIC) (Mazerolle, 2020). Several models were created using different combinations of explanatory variables which were then measured against each other in an AIC test. The model selected used the variables gap ratio, mesoscale topographic index, landform unit, and distance to nearest seed source as determinants of native importance value. The same set of parameters were used in the model analysing variation in native species richness.

Generalised linear models were used to further explore effects of the measured explanatory variables on native regeneration. Models were selected using the AIC test which compared several models with different combinations of parameters. The selected model to determine native species richness used gap ratio, mesoscale topographic index, landform unit, and slope as explanatory variables. The same set of parameters were used in the model exploring native species richness. The significance of the two final models was evaluated using a Wald chi-squared test.

Non-metric multidimensional scaling (nMDS) was used to interpret compositional shifts across the different gap size treatments. The ordination was undertaken using the metaMDS function of the Vegan package (Oksanen, et al., 2019). The ordination used the importance value of each species across all plots. The species importance values were calculated using the method of Allen et al., (1995) whereby each species is weighted by its cover abundance in each tier and then summing the cover weights across all tiers to produce a single importance value for each species in each plot. The following weights were assigned to each RECCE cover class (cover class = weight): 1 = 1.0; 2 = 2.0; 3 = 3.0; 4 = 4.0; 5 = 5.0; and 6 = 6.0.

To further investigate the changes in species composition across treatments, a multivariate statistical model was fitted using the mvabund package (Wang, et al., 2020). An analysis of deviance table was used to determine whether gap size treatment had a significant effect on the composition of species. This method was also used to determine the effect of treatment on individual species by using the 'p.uni = "adjusted"' argument which accounts for the correlation among response variables where species may be interacting with one another, within the ecological system. A linear model modelling the effect of gap ratio on nMDS site scores was also created to further explore the relationship between gap size and species composition.

4. Results

4.1 Species composition

Table 1: Species identified in the Kakapo Bay forest study area and their corresponding code, growth form, life history trait and presence in each gap treatment

Species	Code	Growth Form	Life History	Intact Canopy (Control)	Small Gap	Large Gap
<i>Aristotelia serrata</i>	ARIsr	Tree	Light demanding	✓	✓	✓
<i>Brachyglottis repanda</i>	BRArep	Tree	Light demanding/Intermediate	✓	✓	✓
<i>Carpodetus serratus</i>	CARser	Tree/Shrub	Intermediate		✓	✓
<i>Coprosma colensoi</i>	COPcol	Shrub	Intermediate	✓	✓	✓
<i>Coprosma grandifolia</i>	COPgra	Tree/Shrub	Intermediate	✓		✓
<i>Coprosma lucida</i>	COPluc	Tree/Shrub	Light demanding/Intermediate	✓	✓	✓
<i>Coriaria arborea</i> var. <i>arborea</i>	CORava	Tree	Light demanding/Intermediate			✓
<i>Dicksonia squarrosa</i>	DICsqu	Tree fern	Intermediate			✓
<i>Hoheria populnea</i>	HOHpop	Tree	Intermediate	✓		
<i>Leptospermum scoparium</i>	LEPsco	Tree	Light demanding	✓	✓	✓
<i>Leucopogon fasciculatus</i>	LEUfas	Shrub	Intermediate	✓	✓	✓
<i>Melicytus ramiflorus</i>	MELram	Tree	Light demanding/Intermediate	✓	✓	✓
<i>Schefflera digitata</i>	SCHdig	Tree	Intermediate	✓	✓	✓

A total of 13 indigenous species of trees, shrubs, and tree ferns were identified in the understorey of the 25-year-old *P. radiata* forest. The life history traits of these species vary from intermediate to light demanding, with no shade tolerant species identified. Of the 13 identified species, all but one was found in the large gap plots. Three were missing from both the control and small gap plots, however, the species missing from the control plots tended to be more light demanding than those absent from the small gap plots (Tb.1).

