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ABSTRACT

Areas of high biodiversity and endemism, such as the lowland podocarp-tawa forest type in New Zealand, are at high risk of suffering negative impacts from habitat loss and fragmentation. Shifts in fundamental ecological processes, such as autotoxicity, can exacerbate the effects of human-induced alterations. Restoration activities can help to mitigate the effects of fragmentation and simulation models allow us to improve our understanding of ecosystem dynamics, and are hence useful tools in guiding restoration initiatives. In New Zealand the removal of herbivores by fencing is a common method for restoration, but some recent studies have suggested that fencing alone is insufficient for fragment recovery. Furthermore, the native New Zealand tawa (*Beilschmiedia tawa*) is faced with the challenge of severe recruitment failure in forest fragments, a threat made more severe by its endemic status.

The aim of the present study was to assess the effect of fragmentation and fencing on the regeneration of podocarp-tawa forests of the Waikato region, Northern New Zealand. In **Chapter 2** I focused on the consequences of different types of management (fragmentation and fencing) on the current-day composition and structure of podocarp-tawa forest fragments and the associated abiotic conditions (soil, light and climate). In **Chapter 3** I explored the role of fragmentation and fencing on the survivorship of *B. tawa* seedlings and the factors that could explain the recruitment problems that affects it. Later in **Chapter 4** I tested the potential allelopathic effect of *B. tawa* leaf leachate on germination and growth of *B. tawa*. Finally, in **Chapter 5** I gave a detailed description of the development of a spatially explicit individually-based model (SEIBM) built to represent the long-term dynamics and viability of podocarp-tawa forest and subsequently in **Chapter 6** I used the aforementioned model to

simulate different scenarios to assess the impact of different management and restoration strategies on the long-term persistence of podocarp-tawa forest fragments.

Results from **Chapter 2** showed that in fragmented sites growth rates of seedlings was reduced. Furthermore, our results show that fencing alone is not enough to ensure the viability of forests fragments over time, but it is an important first step. Soil analyses revealed higher water and nutrient content in unfragmented forests versus forest fragments, regardless of whether they were fenced or not. Furthermore, results from **Chapter 3** demonstrated that fencing had no positive effect on seedling growth and survivorship. In addition, in **Chapter 4** I found that *B. tawa* leaf leachate can have a detrimental effect on its own seeds and on the early development stages of its seedlings. The spatial model described in **Chapter 5** showed to perform within plausible ranges. The most sensitive parameters were in general the ones that represented anthropogenic activities and life cycle stages. The model described in **Chapter 5** allowed us to simulate various future scenarios. These future scenarios simulations are compiled in **Chapter 6** were results demonstrated that fenced forest fragments inevitably collapse over time in the absence of other restoration actions. While fencing to remove pressure from large herbivores is a good first step, further restoration actions, such as periodic planting, need to be implemented to secure the persistence of forest fragments.

1. INTRODUCTION

1.1 Background

The negative impacts of unsustainable human activities on natural ecosystems are well known (Hobbs and Harris 2001). Many natural ecosystems have been reduced to small and isolated patches or remnants immersed in a productive matrix comprising, for example, forest plantations, farmland or mining, which, in turn, threatens their long-term survival (Primack et al. 2001). Consequently, it is increasingly necessary to develop and take appropriate actions to ensure the protection and restoration of these remaining ecosystems. The development of tools with which to protect remnant ecosystems within the productive matrix is a priority for their long-term conservation and persistence (Meurk and Swaffield 2000, Moss 2000, Kueffer and Kaiser-Bunbury 2014).

Habitat fragmentation is one of the main processes responsible of the reduction of natural ecosystems to scattered isolated forest remnants (Iida and Nakashizuka 1995, Laurence 2000, Echeverria et al. 2006). Forest fragmentation can be defined as a dynamic process were a large habitat is consecutively reduced to small isolated remnants or patches of forest (Fahrig 2003, Echeverria et al. 2006). The process of forest fragmentation has several demographic consequences for the species occupying them. In particular, changes in the abiotic and biotic conditions due to the ‘edge effect’ can have a profound influence on population and community dynamics (Murcia 1995, Laurance 2000, Broadbent et al. 2008).

The edge effect is the term used to describe a suite of changes in abiotic and biotic conditions at forest edges where fragments are exposed to lateral wind and sunlight that can lead to microclimatic changes (Gascon et al. 2000). Changes in these site conditions can alter the structure and species composition in these fragments (Tabanez and Viana 2000). For example, studies in the Amazon forest have shown that edge effects can alter species distributions, abiotic properties and ecological processes (Ferreira and Laurance 1997, Benitez-Malvido 1998). However, the single strongest negative effect of the edge effect is increased tree mortality (Laurance et al. 2002). Laurance et al. (2000) showed higher mortality of trees in the edges of the fragment, especially of large trees, which can affect the future structure, composition and diversity of tree species in forest fragments. To complicate matters, the distance into which a patch is affected varies for different climatic variables but typically extends from 10 to 50 m (Murcia 1995, Myers and Court 2013), although edge effect impacts up to 300 m have been reported (Gascon et al. 2000, Laurance et al. 2000).

In addition to the negative impact of the loss of forest cover, the remaining forest fragments have to deal with the negative impacts of the surrounding human activities, such as browsing and soil disturbance by domestic stock (e.g. cattle, sheep) (Echeverria et al. 2007, Smale et al. 2008), higher organic nutrient levels by the percolation of fertilizer into the fragments (Stevenson 2004), the introduction of mammalian pests, and altered hydrological regimes by agricultural activities (Dodd 2011). All of the negative factors that affect the fragments (e.g. edge effects, anthropic stressors) are influenced by their size or shape (Laurence et al. 2002, Echeverria et al. 2007). As previously mentioned, edge effects can penetrate up to 100 m or more meaning that, in simple terms, deleterious edge effects may occur throughout fragments where the centre is less than 100 m from the edge (in effect, such small fragments are all 'edge'). Fragments are often linear in shape and complex fragment shapes increase the amount of habitat affected by edge effects relative to more compact geometries of the same area (Ewers and Didham 2007).

Fragmentation and human activities negatively affect population-level processes for plants such as seed dispersal and seedling establishment, ultimately preventing species from colonizing suitable sites (Cramer et al. 2007, Hampe et al. 2008, Herrera and Garcia 2010). Recent studies have shown that recruitment failure in fragmented landscapes can be caused by seed dispersal limitation or by post-dispersal processes such as restrictions in seed survival, germination or seedling establishment (Cramer et al. 2007, Herrera and Garcia 2010). For example, Cramer et al. (2007) show that in Amazonian forests seed dispersal is negatively affected by fragmentation as a result of reduced densities of seed dispersers, especially those of large seeded species and of endemic species. Also, Herrera and Garcia (2010) found that, although in general seed recruitment is positively correlated with the activity of dispersers in the fragments, in some tree species, despite high disperser activity, their recruitment (seed to seedling) was low demonstrating that post-dispersal factors are in play.

Many factors can influence post-dispersal processes in forest fragments and these factors can vary in both their frequency and duration; they include soil composition, canopy cover, patch size, forest community structure, seed and seedling predation, altered microclimates, and continued degradation of the fragment (Bruna 2002, Laurance et al. 2002, Herrera and Garcia 2010, Ismail et al. 2014). For example, Echeverria et al. 2007 found that in the south temperate forest of Chile fragment size was correlated with the abundance and basal area of tree species, although the effect is species specific. In addition, Benitez-Malvido (2002) found that in the Amazon the effect of herbivory on seedlings is increase as the size of the forest fragment decreases, while Cramer et al. (2007) found that the quantity and distance of dispersed seeds were higher in continuous forest than in fragments.

Under stressful conditions such as those seen in fragments, chemical inhibition (allelopathy) could play an important role in plant community dynamics (Muller 1969, Einhellig 1987, Anaya 1999, Gawronska and Golisz 2006). Plants can naturally interfere with each other’s development and thus affect post-dispersal processes. Many plant species produce a large number of secondary chemical compounds that can have inhibitory or stimulatory effects on both conspecific and heterospecific individuals. As the chemical compounds do not target specific species, they can also have a negative effect on individuals of the same species, particularly on their growth, a process called autotoxicity (Friedman and Waller 1985). Few studies have dealt with the allelopathy of New Zealand's native flora (e.g. June 1976, Froude 1980). One of the most important attempts to determine allelopathic interactions was that of Froude (1980) who studied the potential allelopathic effect of 36 plant species and found that the secondary compounds from several species had inhibitory effects on radicle growth. Allelopathy coupled with other stresses in the environment can often enhance allelochemical production and increase the potential for allelopathic interference (Anaya 1999). These underlying ecosystem dynamics have the potential to exacerbate the effects of habitat loss and fragmentation.

Huxel and Hastings (1999) argued that implementing restoration activities can help to offset or at least mitigate the effects of fragmentation. Restoration ecology can be defined as a set of activities seeking to initiate or accelerate the recovery of a degraded, damaged or destroyed ecosystem in terms of its health, integrity and sustainability (Ruiz-Jaen and Aide 2005). The Society of Ecological Restoration International (SER) (2004) recommends the assessment of nine different attributes in order to determine the success of restoration activities, these attributes are: similar diversity and structure to a reference ecosystem, presence of native species, presence of functional groups for long-term stability, physical properties that can support reproducing populations, normal functioning, integration with the landscape, elimination of potential threats, resilience and self-sustainability. In practice, however, most studies only use three of these attributes (diversity, structure vegetation, ecological processes) to determine the success of restoration activities (Ruiz-Jaen and Aide 2005, Shackelford et al. 2013).