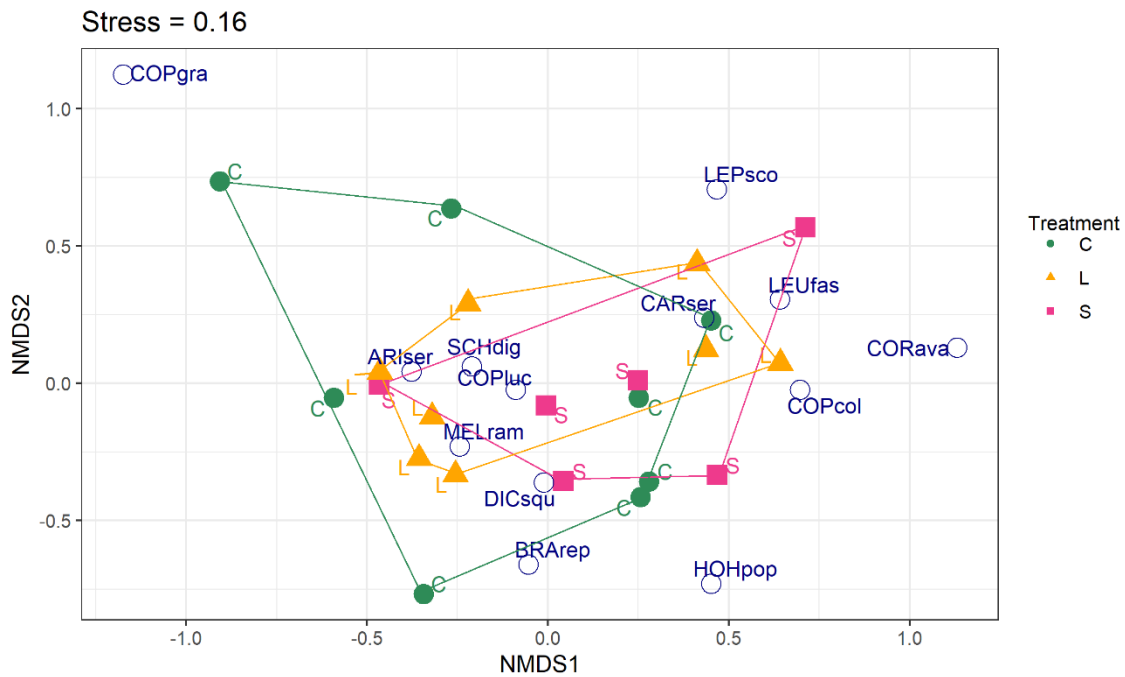


Figure 4: Non-metric multidimensional scaling (nMDS) ordination of species composition across the 22 plots in the Kakapo Bay forest. Treatment codes denote gap size: C = Control; S = Small gap; L = Large gap. Six-letter species codes are defined in Table 1.

The ordination demonstrated a moderate separation in species composition between the small and large gaps, and the intact canopy control (Fig.4). The small and large gap treatments appear to have a relatively similar species composition. The ordination suggests that the control treatment has a wider range of species composition as the plots are more spread in the ordination diagram and six of eight plots are outside the area of the ordination where the small and large gap plots were located. This is supported by the results of the multivariate analysis which showed that the composition of species is different among the canopy treatments ($p < 0.05$). The univariate analysis showed that canopy treatment had the greatest effect on the presence and abundance of *Aristotelia serrata* ($p < 0.05$).

Table 2: Linear model showing the effect of gap ratio of NMDS site scores (Fig.2)

		Estimate	Standard error	t value	Pr(>t)
NMDS1	(Intercept)	-0.1209	0.2426	-0.498	0.624
	Gap ratio	0.3036	0.5596	0.542	0.594
NMDS2	(Intercept)	-0.04941	0.20706	-0.239	0.814
	Gap ratio	0.12410	0.47761	0.260	0.798

The linear model explored the effect of gap ratio on ordination scores, taken from the x and y axes of Figure 2. They found that gap ratio had no significant effect (Tb.2) on ordination scores suggesting that the gap treatments are may not be significantly influencing the composition of species recorded in the *P. radiata* understorey.

4.2 Effect on native species richness

Table 3: Summary statistics of native species richness by treatment (gap size)

Treatment	N	Variable	Mean	Standard deviation
Control	8	Species richness	5.38	1.30
Small	6	Species richness	7	1.90
Large	8	Species richness	7.5	1.93

Species richness was found to be similar between the small gap and large gap treatment plots. The control plots have a lower mean species richness than the plots beneath artificial canopy gaps (Tb.3). However, one-way ANOVA found that this difference was not great enough for canopy gap treatment to have a statistically significant effect on native species richness ($F=3.306$, $p=0.0586$) (Tb.4).

Table 4: One-way ANOVA exploring effect of treatment on native species richness

	df	Sum of Squares	Mean Square	F value	Pr(>F)
Treatment	2	19.44	9.722	3.306	0.0586
Residuals	19	55.87	2.941		

A post hoc pairwise comparison (App. C) further reiterated these findings as there was no significant difference in native species richness between the control and small gap treatments ($p=0.211$); the control and the large gap treatments ($p=0.0566$); and the small gap and large gap treatments ($p=0.853$).

Table 5: ANOVA modelling effects of gap ratio, meso score, landform unit, and distance to native seed source on native species richness

	<i>df</i>	Sum of Squares	Mean Square	F value	Pr(>F)
Gap ratio	1	23.20	23.202	8.395	0.0105 *
Meso score	1	2.01	2.013	0.728	0.4060
Landform unit	2	5.03	2.515	0.910	0.4223
Distance to seed source	1	0.85	0.853	0.308	0.5863
Residuals	16	44.22	2.764		

The ‘best fit’ ANOVA model found that gap ratio does have a significant effect on native species richness ($p<0.05$). The model also included the explanatory variables mesoscale topographic index (meso score), distance to seed source , and landform unit, however, none of these variables were found to have a significant effect on native species richness (Tb.5).

Table 6: Generalised linear model showing effects of gap ratio, meso score, landform unit, and slope on native species richness

	Estimate	Standard error	t value	Pr(>t)
(Intercept)	4.563	1.671	2.730	0.0148 *
Gap ratio	5.481	2.129	2.573	0.0204 *
Meso score	0.052	0.039	1.335	0.2005
Landform unit (Face)	-0.731	0.546	-1.339	0.1992
Landform unit (Gully)	1.232	0.856	1.439	0.1694
Slope	-0.051	0.044	-1.143	0.2700

A generalised linear model was created to model the effects of gap ratio, meso score, landform unit, and slope on native species richness. Gap ratio was found to have a significant effect on native species richness ($p<0.05$). The other explanatory variables included in the model were not found to have a significant effect (Tb.6). These results further reiterate those found in the ANOVA model (Tb.5). An analysis of deviance test found this generalised linear model exploring the effects of explanatory variables on native species richness to be significant ($p<0.05$).

4.3 Effect on native importance value

Table 7: Summary statistics of native species importance value by treatment (gap size)

Treatment	N	Variable	Mean	Standard deviation
Control	8	Native IV	17.6	6.91
Small	6	Native IV	29.2	5.84
Large	8	Native IV	26.8	7.02

Mean native importance value was found to be greatest in plots beneath the small canopy gap treatments. The mean native importance value found beneath the large canopy gap treatments was slightly less than this, and the mean native importance value found beneath the closed canopy in the control plots was noticeably less (Tb.7). This is reflected in the results of a one-way ANOVA which found that canopy gap treatment does have a significant effect on native importance value ($F=6.096$, $p<0.01$) (Tb.8).

Table 8: One-way ANOVA exploring effect of treatment on native importance value

	<i>df</i>	Sum of Squares	Mean Square	F value	Pr(>F)
Treatment	2	545.6	272.80	6.096	0.009 **
Residuals	19	850.2	44.75		

A post hoc pairwise comparison (App. D) revealed that the difference between the native importance value of control treatments and small gap treatments is significant ($p<0.05$). The difference between the control treatments and the large gap treatments was also found to be significant ($p<0.05$). However, the difference in native importance value between the small gap treatments and large gap treatments was not significant ($p=0.784$).

Table 9: ANOVA modelling effects of gap ratio, meso score, landform unit, and distance to native seed source on native importance value

	<i>df</i>	Sum of Squares	Mean Square	F value	Pr(>F)
Gap ratio	1	546.7	546.7	10.749	0.00473 **
Meso score	1	1.0	1.0	0.019	0.89297
Landform unit	2	32.4	16.2	0.319	0.73144
Distance to seed source	1	1.9	1.9	0.037	0.84929
Residuals	16	813.8	50.9		

The ‘best fit’ ANOVA model found that gap ratio also has a significant effect on native importance value ($p<0.01$). As with the model for native species richness, the model also included the explanatory variables meso score, distance to seed source, and landform unit, however, none of these variables were found to have a significant effect on native importance value (Tb.9).

Table 10: Generalised linear model showing the effects of gap ratio, meso score, landform unit, and slope on native importance value

	Estimate	Standard error	t value	Pr(>t)
(Intercept)	24.259	5.987	4.052	0.000925 ***
Gap ratio	27.877	7.629	3.654	0.002140 **
Meso score	0.0514	0.140	0.367	0.718660
Landform unit (Face)	-2.121	1.956	-1.084	0.294354
Landform unit (Gully)	2.473	3.067	0.806	0.431835
Slope	-0.460	1.159	-2.890	0.010659 *

A generalised linear model was created which explored the effects of gap ratio, meso score, landform unit, and slope on native importance value. The model showed that gap ratio has a strong influence on native importance value ($p<0.01$). Meso score and landform unit were not found to have any significant effect on native importance value. Interestingly there was a statistically significant effect of slope on native importance value ($p<0.05$) (Tb.10). An analysis of deviance found this generalised linear model exploring the effect of explanatory variables on native importance value to be highly significant ($p<0.001$).

5. Discussion

5.1 Ecological theory and disturbance regimes

Disturbance regimes are what drives succession in natural forests. Disturbance events create openings in the forest canopy which allows for seedlings to regenerate and eventually form a new forest canopy. Disturbance creates a variety of successional stages throughout a forest, enabling it to remain highly diverse in both species and structure (Duncan, 1993; Lusk & Smith, 1998; Wells et al., 2001).

The creation of a gap in the forest canopy increases the resources available to persisting understorey seedlings and new seedlings establishing. The competition for light is greatly reduced and existing seedlings often respond with rapid growth, as is well illustrated in beech forests (Wardle, 1984). Some later successional species, such as *D. cupressinum*, also find the disturbance of soil associated with gap forming tree windfalls to be favourable for germination (Adams & Norton, 1989). These factors combined allow for an increase in growth and recruitment of species within canopy gaps.

Canopy gaps range in size depending on the level of disturbance. Frequent small gaps are often created by single tree fall in old growth forests, while larger gaps are created by multiple tree falls (Lusk & Smith, 1998). The microclimate created by canopy gaps exists as a gradient from gap centre to the undisturbed canopy understorey and also varies with gap size (McDonald & Norton, 1992). This gradient allows for the maintenance of high species diversity in old growth forests as species which are best suited to various conditions along the gradient can coexist and thrive (Lusk et al., 2009; Lusk & Smith, 1998).

The creation of artificial canopy gaps reflects the frequent, small-scale disturbance regimes experienced in many indigenous forests throughout New Zealand. A diverse forest structure and composition is unlikely to be achieved beneath a single-aged canopy of *P. radiata* due to the very low light conditions beneath the dense canopy and the inevitable harvesting of the trees for timber when the forest is approximately 28 years of age. Over a long period of time (>100 years) the pine trees will begin to senesce and will become increasingly susceptible to windthrow, breakage, and tree death (Woollons & Manley, 2012). It is plausible that a single-aged pine forest could eventually transition to a native forest if it were left unharvested and sufficient seed sources were available. However, for the purpose of achieving ecosystem restoration, this timeline is prolonged and is unlikely to be successful without intervention

and long-term management. This study explored the effect of artificial canopy gap creation as one such management intervention.

5.2 Gap creation effects on native regeneration

The statistical analyses undertaken consistently found a strong effect of treatment and gap ratio on native species importance value. Other measured parameters were found to not have any significant effect on importance value. This suggests that the increased light availability which occurs with artificial canopy gap creation is allowing an increase in the growth, abundance, and recruitment of regenerating plants in the understorey of the mature *P. radiata* canopy.