Restoration activities act at different intensities and can be classified as being either passive or interventionist (active) (Holl and Aide 2011, Hobbs et al. 2011). Passive restoration refers to activities that do not require ongoing active human intervention, but do require the removal of those activities that have a negative impact on the ecosystem (e.g. removal of large herbivores by fencing) followed by ongoing monitoring to ensure the ecosystem is recovering. Interventionist, or active, restoration, on the other hand, requires ongoing activities (e.g. planting of seedlings, efforts to rehabilitate soils) with the aim of recovering lost ecosystems processes to ensure the long term viability of ecosystems.

Passive restoration is mostly used when the negative activities have been acting for a short period of time, and is most effective where stressors can be removed with a single management strategy such as, for example, pest eradication. Active restoration, on the other hand, is typically required when the ecosystem has been exposed to long-term degradation (Zahawi et al. 2014) and may have passed critical thresholds beyond which it has lost resilience (Suding and Hobbs 2009). Currently, passive restoration is the most widely adopted approach in the world (Melo et al. 2013). For example, in New Zealand the removal of herbivores by fencing, often alongside non-native pest eradication, is a widely method used for restoration (Dodd et al. 2011, Burns et al. 2012). However, some studies have suggested that fencing alone is not sufficient for such forest fragments to recover to a state similar to that of more intact forest (Burns et al. 2011, Myers and Court 2013). The widespread use of the passive restoration approach could be explained by the comparatively low cost, and it has been suggested that passive restoration is more cost effective than active restoration. Birch et al. 2010 evaluated the cost effectiveness of passive and active restoration activities in dry land forest in Argentina, Mexico and Chile using a cost benefit analysis. The authors compared the cost of different restoration scenarios (passive and active restoration) plus the ecosystem services that restoration will bring minus the lost in income from livestock production. Their results showed that the most cost-effective restoration activities are passive. However, Norbury et al. (2014) suggested that depending on the size of the fragment sometimes active restoration will be cheaper. In fact, the authors argued that in small fragments (1 ha) the use of a pest proof fence is more cost effective. But in larger fragments (> 219 ha) a combination of fencing (cat and ferret proof) and pest control will be more economical sound.

Active restoration may be very expensive depending on the scale in space and time of the restoration project and the desired outcomes. In such contexts it is extremely challenging, both logistically and economically, to experimentally compare different management activities playing out over decades. Although, some studies have shown that active intervention is not necessary or in some cases detrimental to the recovery of the target ecosystems (e. g. Murcia 1997, Sampaio et al. 2007), the appropriate restoration strategy will depend on the current state and type of ecosystem, particular conditions and past degradation history (Muñiz-Castro et al. 2006, Holl and Aide 2011, Stanturf et al. 2014). For example, Rodrigues et al. (2011) developed a regional scale restoration plan in Atlantic Forest biome in Brazil which showed that some areas were able to recover by themselves but others would need active intervention (e.g. seed and seedlings introduction, enrichment) because of the nature of the past degradation or the current context of the target areas (e.g. scarcity of propagules, absent of dispersers).

The decision of what restoration approach (passive or active) to be used seems to be made on a case by case basis and can become a complex process especially when extended scales (large areas and/or many fragments) are being considered (Holl and Aide 2011, Stanturf et al. 2014). Ecological models can be useful tools to help with the complex decision-making process required to determine which restoration approach to adopt. Ecological models are helpful in assessing the factors that affect forest fragments and the future prospects for these fragments under different restoration approaches. Simulation models can help in the conservation and restoration of degraded systems by improving our understanding of such systems' dynamics, by allowing the assessment of different future scenarios, and by providing qualitative and quantitative predictions for the development of management actions (Holl et al. 2003). Models also allow us to evaluate combinations of restoration activities to determine which combination will have the highest rate of success without waiting decades or investing large sums of money (Crossman and Bryan 2009). Even where formal empirical comparison using frameworks such as adaptive management (Walters 1986) is being implemented, models provide a crucial first-step in designing the experiment and identifying appropriate 'treatments'.

Although in New Zealand ecological restoration is an active discipline with a great number of dynamic projects and success stories, many restoration projects have been primarily focused on the management of invasive species and to a lesser extent improving connectivity between remnants, enhancing buffers around remnants, and creating additional habitat. Relatively few projects, however, are incorporating a landscape-scale approach (Norton, 2009). This is likely due to the difficulties presented by the sheer scale of landscape-level dynamics, but developing predictive ecological models can go a long way to overcome the challenges faced by large-scale restoration projects (Meurk and Hall 2006).

1.2 Podocarp-tawa forest in northern New Zealand

Areas of high biodiversity and endemism are at greater risk of suffering negative impacts from ecosystem alterations than other areas (Myers et al. 2000). Such is the case of the lowland podocarp-tawa forest type in New Zealand, which is currently fragmented, under exotic herbivore pressure, suffering invasion by exotic weeds and potentially experiencing recruitment and seed dispersal failure (Dodd and Power 2007, Smale et al. 2008, Innes et al. 2010, King et al. 2011). Fragmentation in areas where podocarp-tawa forest was once widespread is acute; forest across the Waikato, for example, has been reduced to nearly 5000 small fragments (average size of 97 ha) of which more than 95 % are 25 ha or smaller (Waikato Regional Council 2009). The recruitment problems that affect podocarp-tawa type forest, especially *B. tawa* (tawa) fragments, could have negative long-term effects on forest structure and composition.

1.2.1 *Beilschmiedia tawa*

B. tawa is usually referred to in New Zealand by its Māori name, tawa, which means "purple" and probably refers to the colour of its fruit (Figure 1.1a). It is member of the mainly tropical family Lauraceae, and and its genus (*Beilschmiedia*) has approximately 250 species (Kostermans 1964). Tawa is an endemic evergreen that can reach a height of 35 m and a diameter of 1 m (Allan 1982) and is one of only two members of *Beilschmiedia* in New Zealand (the other being *B. taraire*, also a canopy-dominant northern species). It has dark, smooth bark and produces crowns < 30 m in diameter, but larger crowns are not uncommon (Figure 1.2). The leaves of tawa are lanceolate and appear yellow-green in colour. Flowers are small (2 – 3 cm in diameter) and green. The ripe fruit appears purple and pendulous (drupe), and measures between 15 – 25 mm in length (Roper 1967). The native New Zealand pigeon kererū (*Hemiphaga novaeseelandiae*), which is itself in decline, is a common disperser of *B. tawa* (Campbell and Atkinson 2002) (Figure 1.1b and 1.1c).

Figure 1.1 **(a)** Detail of tawa leaves and its purple fruit, **(b)** kererū (*Hemiphaga novaeseelandiae*), **(c)** a *Beilschmiedia tarairi* seed shortly after being excreted by a kererū. *B. tarairi* and *B. tawa* seeds are of similar size and shape.

Figure 1.2 Photos of *B. tawa* as a canopy dominant in the Waikato region, North Island, New Zealand.

In general, *B. tawa* do not establish in large canopy gaps but in small gaps, preferentially in moist and deeply shaded sites, under emergent mature podocarps and under light or decaying hardwood canopies (Knowles and Beveridge 1982, West 1986). A germination experiment performed by West (1986) showed that a warm and humid environment is required, substrate composition was not important and litter depth and density did not impede germination. In addition, cold temperatures seemed to slow germination. *B. tawa* seedlings have been classified as shade-tolerant and can persist under the canopy for decades or centuries (Smale 2008). West (1986) showed that there was a high mortality of seedlings in simulated large gaps and low mortality under shade simulated situations. *B. tawa* seedlings under simulated large gaps were more prone to desiccation, suggesting a potentially high sensitivity to drought. In terms of growth, although, *B. tawa* is a shade-tolerant species it showed optimal growth rates under intermediate light situations (e.g. in small gaps) when all the other conditions were maintained in their normal ranges.

B. tawa is distributed throughout the North Island and the northern part of the South Island (Wiser et al. 2011). At the southern limit of its distribution there are several stands of tawa, all in remnant forest patches, suggesting that tawa was formerly more widespread in coastal areas north of Kaikoura (West 1986). Tawa can be found in the major forest communities of New Zealand (Wardle 1991). Throughout its range, however, *B. tawa* is most frequently found in association with podocarps, particularly rimu (*Dacrydium cupressinum*). The selective logging of podocarps by Europeans has reduced what were once mixed stands with significant podocarp specimens to a composition that is now dominated by tawa (West 1986). However, across parts of its range tawa regeneration failure is evident in podocarp-tawa fragments (Burns et al. 2011).

Recruitment failure in tree species is not uncommon and has been shown to be an issue affecting forest species from Brazil (Uriarte et al. 2010), to Canada (Caspersen and Saprunoff 2004), and from India (Ismail et al. 2014) to Spain (Carnicer et al. 2013). These studies show that there a variety of factors can cause recruitment failure such as elevated inbreeding caused by fragmentation, increased degradation of forest fragments, changes in light patterns, lack of suitable substrate, limited seed dispersal, limited seed supply and climate effects among others. The factors that affect recruitment in some cases can be species- specific and vary with the degree of degradation of the affected sites. In the case of *B. tawa* seed limitation does not appear to be the cause of recruitment failure (Knowles and Beveridge 1982, West 1986) and therefore other potential factors cannot be discounted.

Studies on *Beilschmiedia* have identified several allelopathic compounds. Russell and Fraser (1969) found alkaloids in *B. tawa* fruits, while Cambie et al. (1961) found leucoanthocyanins in the leaves. Leucoanthocyanins have been described as germination and growth inhibitors in some plant species (Rawat et al. 1998). Froude (1980) determined that *B. tawa* had a moderate inhibitory effect on radicle growth in in cress (*Lepidium sativum*) and *Weinmania racemosa*. It is not known whether these leucoanthocyanins have an inhibitory effect on its own seeds and seedlings. In addition, and as mentioned earlier, the decline of kererū, one of tawa's main seed dispersers, could also be playing a role in the lack of regeneration of *B. tawa*. In a study on vertebrate seed dispersers, Babweteera and Brown (2009) showed that assemblages of forest specialists were less abundant in heavily disturbed forests, and that frugivores were mainly small-bodied species that spat seeds beneath fruiting trees compared to large-bodied species in the less disturbed forests that ingested and carried away the seeds. This evidence seems to suggest that the quantity of seeds dispersed in heavily disturbed forests could be reduced due the absence of large frugivores (Kelly et al. 2010). There is, therefore, a pressing need for studies in post-dispersal processes to help to clarify and isolate the factor or factors responsible for the recruitment limitation being observed.