The analyses also showed a significant effect of gap ratio on the number of native species (richness). As with species importance value, other measured parameters did not have any significant effect on native species richness. The effect of treatment on species richness was, however, not significant. The difference between treatment and gap ratio as an explanatory variable is likely responsible for this difference as gap ratio accounts for the variability of gap sizes between treatments due to the spacing of the planted pine. The results suggest that artificial canopy gap creation does have a significant effect on native species richness, but it is not as strong as the effect on native importance value.

The findings of the analyses show that the presence of artificial canopy gaps is strongly affecting the abundance and growth of regenerating light demanding and intermediate native plants. The abundance, growth, and diversity of species within small and large canopy gaps were found to be significantly greater than beneath the closed canopy control treatment. These findings are congruent with the light demanding characteristics of many early and mid-successional native species (Baxter & Norton, 1989; Tulod & Norton, 2020). The results also suggest that artificial canopy gap creation can be a successful tool in stimulating the regeneration of native species beneath the canopy of a mature *P. radiata* forest.

5.3 Factors affecting regeneration

The disturbance regime of a forest is what drives its succession and species turnover (Duncan, 1993; Lusk & Smith, 1998; Wells et al., 2001). The creation of artificial canopy gaps mimics a small-scale disturbance such as tree fall and creates more varied and favourable conditions in the understorey for species to regenerate. This research found a small subset of earlier successional species throughout all the plots measured. There was a distinct lack of later successional species and a relatively low total richness comprised of just

thirteen native species. The typical light-demanding early coloniser *A. serrata* was frequently found throughout small and large gap plots. Other more shade tolerant early-successional species such as *Schefflera digitata*, *Melicytus ramiflorus*, and *Brachyglottis repanda* were also frequently recorded in the plots. The presence and abundance of these species suggests the forest succession is moving towards the establishment and growth of later successional canopy species such as *P. totora* and *B. tawa*, although these species had yet to establish at the site.

The absence of later successional species within the study site is likely due to several factors. The site for this study was a grazed pasture for a significant period before it was established as a plantation pine forest. New Zealand native vegetation does not have long lived seeds so it is highly unlikely that there would be any contribution of a soil seed bank to regeneration at this site (Moles & Drake, 1999).

Limitations related to seed dispersal are also likely to affect the regeneration of native species. Areas of native forest were identified within relatively close proximity to the site (<2 km), however, these are secondary forests which have regenerated after having been historically cleared for grazing. These regenerated forests also lacked later successional canopy species due to a lack of nearby old growth forest to provide an effective seed source. The mechanism for seed dispersal may also be lacking as many later-successional indigenous tree species have large fruits which require dispersal through frugivorous birds (Clout & Hay, 1989). This is also a possible explanation for the lack of regionally typical later successional species in the study area. For example, both *B. tawa* and *Pectinopitys ferruginea* are reliant on the kererū (*Hemiphaga novaeseelandiae*) to disperse their large fruits. Other species of birds such as tūī (*Prosthemadera novaeseelandiae*) and korimako (*Anthornis melanura*) also act as dispersers of fleshy fruits, of which 70% of common indigenous woody species possess (Clout & Hay, 1989). Nearby stands of old growth forest are highly important as seed sources for regenerating forest. The isolation of many areas of regenerating forest from seed sources is a likely cause of the lack of later successional species establishing. The existence of old growth or mature indigenous forest in the adjacent landscape matrix is crucial for the presence of seed sources and populations of seed dispersing birds (Forbes et al., 2019). This further reiterates the need for ecosystem restorations as these will improve the landscape matrix and help to facilitate the regeneration of vegetation in adjacent areas as well as improve landscape biodiversity and forest patch connectivity. The lack of effective seed

sources and dispersal mechanisms at this site, and at many other similar restoration sites throughout the country, emphasises the need for enrichment planting to ensure later-successional species will establish in the restored ecosystem.

5.4 Management considerations

The results of the analyses found that there was a significant difference between the growth, abundance, and richness of species in the understorey of small and large gaps compared to the closed canopy control. However, no statistically significant difference was found between the growth, abundance, or richness of species in the understorey of the small gap compared to the large gap treatment. Minor differences in mean species richness and mean importance value were noted between the two treatments, however, this difference was not great enough to produce a statistically significant result. These findings suggest that the presence of gaps is substantially more important than the size of the canopy gap, at least in the context of the gap sizes included in this study. Therefore, for landowners wishing to transition a single-aged *P. radiata* forest to an indigenous forest, the focus should be on the creation of canopy gaps throughout the forest, rather than the size of the individual gap. Canopy gaps could be created by felling small groups of mature trees, as was the process for this study, or by leaving gaps in the forest when planting for forest establishment. A progressive thinning regime could also be adopted to gradually remove the pine canopy trees and allow native regeneration to eventually become the dominant cover.

The creation of canopy gaps does not guarantee that a successful ecological restoration will be achieved. There are often significant limitations preventing a full suite of species from regenerating in secondary forests. As mentioned in the previous section, one of these limitations is adequate seed sources and seed dispersal mechanisms. Research has suggested that enrichment planting is likely to be critical for the establishment of indigenous canopy species in the face of seed dispersal limitations (Forbes et al., 2016, 2020; Norton et al., 2018; Tulod et al., 2018; Tulod & Norton, 2020). The light environments produced from artificial canopy gap creation produces more favourable conditions for the establishment and growth of mid and later successional species (Tulod et al., 2018). Enrichment planting of species such as *P. totora* and *B. tawa* beneath canopy gaps could help to facilitate a more successful ecosystem restoration. It is important that the species selected for enrichment planting are well-suited to the region, site, and light environments within canopy gaps for optimum restoration. Eco-sourcing high quality plant material is essential for successful growth when

planted and to ensure that appropriate genetic material is being introduced into the natural environment (Norton et al., 2018).

Herbivory is a key limitation often faced in ecological restoration. Ungulates browse regenerating species and cause their growth to be stunted and may result in seedling death. The occurrence of browsing also tends to increase with gap creation which acts as a further barrier to regeneration (Forbes et al., 2016). Browsing from ungulates and other mammalian pests is known to alter the structure and function of indigenous forests. Ungulates can be excluded effectively with fencing and populations of other mammalian pests can be reduced through pest control. These actions will aid in ecosystem restoration as there will be an increase in regenerating plants, an increase in invertebrate populations, and an increase in litter mass other than pine needles (Wardle, et al., 1999; Dodd, et al., 2011). Therefore, the exclusion and control of browsing mammals is vital in allowing a full suite of species to regenerate freely, facilitating the effective restoration of forest ecosystem processes.

The results of this research suggest that the transition of a pine forest to an indigenous forest may be possible with the assistance of artificial canopy gaps. However, the transition is likely to require a significant period of time and can be expected to result in the regeneration of a limited subset of forest species if management interventions are not taken. There is also a requirement for ungulate exclusion, control of other mammalian pests, and enrichment planting to support in the restoration of the indigenous ecosystem. It is critical that any ecological restoration project has a high level of long-term management throughout. The restoration should be based on a local reference system to act as a guide to appropriate species for enrichment planting and for setting targets regarding the functions and systems of the site. The level of input and intervention required will depend on the level of resilience and degradation of the site. The Kakapo Bay forest has been highly modified from its natural environment for a long period and is likely to require a higher level of restoration inputs and intervention to progress the forest towards an indigenous forest ecosystem. Finally, it is vital that clear targets, goals, and objectives are defined for the ecological restoration project (McDonald et al., 2016). Monitoring of key variables will help to quantify progress and identify areas which require further attention. A high level of long-term management and involvement will give the greatest possibility of an ecological restoration being successful.

5.5 Limitations

There are some limitations to the research conducted in this dissertation. The statistical analyses looked for a significance level of $p < 0.05$. This means that the result can be called significant with a confidence level of 95%. This leaves of 5% chance that a false positive result may be returned. In this study one of the statistical analyses found slope to have a significant effect on native species importance value to a 95% confidence level (Tb.10). Due to the relatively homogenous slope profile of the site and from what was observed in the field, this result is likely to be a false positive. Other results in this dissertation may be subject to this phenomenon.

The RECCE method used to gather abundance by cover class data is a subjective method. The canopy cover of each species in the different height tiers is determined by a best estimate by sight. There will be some level of variability in this method of data collection, however, this has been reduced in this study by all data being gathered by the same person, over the course of two consecutive days.

This study is missing two small gap treatments due to circumstances beyond control. The other two treatments had two more plots than the small gap treatment which may have affected the consistency of the results. A larger sample size would also improve the reliability of the results. Repeated studies across different sites with different climatic conditions would be a valuable contribution to this field of research and would aid to further understand the factors which drive regeneration beneath pine canopies and how they can be managed to improve biodiversity. Further research into other canopy manipulation methods, such as progressive thinning, would also provide useful insight. A long-term study on the response of understorey vegetation to canopy manipulation would also help to grow the field of expertise in transitioning pine forest to native forest.

6. Conclusion

The results of this research have provided evidence that artificial canopy gap creation has a positive effect on the growth, abundance, and richness of native regenerating species in the understorey of a mature *P. radiata* forest. The small and large gap canopy treatments were both found to significantly improve growth, abundance, and species richness of regenerating species when compared to the closed canopy control treatment. However, there was no significant difference between the growth, abundance, or richness of species beneath small and large canopy gaps. This shows that the presence of canopy gaps is more important for stimulating regeneration than the size of each canopy gap, at least for the range of gap sizes included in this study. Therefore, if a forest owner wished to transition a single-aged pine forest to an indigenous forest it is strongly advised that artificial canopy gaps are created to allow for favourable understorey conditions for the establishment and growth of regenerating species.

A common limitation to successful ecosystem restoration which has been identified is a lack of adequate seed sources and dispersal mechanisms. In this study an absence of later successional species was noted in the understorey of the forest. The lack of nearby old growth or mature indigenous forest is likely to be the cause of this absence. Intervention in the form of enrichment planting of later successional species beneath canopy gaps is likely to be necessary to successfully restore a structurally diverse forest. Enrichment planting will also further help to accelerate succession towards a mature indigenous forest.

The effects of herbivory have also been noted as a limitation to ecosystem restoration. Browsing can stunt growth, kill seedlings, and alter the composition of species regenerating. To allow species to regenerate freely and to ensure the survival of palatable species, herbivores must be excluded through a combination of effective fencing and pest control. These actions will also assist in restoring the functionality of the ecosystem regarding flora and fauna populations.

The findings of this research suggest artificial canopy gaps can be useful in promoting natural regeneration beneath mature pine canopy. However, it is imperative that ecological restoration is treated as a long-term project with management and monitoring throughout the process. Clear goals and objectives will keep the project on track and bring attention to areas where there may be shortcomings. Restoring indigenous forests with the aid of pine trees as a

nurse crop appears to be a viable option in the context of this research, and artificial canopy gaps will likely be essential in providing the conditions required for species to regenerate in the forest understorey.