1.3 Current management activities of podocarp–tawa forest fragments

Selective logging has left what were once mixed podocarp-tawa forests in a state where they are often dominated by *B. tawa* (West 1986). However, the pressure from logging in these *B. tawa*-dominant forests has largely disappeared. Nowadays, the main factors affecting these forest types are the browse pressure exerted by exotic mammals such as fallow deer (*Dama dama*) and brushtail possums (*Trichosurus vulpecula*) and the reduction of seed dispersal by the native pigeon or kererū (Knowles and Beveridge 1982, Dodd 2011).

Herbivores can have a negative impact on regeneration of plants and also on soil properties (Hulme 1996, Hanley and Sykes 2009, Wardle et al. 2001). In response to these and other pressures various management strategies have been applied to remnant podocarp-tawa forest areas. One common management practice in New Zealand is the fencing of forest fragments to exclude large herbivores, often followed by small mammalian pest control (Dodd et al. 2011, Burns et al. 2012). Fencing ranges from the total exclusion of all mammals (e.g. via predator-proof fences) to just the exclusion of large mammalian herbivores (e.g. livestock such as cattle and sheep) (Figure 1.3). It is logical to think that if fences are installed and exotic herbivores excluded then, eventually, some of the negative effects of herbivores will be removed and the forest will recover its resilience as it returns to a more intact state. Unfortunately, and despite the seeming logic of this statement, the success of fencing in supporting long-term recovery of forest fragments has not been critically analysed, at least in New Zealand (Burns et al. 2011).

Figure 1.3 Fencing can exclude large herbivores such as cattle from forest fragments. Note the fenced forest fragment in the far right.

1.4 Examples of restoration projects in New Zealand

Over the last 750 years the Waikato region of the central North Island of New Zealand has experienced a marked loss of forest and accompanying fragmentation (Waikato Regional Council 2009). To counter this loss of native forest, a wide range of initiatives ranging in scope have been implemented across the region. Looking at two of these initiatives showcases a few of the key features of modern conservation and restoration activities in productive landscapes in New Zealand. At one end of the spectrum Mt. Maungatautari could be considered a flagship for mainland island habitats; an expensive long-term endeavour geared towards pest eradication and reintroduction of native species. By contrast Te Miro, part of the Hamilton Halo Project, is perhaps a more typical restoration initiative with ongoing pest control, but designed to provide spillover benefits as part of a larger conservation effort.

1.4.1 Maungatautari Ecological Island

The decline of the vegetation on Mt. Maungatautari (Waikato region, central North Island*)* is typical of the fate of forests in the 20th century in New Zealand. Maungatautari Mountain was first deemed a nature reserve in 1912. In the late 19th and early 20th century rabbits posed a great threat to the farmer/settlers of the Waikato region and to Māori cultivation. However, the arrival of the brushtail possum in the 1950s was much more devastating, and by the 1980s the remaining forest on the mountain was showing signs of severe browsing damage (Scott 2003).

Almost 100 years after Maungatautari was first made a reserve, the Maungatautari Ecological Island Trust (MEIT) was formed in 2002. The MEIT aims “to protect the forest by eradicating non-native pest species and reintroducing native species” (Kaval 2004, p. 3). The 3400 ha of forest on Mt Maungatutari are now enclosed by 47 km of predator-proof fence, at an estimated cost of $20 million NZD (Kaval 2004) (Figure 1.4). The enclosed area is completely surrounded by pastureland and is the largest ecological ‘mainland island’ in New Zealand. Since the completion of the pest-proof fence in 2004, 14 mammal species have been totally eradicated from Maungatautari, including cats (*Felis catus*), ship rats (*Rattus rattus*), stoats (*Mustela erminea*), rabbits (*Oryctolagus cuniculus*), possums, deer, and goats (*Capra hircus*) and native bird populations, e.g. stitchbird (Notiomystis cincta) and kaka (*Nestor meridionalis*) are gradually being re-introduced (Kaval 2004, Smuts-Kennedy and Parker 2013).

Figure 1.4 Predator-proof fence surrounding the 3400 ha Maungatautari Ecological Island, Waikato region, North Island, New Zealand

1.4.2 Te Miro Scenic Reserve

The Te Miro Scenic Reserve is located in the farming locality of Te Miro, 15 km northeast of

Cambridge. Te Miro Scenic Reserve is a 400 ha Department of Conservation (DoC) area. The most common native tree species in the reserve include tawa, rimu, pukatea (*Laurelia novae-zelandiae*), rewarewa (*Knightia excelsa*) and, of course, miro (*Prumnopitys ferruginea*) trees. It is popular with hunters who use the reserve during the fallow deer hunting season.

In 2007 DoC, along with the Biosecurity Heritage Group of the Waikato Regional Council began the “Hamilton Halo Project” with the objective of boosting native bird populations, mainly tui (*Prosthemadera novaeseelandiae*), kererū *(H. novaeseelandiae)* and bellbird (*Anthornis melanura*), throughout the region. These species are important pollinators and seed dispersers for native plants and play a vital role in ecosystem dynamics (Kelly et al. 2010). The Hamilton Halo Project is one of the few landscape-level restoration projects in New Zealand.

The Halo project set out to achieve its goal via mammalian pest control, mainly of rats, possums and other small mammals, alongside planting and weed control. Even though Te Miro is not fenced like Maungatautari, the Halo project has resulted in increases in tui and bellbird sightings in the area and has suppressed pest populations (Hamilton Halo Project Report 2012).

1.5 Objectives

The research presented in this thesis focuses on the role of post-dispersal processes in the apparent recruitment failure of *B. tawa* in forest fragments. To this end, I carried out field experiments on *B. tawa* seedlings in areas with different management regimes; unfragmented forests, fenced and unfenced forest fragments. I measured both biotic and abiotic variables to determine which factors or combination of factors can best explain the observed recruitment failure. I also assessed vegetation composition and structure in podocarp-tawa forests using a multivariate approach, and whether *B. tawa* leaf leachate had allelopathic properties and determined its effect on growth of *B. tawa* seeds. Building on the outcomes of this field-based research I developed a forest simulation model by integrating the field-derived information to evaluate the long-term viability of *B. tawa* forest patches. The model is designed to provide information that will help to identify restoration needs and the types of management intervention that may be necessary to protect these remnant forest patches. Figure 1.3 presents a diagram highlighting the topics in this thesis and the relationships between them.

In summary, New Zealand podocarp-tawa forests are at present reduced, fragmented, and under anthropic stress. These factors have important effects for the demography of tree species and the dynamics in the remaining forest fragments. The use of fences to remove pressure from large mammalian herbivores is a common management tool in New Zealand its long-term effects on the viability of forest fragments remains undetermined. This thesis will address post-dispersal processes in light of the apparent regeneration failure of tawa in forest fragments.

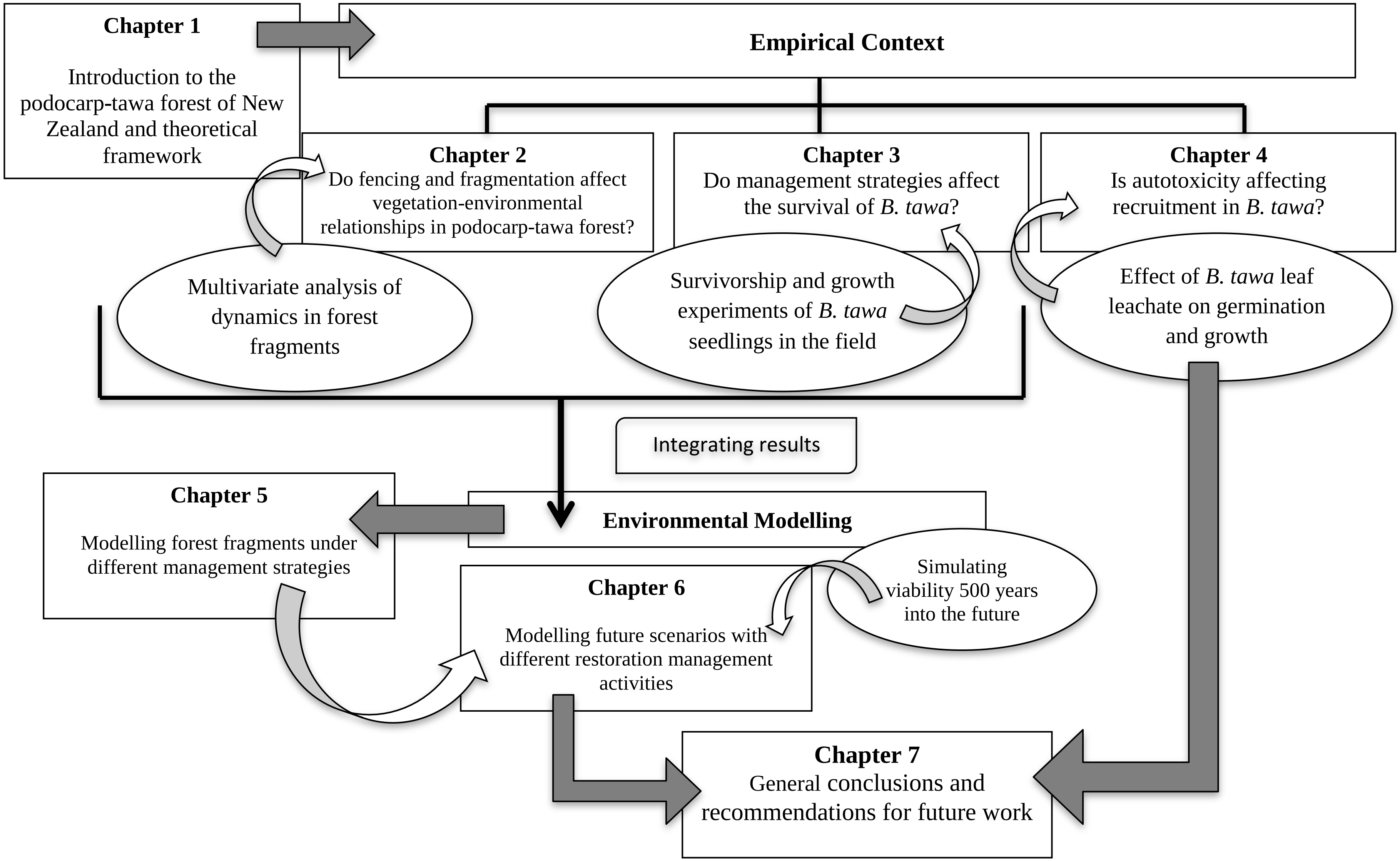


Figure 1.3 Flow chart of thesis structure highlighting the relationships between each chapter and its topics.