Figure 5: Regenerating native species in a canopy gap, in the understorey of the Kakapo Bay forest, Port Underwood, Marlborough Sounds

References

- Adams, J. A., & Norton, D. A. (1989). Soil and vegetation characteristics of some tree windthrow features in a South Westland rimu forest. *Journal of the Royal Society of New Zealand*, 21, 33-42.
- Allen, R. B., Platt, K. H., & Coker, R. E. (1995). Understorey species composition patterns in *Pinus radiata* plantation on the Central North Island volcanic plateau, New Zealand. *New Zealand Journal of Forestry Science*, 25(3), 301-317.
- Baret, S., Cournac, L., Thebaud, C., Edwards, P., & Strasberg, D. (2008). Effects of Canopy Gap Size on Recruitment and Invasion of the Non-Indigenous *Rubus alceifolius* in Lowland Tropical Rain Forest on Reunion. *Journal of Tropical Ecology*, 24, 337-345.
- Baxter, W. A., & Norton, D. A. (1989). Forest recovery after logging in lowland dense rimu forest, Westland, New Zealand. *New Zealand Journal of Botany*, 27(3), 391-399.
- Brockerhoff, E. G., Ecroyd, C. E., Leckie, A. C., & Kimberley, M. O. (2003). Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand. *Forest Ecology and Management*, 185, 307-326.
- Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P., & Sayer, J. (2008). Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation*, 17, 925-951.
- Carnevale, N. J., & Montagnini, F. (2002). Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. *Forest Ecology and Management*, 163, 217-227.
- Christian, D. P., Hoffman, W., Hanowski, J. M., Niemi, G. J., & Beyea, J. (1998). Bird and mammal diversity on woody biomass plantations in North America. *Biomass and Bioenergy*, 14(4), 395-402.
- Clout, M. N., & Hay, J. R. (1989). The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology*, 12, 27-33.
- Coates, K. D., & Burton, P. J. (1997). A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management*, 99, 337-354.
- Dodd, M., Barker, G., Burns, B., Didham, R., Innes, J., Carolyn, K., . . . Watts, C. (2011). Resilience of New Zealand indigenous forest fragments to impacts of livestock and pest mammals. *New Zealand Journal of Ecology*, 35(1), 83-95.
- Duncan, R. P. (1993). Flood disturbance and the coexistence of species in lowland podocarp forest, south Westland, New Zealand. *Journal of Ecology*, 81, 403-416.
- FAO & UNEP. (2020). *State of the World's Forests 2020*. Rome: FAO and UNEP.
- FOA. (2019). *Facts and Figures 2018/2019*. Forest Owners Association.

- Forbes, A. S., Norton, D. A., & Carswell, F. E. (2016). Artificial canopy gaps accelerate restoration within an exotic *Pinus radiata* plantation. *Restoration Ecology*, 24(3), 336-345. doi:<https://doi-org.ezproxy.canterbury.ac.nz/10.1111/rec.12313>
- Forbes, A. S., Norton, D. A., & Carswell, F. E. (2019). Opportunities and limitations of exotic *Pinus radiata* as a facilitative nurse for New Zealand indigenous forest restoration. *New Zealand Journal of Forestry Science*, 49(6).
- Forbes, A. S., Wallace, K. J., Buckley, H. L., Case, B. S., Clarkson, B. D., & Norton, D. A. (2020). Restoring mature-phase forest tree species through enrichment planting in New Zealand's lowland landscapes. *New Zealand Journal of Ecology*, 44(1), 3404.
- Hurst, J. M., & Allen, R. B. (2007). *The RECCE Method for Describing New Zealand Vegetation - Expanded Manual*. Lincoln: Landcare Research.
- Laffan, M. D., & Daly, B. K. (1985). Soil resources of the Marlborough Sounds and implications for exotic production forestry. 1. Soil resources and limitations to exotic forest growth. *New Zealand Journal of Forestry*, 30(1), 54-69.
- Lamb, D. (1998). Large-scale Ecological Restoration of Degraded Tropical Forest Lands: The Potential Role of Timber Plantations. *Restoration Ecology*, 6(3), 271-279.
- Lu, Y., Ranjitkar, S., Harrison, R. D., Xu, J., Ou, X., Ma, X., & He, J. (2017). Selection of Native Tree Species for Subtropical Forest Restoration in Southwest China. *PLoS One*, 12.
- Lusk, C. H., & Smith, B. (1998). Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology*, 79(3), 795-806.
- Lusk, C. H., Duncan, R. P., & Bellingham, P. J. (2009). Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp-broadleaved forest. *New Zealand Journal of Ecology*, 33(1), 83-89.
- Mazerolle, M. J. (2020, August 26). *Model Selection and Multimodel Inference Based on (Q)AICC(c)*. Retrieved from Package 'AICcmodavg': <https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf>
- McDonald, D., & Norton, D. A. (1992). Light environments in temperate New Zealand podocarp rainforests. *New Zealand Journal of Ecology*, 16(1), 15-22.
- McDonald, T., Jonson, J., & Dixon, K. W. (2016). National standards for the practice of ecological restoration in Australia. *Restoration Ecology*, 24(S1), S4-S32.
- McNab, W. H. (1993). A topographic index to quantify the effect of mesoscale landform on site productivity. *Canadian Journal of Forest Research*, 1100-1107.
- Ministry for the Environment. (2020, June 17). *Overview of the New Zealand Emissions Trading Scheme reforms*. Retrieved from Ministry for the Environment: <https://www.mfe.govt.nz/overview-reforming-new-zealand-emissions-trading-scheme>
- Moles, A. T., & Drake, D. R. (1999). Potential contributions of seed rain and seed bank to regeneration of native forest under plantation pine in New Zealand. *New Zealand Journal of Botany*, 37(1), 83-93.

- Norton, D. A. (2009). Species Invasions and the Limits to Restoration: Learning from the New Zealand Experience. *Science*, 325, 569-571.
- Norton, D. A., & Forbes, A. (2013). Can exotic pine trees assist in restoration? *Applied Vegetation Science*, 16, 169-170.
- Norton, D. A., Butt, J., & Bergin, D. O. (2018). Upscaling restoration of native biodiversity: A New Zealand perspective. *Ecological Management & Restoration*, 19, 26-35.
- Ogden, J., Braggins, J., Stretton, K., & Anderson, S. (1997). Plant species richness under *Pinus radiata* stands on the Central North Island volcanic plateau, New Zealand. *New Zealand Journal of Ecology*, 21(1), 17-29.
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . . Wagner, H. (2019, September 1). *Package 'vegan'*. Retrieved from Community Ecology Package: <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Onyekwelu, J. C., & Olabiwonnu, A. A. (2016). Can forest plantations harbour biodiversity similar to natural forest ecosystems over time? *International Journal of Biodiversity Science, Ecosystem Services & Management*, 12(1-2), 108-115.
- Pawson, S. M., Brockerhoff, E. G., Meenken, E. D., & Didham, R. P. (2008). Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. *Biodiversity Conservation*, 17, 1127-1148.
- Pawson, S. M., Ecroyd, C. E., Seaton, R., Shaw, W. B., & Brockerhoff, E. G. (2010). New Zealand's exotic plantation forests as habitats for threatened indigenous species. *New Zealand Journal of Ecology*, 34(3), 342-355.
- Pejchar, L., Gallo, T., Hooten, M. B., & Daily, G. C. (2018). Predicting effects of large-scale reforestation on native and exotic birds. *Diversity and Distributions*, 24, 811-819.
- R Development Core Team. (2020). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. Vienna, Austria. Retrieved from <http://www.r-project.org/>
- Rouvinen, S., & Kouki, J. (2011). Tree regeneration in artificial canopy gaps established for restoring natural structural variability in a Scots pine stand. *Silva Fennica*, 45(5), 1079-1091.
- Schneider, E. E., & Larson, A. J. (2017). Spatial aspects of structural complexity in Sitka spruce - western hemlock forests, including evaluation of a new canopy gap delineation method. *Canadian Journal of Forest Research*, 47(8), 1033-1044.
- Tulod, A. M., Norton, D. A., & Sealey, C. (2018). Canopy manipulation as a tool for restoring mature forest conifers under an early-successional angiosperm canopy. *Restoration Ecology*, 27(1), 31-37.
- Tulod, A., & Norton, D. A. (2020). Regeneration of native woody species following artificial gap formation in an early-successional angiosperm forest in New Zealand. *Ecological Management and Restoration*, 1-8.
- Walls, G. Y., & Laffan, M. D. (1986). Native vegetation and soil patterns in the Marlborough Sounds, South Island, New Zealand. *New Zealand Journal of Botany*, 24(2), 293-313.

- Wang, Y., Naumann, U., Eddelbuettel, D., Wilshire, J., Warton, D., Byrnes, J., . . . Wright, S. (2020, February 27). *Statistical Methods for Analysing Multivariate Abundance Data*. Retrieved from Package 'mvabund': <https://cran.r-project.org/web/packages/mvabund/mvabund.pdf>
- Wardle, D. A., Bonner, K. I., Barker, G. M., Yeates, G. W., Nicholson, K. S., Watson, R. N., & Ghani, A. (1999). Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs*, 69(4), 535-568.
- Wardle, J. (1984). *New Zealand Beeches: Ecology, Utilisation, and Management*. New Zealand Forest Service.
- Wells, A., Duncan, R. P., & Stewart, G. H. (2001). Forest dynamics in Westland, New Zealand: the importance of large, infrequent earthquake-induced disturbance. *Journal of Ecology*, 89, 1006-1018.
- Woollons, R. C., & Manley, B. R. (2012). Examining growth dynamics of *Pinus radiata* plantations at old ages in New Zealand. *Forestry: An International Journal of Forest Research*, 85(1), 79-86.
- Zhu, J., Matsuzaki, T., Lee, F., & Gonda, Y. (2003). Effect of gap size created by thinning on seedling emergency survival and establishment in a coastal pine forest. *Forest Ecology and Management*, 182, 339-354.