2. EFFECTS OF FRAGMENTATION AND FENCING ON VEGETATION COMPOSITION, STRUCTURE AND ENVIRONMENT OF FOREST FRAGMENTS

2.1 Introduction

In present-day northern New Zealand landscapes, including podocarp-tawa type communities, forests are often highly fragmented (Ewers et al. 2006). Fragmentation can negatively affect seed dispersal and seedling establishment, preventing plant species from colonizing suitable sites (Bach and Kelly 2004; Herrera and Garcia 2010 and references therein,). Herrera and Garcia (2010) note that it remains uncertain whether recruitment failure in fragmented landscapes is caused by seed limitation or by an interruption of post-dispersal processes such as seed survival, germination or seedling establishment, or a combination of these factors. In the case of *Beilschmiedia tawa*, previous studies have described recruitment failure in some fragments in the Waikato (Burns et al. 2011). However, seed limitation does not appear to be the cause of recruitment failure because reasonable levels of seedfall have been reported (Knowles and Beveridge 1982, West 1986). Therefore, studies of post-dispersal processes are needed to clarify the factor or factors responsible for recruitment limitation in this species.

Both abiotic and biotic factors can influence post-dispersal processes in forest fragments and these effects can vary in both their frequency and duration. Factors that can affect post-dispersal processes include soil composition, canopy cover, patch size, forest community structure, altered microclimates, and continued degradation of the fragment (Ismail et al. 2014). Because of the many effects operating on vegetation fragments, it is difficult to isolate the pure effect of fragmentation alone (Ewers and Didham 2006).

As mentioned in Chapter 1, a common management practice for forest fragments in New Zealand is to fence them off to remove the impacts of large herbivores (Smale et al. 2005; Burns et al. 2012). This is sometimes followed by small mammalian pest control (Dodd et al. 2011). However, some studies suggest that fencing alone is not sufficient for the fragments to recover (Burns et al. 2011, Myers and Court 2013). In this chapter I assess the impact of fragmentation and fencing on podocarp-tawa forest. We wanted to explore the effects of fragmentation and fencing on the current-day composition and structure of the vegetation in the fragments, and the abiotic conditions (soil, light and climate) experienced within them. In addition, I wanted to determine whether fencing fragments has a positive effect on *B. tawa* recruitment. To accomplish these objectives I collected a broad suite of biotic (e.g. community composition, species abundance, stand structure) and abiotic data (e.g. soil nutrients and physical characteristics, air temperature, canopy density) in unfragmented forests, and fenced and unfenced fragments.

To account for fragmentation I merged the data from the fenced and unfenced fragments and compared them with the unfragmented forest data when possible. To determine the effect of fencing I used the data from fenced and unfenced fragments separately and contrasted these with the unfragmented forest. I first present the results for the biotic and then for the abiotic data. The biotic section is organised into two components:

- Vegetation analyses: analysis of tree and seedling compositional data across sites experiencing fragmentation and under different management regimes using nMDS and mvabund.
- Tree coring: results of age-increment cores taken from trees at sites under different types of management to establish an age range for recruitment failure at each site.

The abiotic section results are also organised into two components:

- Soil analysis, canopy cover and litter depth: PCA analysis to determine whether there is a relationship between fragmentation, the type of management and abiotic variables.
- Temperature and humidity measurements: Correlation analyses were performed to determine whether temperature and humidity were correlated. Monthly mean, maximum mean, minimum mean temperatures and daily range temperatures were analysed graphically.

2.2 Methods

2.2.1 Study area

The study area was located near Cambridge in the Waikato region, North Island, New Zealand (Figures 2.1 and 2.2). Within this area, I identified three locations each centred on a large unfragmented forest – Te Miro, Maungatautari North and Maungatautari South. Within each location I also identified a fenced forest fragment and an unfenced forest fragment (Figures 2.1 and 2.3). The unfragmented forests occurred within the Maungatautari and Te Miro Scenic Reserves, while forest fragments were all located on private land (Table 2.1). We considered that ‘fenced’, fragments must have been continuously fenced for at least 20 years to avoid changes that occur immediately following fencing (Burns et al. 2011). Some of the fenced fragments had been previously included in a study of vegetation dynamics in fragmented landscapes (Burns et al. 2011, Dodd et al. 2011) and were classified in a similar way by those authors.

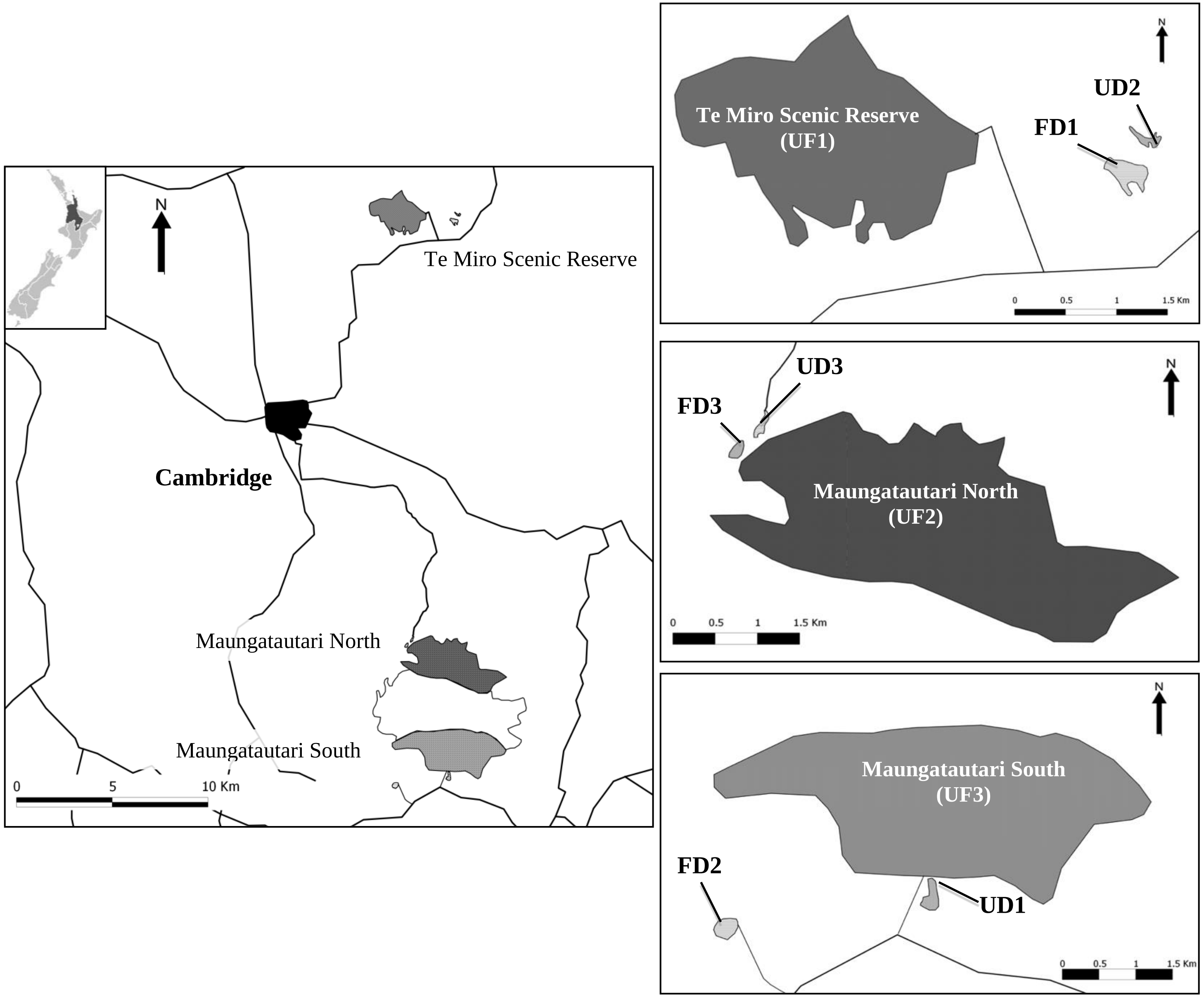


Figure 2.1 Map of the study site, near Cambridge in the Waikato region, North Island, New Zealand. Study sites as per Table 2.1

Figure 2.2 Typical scenery of the Waikato region (south of Cambridge) where forest fragments can be seen interspersed with pastureland; Lake Karapiro is in the middle ground.

A variety of mammalian herbivores can be found in the study area. The unfragmented forest of Maungatautari is protected by a predator-proof fence (see Chapter 1) (Burns et al. 2012), while the Te Miro site only has a fence that prevents access to large mammals, plus a small mammalian herbivore eradication plan. However, fallow deer (*Dama dama*) have been documented in the Te Miro reserve (Gudex 1959, DoC 2014). The fencing used in the forest fragments only prevented access by large mammalian herbivores such as cattle (*Bos taurus*) and sheep (*Ovis aries*), and I detected the presence of rabbits (*Oryctolagus cuniculus*) in the fragments. Furthermore, ship rats (*Rattus rattus*) have been reported in forest fragments in this region (Innes et al. 2010, King et al. 2011). Gudex (1959) reported the presence of brushtail possums (*Trichosurus vulpecula*) in high numbers in the region in the past. Currently, possums are still in the region, as reported by the landowners of the study sites.

Table 2.1 Locations of study sites ordered by treatment and area.

Treatment	**Site name**	**Location**	**Area (ha)**
Fenced (FD)	FD1	37°47'47" S, 175°34'13" E	8
	FD2	38° 3'35" S, 175°32'12" E	5
	FD3	37°59'60" S, 175°32'53" E	2
Unfenced (UD)	UD1	38° 3'30" S, 175°33'46" E	5
	UD2	37°47'46" S, 175°34'17" E	2
	UD3	37°59'58" S, 175°32'47" E	2
Unfragmented forest (UF)	UF1	37°47'35" S, 175°33'15" E	>350
	UF2	38° 0'19" S, 175°34'38" E	>700
	UF3	38° 3'13" S, 175°34'0.62" E	>700

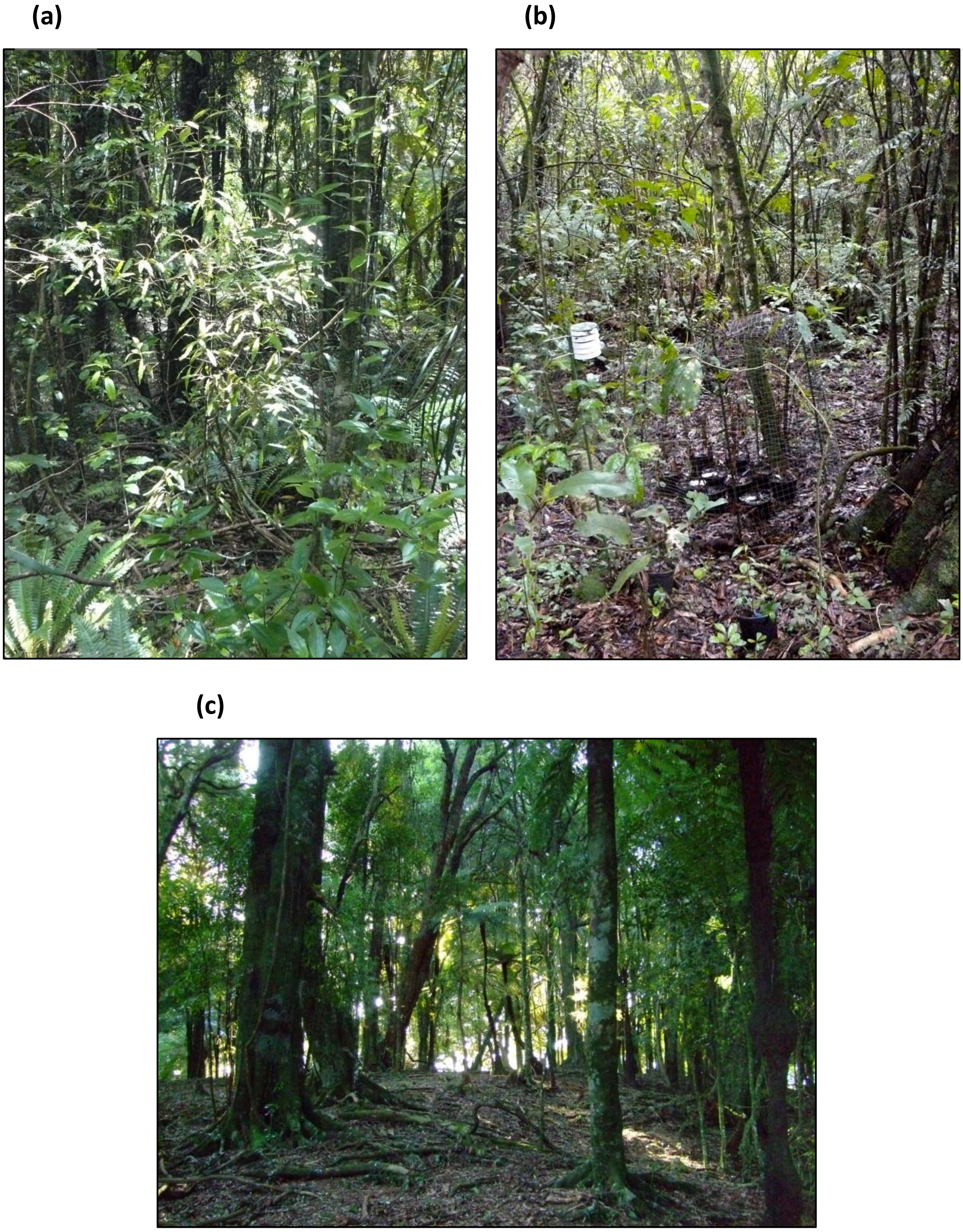


Figure 2.3 Typical understory conditions in each of the study sites experiencing different levels of management, (a) unfragmented native forest (Maungatatutari Scenic Reserve), (b) fenced fragment (FD2 site), (c) unfenced fragment (UD1 site). Note the relative lack of regenerating understorey in the unfenced fragment (c).

2.2.2 Data collection

Vegetation analysis

To assess the vegetation composition and structure of each site I used the point-centered quarter (PCQ) approach (Mitchell 2007), using the modified method described by Perry et al. (2010). Eighteen points were assessed at all but one of the nine study sites. At this site, an unfenced fragment (UD2), only 14 measurements could be independently located within the fragment. Thus, in total, I recorded *n* = 158 PCQ points across nine locations. Although the PCQ method has been criticised (e.g. Bryant et al. 2005) it is capable of picking out relative trends in community composition of the type that are of interest in this study (White et al. 2008). At each of the experimental areas I used the enclosures described in Chapter 3 as the focal point for three 50 m transects each following a constant bearing and so forming a Y-shape (Figure 2.4a).

At each point a modified PCQ method was used. First the space around each PCQ point was divided into quarters. In each quarter I recorded the distance to the closest tree with a diameter at breast height (dbh) > 5 cm, and identified its species. This tree was designated as the ‘focal tree’ of the quarter. Additionally, in each quarter the identity of the next nearest tree with a dbh > 5 cm and the species of the seedling or sapling (dbh < 5 cm) most likely to replace the focal tree (following Ogden 1983, and Perry and Enright 2007) was recorded. The ‘replacement species’ was that species deemed most likely to replace the focal tree in the event of its immediate death. The identity of all tree species and saplings/seedlings within a radius of 3 m of the PCQ station was recorded.

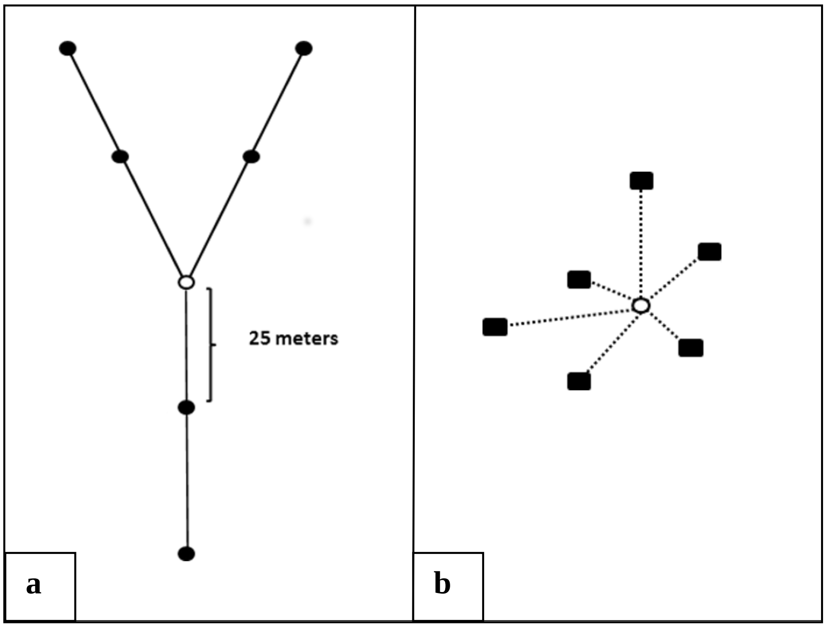


Figure 2.4 Schematic representation of the layout of the (a) enclosures (open circles) and PCQ plots (filled circles) and the (b) regeneration plots (filled squares).

Tree coring

To determine the age structure of B. tawa populations across the sites I took increment core samples from individuals of different sizes. We classified potentially sampled trees as small (0 – 20 cm dbh), medium (20 – 50 cm dbh) or large (> 50 cm dbh) and obtained age-increment cores from approximately equal numbers in each size category at each site. Young trees were targeted because I wanted to have a sense of the youngest tree in each area. The trees were cored as close to the base as possible. Because the abundance of individuals falling into each of the different size classes varied from site-to-site, the number of trees cored also varied between sites (5 – 12 per site). The cores were dried at room temperature, mounted and fixed using wood glue and sanded using 120-grit through 400-grit sandpaper until the rings were clearly visible. The rings were counted under a stereo-microscope (Olympus® sz61) (6.7 to 45× magnification).

Soil analysis

We collected three composite soil samples from each experimental area each of which was collected within 20 m of each of the previously mentioned enclosures (*n* = 27). To avoid differences due to variability in time, all of the samples were collected under similar antecedent weather conditions and in the same week.