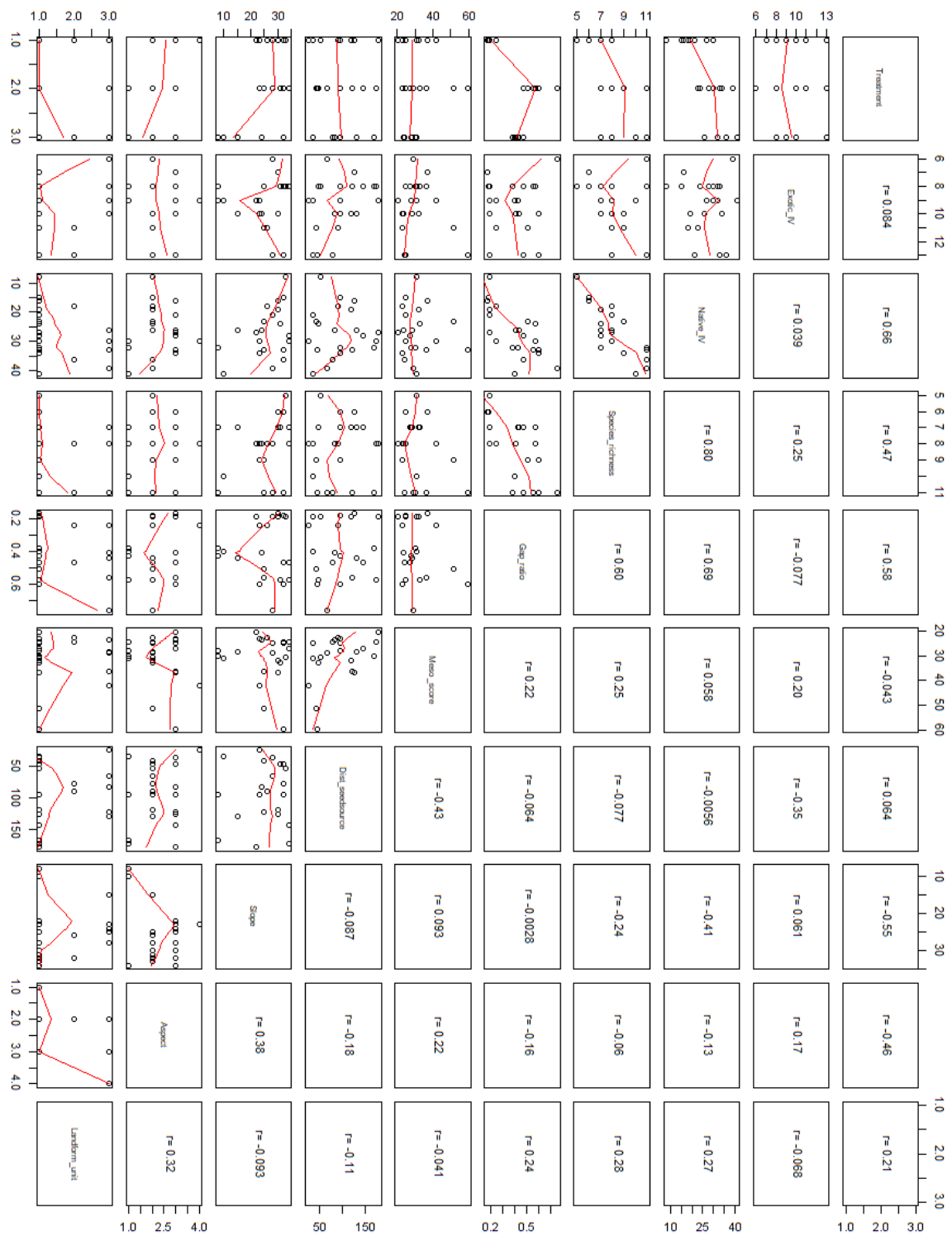
Appendices

Appendix A

Appendix A: Native species importance values. Kakapo Bay Forest, Marlborough Sounds, New Zealand. Site codes refer to treatment (L = Large gap, S = Small gap, C = Control). Species codes are the six letter codes assign by the National Vegetation Survey. Species corresponding to each code are given in Table 1.

Site	ARlser	BRAre	CARser	COPcol	COPgra	COPluc	CORava	DICsqu	HOHpop	LEPsc	LEUfas	MELram	SCHdig
L	9	1	2	0	2	2	0	0	0	2	0	8	9
S	5	0	0	0	0	2	0	0	0	0	0	10	11
S	5	5	2	2	0	2	0	2	0	0	0	9	6
C	0	0	0	0	0	2	0	0	0	0	0	6	6
C	0	3	0	0	0	0	0	0	0	0	0	2	2
L	5	2	0	0	0	2	0	2	0	0	0	8	11
C	0	0	0	2	0	4	0	0	0	6	2	6	6
C	0	2	0	1	0	2	0	0	0	0	2	5	8
L	2	0	0	0	0	2	0	0	0	0	0	9	8
L	2	2	2	2	0	2	0	0	0	4	2	7	9
C	0	4	0	2	0	2	0	0	0	0	0	2	6
L	2	0	0	2	0	2	2	0	0	4	0	4	6
S	0	0	0	2	0	0	0	0	0	9	2	0	10
L	8	4	0	0	0	2	0	0	0	0	0	7	5
S	3	7	0	0	0	2	0	0	0	2	2	11	11
C	0	5	0	2	0	2	0	0	4	0	0	6	11
L	8	2	0	0	0	2	0	0	0	0	0	10	5
C	2	0	0	0	0	2	0	0	0	6	0	0	7
S	0	7	0	1	0	2	0	0	0	0	0	7	6
S	2	4	0	2	0	4	0	0	0	2	2	9	7
L	6	0	2	2	2	2	0	0	0	6	2	4	8
C	2	0	0	0	4	0	0	0	0	0	0	0	7

Appendix B



Appendix B: Scatterplot matrix of variables measured at Kakapo Bay, Port Underwood, Marlborough Sounds

Appendix C

Treatment	diff	lwr	upr	p adj
Small-Control	1.625	-0.728	3.978	0.212
Large-Control	2.125	-0.053	4.303	0.057
Large-Small	0.500	-1.853	2.853	0.853

Appendix C: Post hoc tukey test of one-way ANOVA: effect of treatment on native species richness

Appendix D

Treatment	diff	lwr	upr	p adj
Small-Control	11.542	2.263	20.719	0.013*
Large-Control	9.125	0.628	17.622	0.034*
Large-Small	-2.417	-11.594	6.761	0.784

Appendix D: Post hoc tukey HSD test of one-way ANOVA: effect of treatment on native species importance value