Levels of nitrogen and carbon were estimated using the dry combustion method (Bisutti et al. 2004) with an elemental analyser (LECO TRUSPEC CN, St. Joseph, MI, US). We used the Bray and Kurtz N°1 method as an index of available phosphorus (Bray and Kurtz 1945). The pH of the soil was measured in a supernatant liquid with a digital pH meter and the water content was estimated using the gravimetric method (Kalra and Maynard 1991). Bulk density was calculated as dry soil weight divided by the total soil volume. All analyses were performed using facilities at the School of Environment, University of Auckland.

Canopy density

To estimate canopy density and complexity at each site I took nine digital colour canopy photos (*n* = 81 in total) following Goodenough and Goodenough (2012). This technique does not require expensive equipment (e.g. fish-eye lenses), and it is quicker and more flexible (e.g. there is no need take photographs under uniformly overcast skies). The photos were taken at the first PCQ point of each transect. All of the photographs were taken approximately 1 m from the ground with the camera parallel to the ground mounted on a tripod. All pictures were taken using a Canon EOS 50D camera.

Litter depth

Litter depth – defined as the loose organic material layer on top of the topsoil – was measured at the centre of each sub-quadrat of the natural regeneration plots (see Section 3.3.2) ($n = 648$) using a steel tape-measure.

Temperature and humidity

At each of the experimental areas I placed three *ibutton*® sensors, two that measured temperature and one that measured humidity/temperature ($n = 27$). Each sensor was mounted on a custom-made radiation shield fixed by a pole at 1 m above the ground (Figure 2.5). The custom-made radiation shields were based on a design by Scottech ™ Radiation Shields, and have been shown to function as well as those that are commercially available (Tarara and Hoheisel 2007).

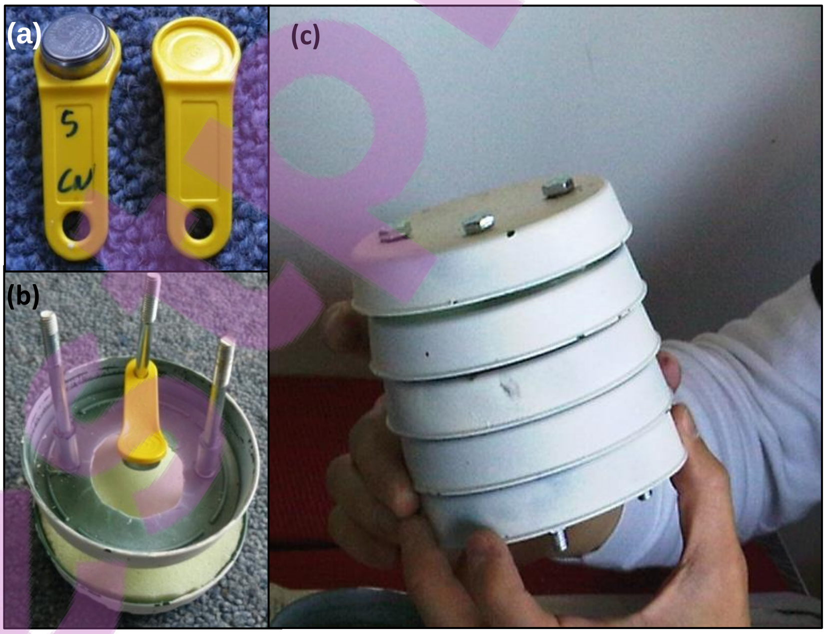


Figure 2.5 Detail of *ibutton*® sensors (a) mounted on a handmade radiation shield (b) and a view of the radiation shield ready for deployment in the field (c).

The temperature and humidity sensors were set to record every two hours. Temperature was recorded from November 2011 to January 2014. Humidity was measured from May 2012 to January 2014. Some of the sensors failed or disappeared altogether (presumably due to disruption by large animals) and although they were replaced as quickly as possible, some data loss was unavoidable.

2.2.3 Data analysis

All the analyses described in this section were carried out using R-2.15.1 (R Core Team 2010), unless otherwise stated.

Vegetation analysis

Using composition and dbh data from the PCQ measurements I calculated the frequency, density and basal area of canopy and subcanopy trees; mean density calculations were made following Pollard (1971). I also calculated the size frequency of *B. tawa* trees. We used non-metric multidimensional scaling (nMDS) (Gauch 1982) to ordinate and graphically represent the PCQ data (see ‘Vegetation analysis’ in Section 2.2.2) using the “*vegan*” R package (Oksanen et al. 2013). In the nMDS analysis I used all the PCQ points, although this means that, in a strict statistical sense, I used pseudo replicates I did not, however, perform any formal statistical analysis with these pseudo-replicates and used them instead to represent the data graphically to look for trends within each of the sites. The amin goal of this exploratory visual analysis was to determine whether some of the characteristics of the PCQ points in fenced and unfenced fragments were similar to those seen at the continuous forest sites. The data matrices from the different sites used in this analysis were weighted such that the individuals in each quarter closest to the centre point were given a weighting of two. A weighting of two was also given to the next nearest species plus one added to each species appearing as a seedling/sapling. If an individual was a replacement species and it did not appear in the other categories a weighting of one was apportioned to it. The maximum score that an individual species could attain at a point was 17 points (following Perry et al. 2010). This scoring method was designed to more strongly reflect the presence of canopy tree species over the subcanopy trees and the sapling bank.

To evaluate differences in community composition across the different levels of management (unfragmented forest, fenced fragments and unfenced fragments) I used a multivariate form of generalized linear models (Warton 2011) as implemented in the "*mvabund"* package (Wang et al. 2013). We used this approach because *mvabund* does not confound location with dispersion effects as more widely used tests such as PERMANOVA and ANOSIM can do (Warton et al. 2012). For these analyses data were pooled across the PCQ stations within each site to avoid pseudo-replication. We used mean density data per site obtained from the analysis of the PCQ points data for canopy trees and subcanopy trees (n = 9), and seedling data from the regeneration plots for seedlings (n = 9) (see Section 3.2.2). First I performed a general analysis with all species, canopy and subcanopy trees. To classify species as canopy or subcanopy I used the current position in the canopy and not the potential dominance of the trees. We then analysed the canopy trees and subcanopy trees individually; I considered *Alectryon excelsus*, *Beilschmiedia tawa*, *Dacrydium cupressinum*, *Knightia excelsa*, *Laurelia novae-zelandiae*, *Litsea calicaris* and *Rhopalostylis sapida* as canopy species and *Hedycarya arborea, Piper excelsum, Melicytus ramiflorus, Myrsine australis*, *Prumnopitys ferruginea* and *Schefflerra digitata* as subcanopy species. Seedling data were analysed separately following the same methodology and classification described above.

We used a reduced model with level of management and site, plus a level of management-site interaction (canopy seedlings ~ level of management + site + treatment × block) and an additive model with level of management, water content, nitrogen and carbon as factors (canopy seedlings ~ level of management + water content + nitrogen + carbon). We chose these factors because a principal components analysis suggested that they could explain some of the differences in species abundance across the different management types (see Soil analysis, canopy density and litter depth in this Section).

Tree coring

Tree age was estimated by counting the number of rings in each core and adding the years it takes the tree to grow to coring height. To calculate the number of years needed to grow from the base to the coring height an average height increment of 4.41 cm per year was used (West 1986 based on Ogden and West 1981). In the case that the cores did not hit the centre of the sampled trees, I calculated the reliability of the cores by dividing the core length by the dch (diameter at core height) of the tree multiplied by 0.5. If the value was less than 0.8 I discarded those cores. If the reliability value was more than or equal to 0.8, I subtracted the core length to the radius of the tree using their dch. The resultant difference is multiplied by the growth rate, following West (1986). The growth rate was calculated using the innermost 10 rings of each core (West 1986, Norton et al. 1987). I calculated descriptive statistics for age and dbh for each management type and graphical analysed of age frequency distributions.

Soil analysis, canopy density and litter depth

Canopy density and canopy aggregation (spatial complexity) were calculated using the CanopyDigi software (Goodenough and Goodenough 2012). As my canopy photos were in colour and CanopyDigi needs monochrome images, the photographs were transformed using the batch conversion option incorporated in the software GIMP (Kimball and Mattis 2013) (Figure 2.6).

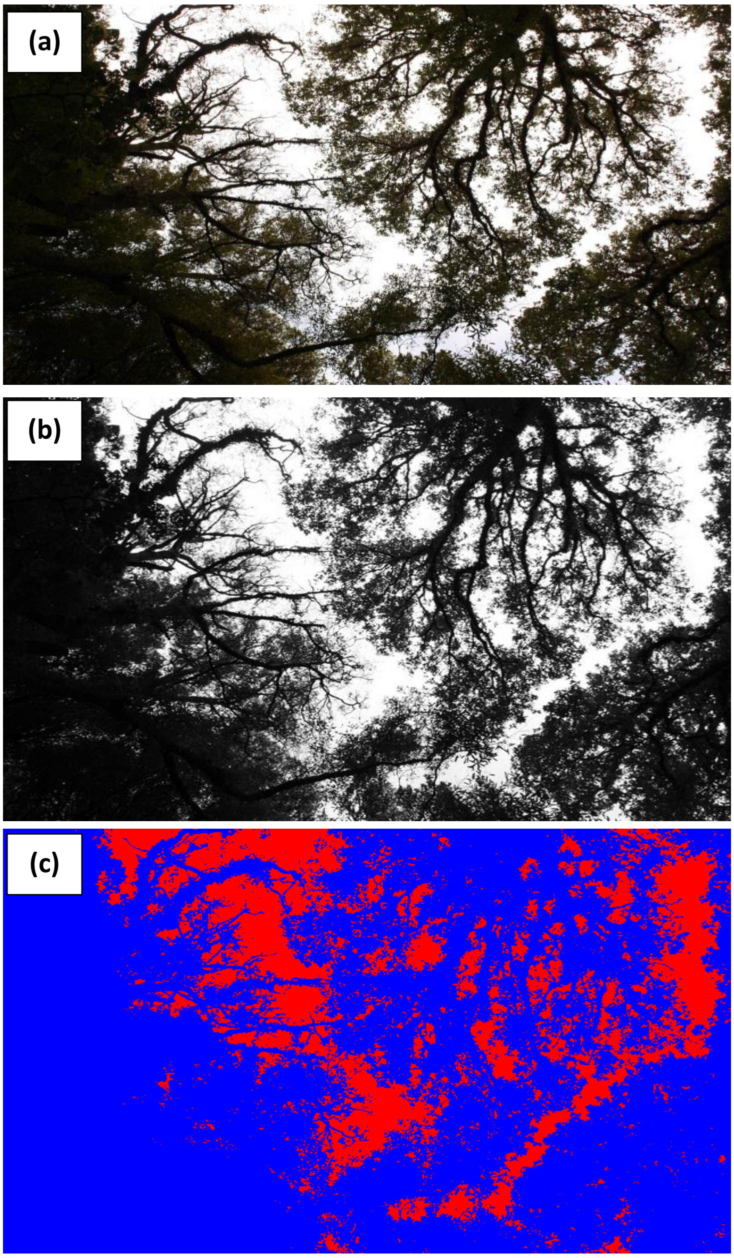


Figure 2.6 Sequence of photographs before and after they were processed by CanopyDigi. (a) Original photograph, (b) transformed monochrome photograph and (c) output from CanopyDigi analysis (threshold = 155). Blue corresponds to tree canopy and red to canopy (light) gaps.

CanopyDigi polarises monochrome images using a user-defined threshold to generate dark canopy pixels and light sky pixels. We generally adopted a threshold value (grey-scale value of 155), although occasionally this needed to be adjusted to obtain an acceptable image (Figure 2.6).

To characterise the abiotic conditions across the sites (unfragmented forest, unfenced, fenced), I performed a principal component analysis (PCA) (Jackson 1999) using the R package "*FactoMineR*" (Le et al. 2008). We included nitrogen, carbon, phosphorus, water content, bulk density, pH, canopy, canopy aggregation and litter depth in the PCA analyses. Four of the eight variables (nitrogen, phosphorus, bulk density, and pH) were non-normal but transformations (e.g. $\log_{10}$, fourth-root) did not improve this, so I opted to use the raw data.

A Friedman test, based on 9999 Monte-Carlo resamplings, was used to evaluate differences in soil conditions (nitrogen, carbon, phosphorus, water content, bulk density and pH), canopy density and litter depth across the different treatments (unfragmented forest, unfenced, fenced; $n = 9$). For this analysis I used the "*coin*" package in R (Hothorn et al. 2008).

Temperature and humidity

The sensors were placed in the study sites at slightly different times and therefore I used the data from December 2011 to mid-January 2013 to ensure the data were as continuous as possible. From November 2012 and January 2013 only one of the sensors was recording in each of the sites. However, the differences between the sensors within the same fragment were less than 0.5 °C in most cases and so I considered it reasonable to use the data from just one sensor as representative of the fragment as a whole.

The humidity measurements were more discontinuous than those of temperature. To determine whether temperature could be used as a proxy for humidity I performed a Pearson's correlation analysis on temperature and humidity using the period from February 2013 to January 2014. The mean, maximum and minimum temperatures were analysed graphically as was the daily temperature range.

2.3 RESULTS

2.3.1 Vegetation analysis

We analysed the size-frequency distribution of *B. tawa* under different types of management. At the three unfragmented forest sites, tawa shows that most individuals falling in the smaller and intermediate size classes and relatively few in the larger size classes (Figure 2.7). In stark contrast in the fenced forest fragments most of the individuals are in larger (> 20 cm) diameter classes with few individuals in the smaller classes. The population size structure in the unfenced forest fragments was similar to those seen in the fenced fragments, with most of the individuals present falling into the larger size classes (Figure 2.7). The percentage of individuals belonging to the sapling size-class (1 – 5 cm dbh) in fenced and unfenced fragments is nine-times lower than in the unfragmented forest. The absence of saplings (1 – 5 cm dbh) is consistent across the fragments irrespective of fencing.

As described in Section 2.2, composition data from the PCQ stations allowed us to calculate frequency (proportion of PCQ stations where the species was present), mean density and mean basal area of canopy and subcanopy trees. Densities of B. *tawa*, *K excelsa* and *L. novae-zelandiae* were proportionally higher in the unfragmented forest than in the fragmented sites (fenced and unfenced fragments), although these differences were not significant (*n* = 9)

(Table 2.2), but basal area were consistent across them. Subcanopy species density and basal area were higher in the fragmented sites than in the unfragmented forest but only *P. excelsum* was significantly different (Density: Z= -2.07, n = 9, p = 0.04; Basal area: Z= -2.07, n = 9, p = 0.04) (Table 2.3). Fenced fragments had high densities and basal areas of subcanopy species *P. excelsum* and *M. ramiflorus* (Table 2.3), although only *P. excelsum* was marginally significant in comparison with the forest fragments (Z = 1.99, n = 9, p = 0.09).

B. tawa and *L. novae-zelandiae* had the highest densities and were the most frequent canopy tree species across all three management types. Fenced fragments had the lowest mean density of *B. tawa* and *L. novae-zelandiae* of the management types (Table 2.2). The canopy-dominant podocarp *D. cupressinum* is present in low numbers in the unfragmented forest and fenced fragments, but is completely absent from the unfenced fragments.

H. arborea and *M. ramiflorus* were the most abundant and frequent subcanopy tree species in the forest sites (Table 2.3), with *P. excelsum* widespread in the fenced and unfenced fragments and *M. ramiflorus* common in the fenced fragments (Table 2.3). Canopy tree species, such as *B. tawa* and *L. novae-zelandiae,* accounted for the majority of the stand basal area (Tables 2.2 and 2.3). In general, *B. tawa* had a higher basal area than *L. novae-zelandiae* except in the fenced fragments. Although *D. cupressinum* was only present in low numbers it accounted for 11 % of the basal area in the unfragmented forest (suggesting that it was present as scattered large individuals). On the other hand, in the fenced fragments *D. cupressinum* barely contributed to stand-level biomass (0.2 % of standing BA), indicating that the few individuals present in those sites were probably juveniles.

Of the subcanopy species, *M. ramiflorus* and *H. arborea* had the highest basal area across all management types. *M. ramiflorus* had a higher basal area than *H. arborea* in fenced and unfenced fragments. *P. excelsum* basal area was markedly higher in the fragmented sites but was especially high in the fenced fragments (Table 2.3 and Figure 2.8).

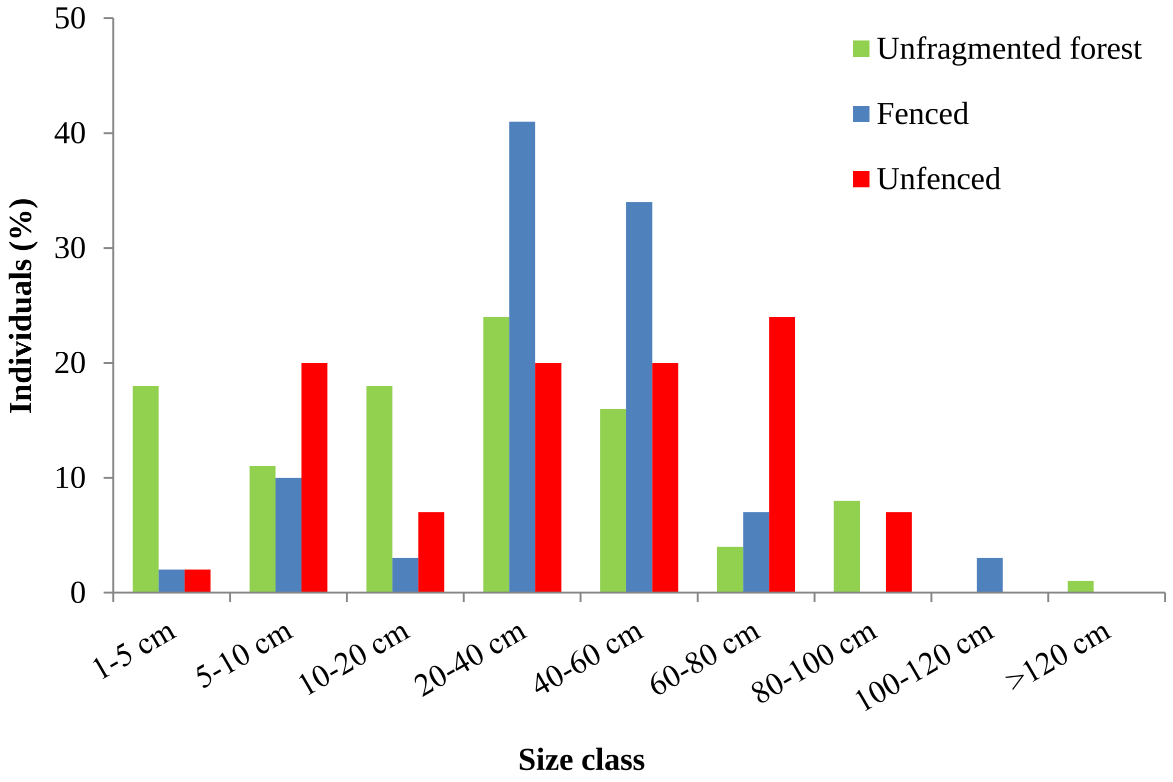


Figure 2.7 Percentage of individuals of *B. tawa* trees in the unfragmented forest, fenced forest fragment and unfenced forest fragment by size class. Calculations are based on n = 62 for *B. tawa*, n = 54 for unfragmented forest, n =29 for fenced forest fragment and n = 50 for unfenced fragment. Size-class 1-5 cm comes from preliminary sapling plots.

Table 2.2 Species (a) frequencies (proportion of PCQ points at which species was focal), (b) mean density ± SD (individuals [greater than 5 cm dbh] per ha) and (c) mean basal area (m^2/ha) ± SD for canopy tree species by type of management.

(a)

Species	Forest	Fenced	Unfenced
A. excelsus	0.00	0.01	0.04
B. tawa	0.29	0.13	0.25
D. cupressinum	0.00	0.01	0.00
K. excelsa	0.09	0.05	0.04
L. novae-zelandieae	0.25	0.10	0.19
L. calicaris	0.01	0.01	0.03
R. sapida	0.02	0.00	0.01

(b)

Species	Forest (ind/ha)	Fenced (ind/ha)	Unfenced (ind/ha)
A. excelsus	0	8 ± 7	17 ± 21
B. tawa	164 ± 83	76 ± 50	102 ± 60
D. cupressinum	2 ± 4	7 ± 13	0
K. excelsa	46 ± 10	28 ± 37	37 ± 20
L. novae-zelandieae	140 ± 46	68 ± 41	147 ± 179
L. calicaris	5 ± 5	12 ± 13	14 ± 17
R. sapida	8 ± 14	4 ± 6.4	6 ± 10
Total	365	203	323

(c)

Species	Forest (m^2/ha)	Fenced (m^2/ha)	Unfenced (m^2/ha)
A. excelsus	0	1.23 ± 1.35	0.9 ± 1.35
B. tawa	24.06 ± 2.93	15.21± 1.95	24.41 ± 22.99
D. cupressinum	5.01 ± 8.66	0.18 ± 0.32	0.00
K. excelsa	1.73 ± 0.99	4.23 ± 4.34	1.16 ± 1.06
L. novae-zelandieae	17.18 ± 3.94	33.84 ± 32.34	9.35 ± 7.1
L. calicaris	0.14 ± 0.23	1.45 ± 2.47	1.36 ± 1.25
R. sapida	0.25 ± 0.44	0.06 ± 0.11	0.29 ± 0.51
Total	48.37	56.02	34.47

Table 2.3 Species (a) frequencies (proportion of PCQ points where species was focal), (b) mean density ± SD (individuals [greater than 5 cm dbh] per ha) and (c) mean basal area (m^2/ha) ± SD by dominant sub canopy tree species and type of management.

(a)

Species	Forest	Fenced	Unfenced
H. arborea	0.11	0.05	0.14
P. excelsum	0.01	0.44	0.13
M. ramiflorus	0.12	0.15	0.12
S. digitata	0.06	0.02	0.05

(b)

Species	Forest (ind/ha)	Fenced (ind/ha)	Unfenced (ind/ha)
H. arborea	63 ± 29	31 ± 17	90 ± 58
P. excelsum	4 ± 7	368 ± 273	75 ± 98
M. ramiflorus	64 ± 14	99 ± 84	87 ± 84
S. digitata	31± 27	13 ± 1	52 ± 86
Total	162	511	304

(c)

Species	Forest (m^2/ha)	Fenced (m^2/ha)	Unfenced (m^2/ha)
H. arborea	1.06 ± 0.67	0.67 ± 0.33	3.56 ± 0.73
P. excelsum	0.01 ± 0.03	1.94 ± 1.55	0.66 ± 0.98
M. ramiflorus	2.73 ± 1.22	5.70 ± 5.16	2.52 ± 2.66
S. digitata	0.28 ± 0.25	0.07 ± 0.04	0.33 ± 0.57
Total	4.08	8.38	7.07

Figure 2.8 An example of a *P. excelsum* thicket in a fenced fragment (FD3 site).

Canopy and subcanopy trees

Ordination (nMDS) of the canopy and subcanopy tree species abundances showed that unfragmented forest PCQ points were compositionally similar to each other although they did not form a cluster that was clearly separated from the fragmented, whether fenced or unfenced, PCQ points (Figure 2.9). In fact, some of the fenced fragments and unfenced fragments PCQ points appeared to be compositionally quite similar to the unfragmented forest communities (Figure 2.9). In the case of the fenced fragments, all of the PCQ points that fell within the unfragmented forest cluster are from the same fenced fragment site (FD1). For unfenced fragments the PCQ points that were compositionally similar to the unfragmented forest PCQ points came from UD1 and UD2.

B. tawa was present at the majority of the points across all management types and sites (Figure 2.9). However, *B. tawa* weighted abundance scores were higher in the cluster formed by the unfragmented forest plots (5.7 ± 3.8; mean ±1 SD; *n* = 54) and tended to lessen toward the cluster formed by the fenced fragments (2.9 ± 3.7; *n* = 54) (Table 2.2).

Ordination of the canopy tree species alone showed a similar pattern to that seen when both canopy and subcanopy species were considered (Figure 2.10a). The unfragmented forest PCQ points formed a somewhat cohesive group, but this grouping also contained some points from both the fenced and unfenced fragments. We could not separate out PCQ points of fenced fragments as opposed to unfenced fragments in the ordination space. An nMDS of the subcanopy trees alone showed a more diffuse unfragmented forest cluster (Figure 2.10b), which suggests that the relative abundances of subcanopy tree species varied across the different unfragmented forest PCQ plots. On the other hand, the fenced fragments PCQ points formed a more cohesive group indicating that subcanopy tree species had similar relative abundances across the three fenced fragments.

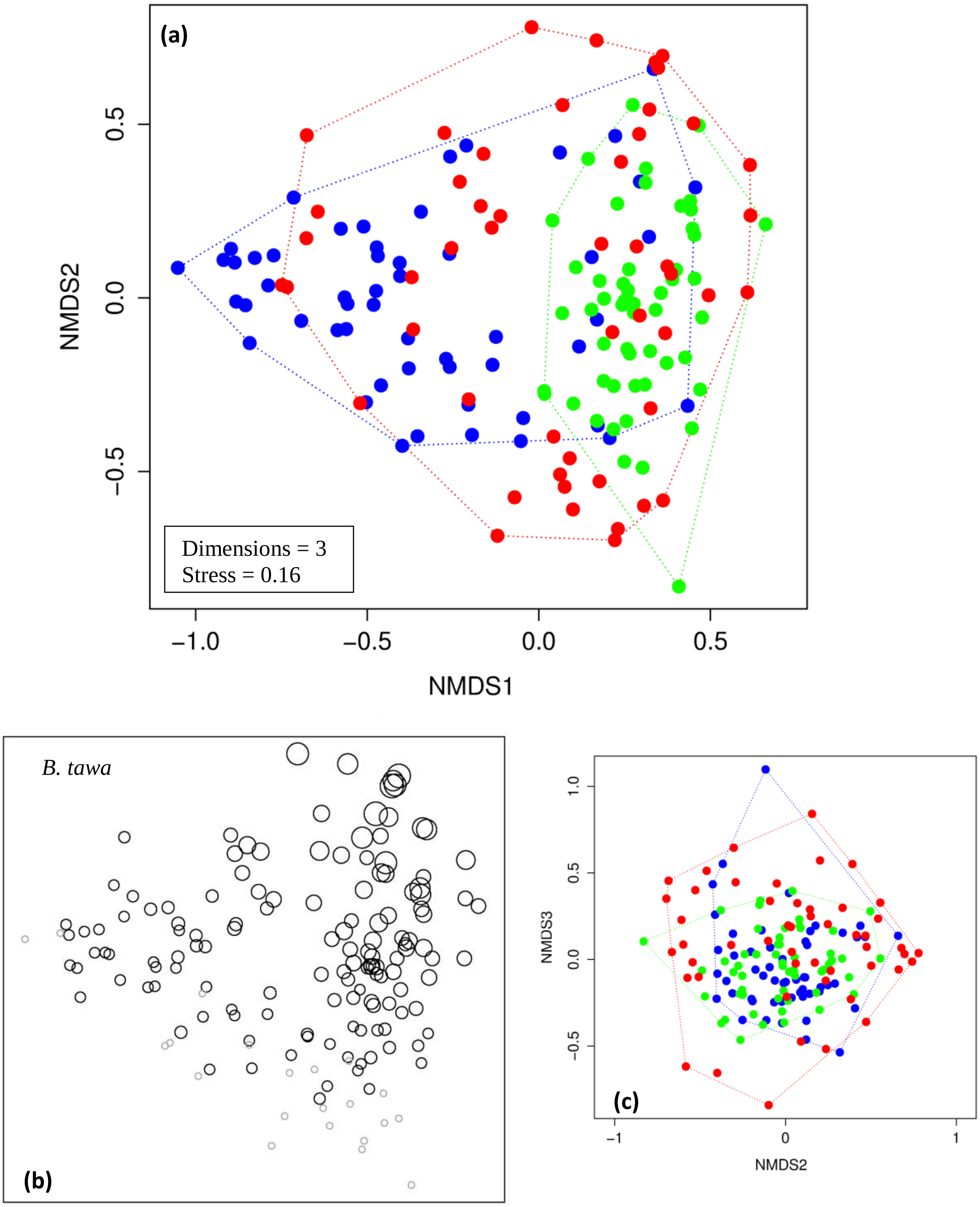


Figure 2.9 nMDS ordinations of all canopy and subcanopy tree species (dimension 1 vs. 2) (a). Green circles represent unfragmented forest, blue circles fenced fragments and red circles unfenced fragments; blue and red circles together represent the fragmentation effect. (b) occurrence of *B. tawa* individuals across the 158 points; the size of the circle is proportional to the species' dominance at a site. Greyed circles indicate plots where *B. tawa* was absent. Dashed lines indicate area in ordination space occupied by each management type, (c) the ordination of dimension 2 vs 3.

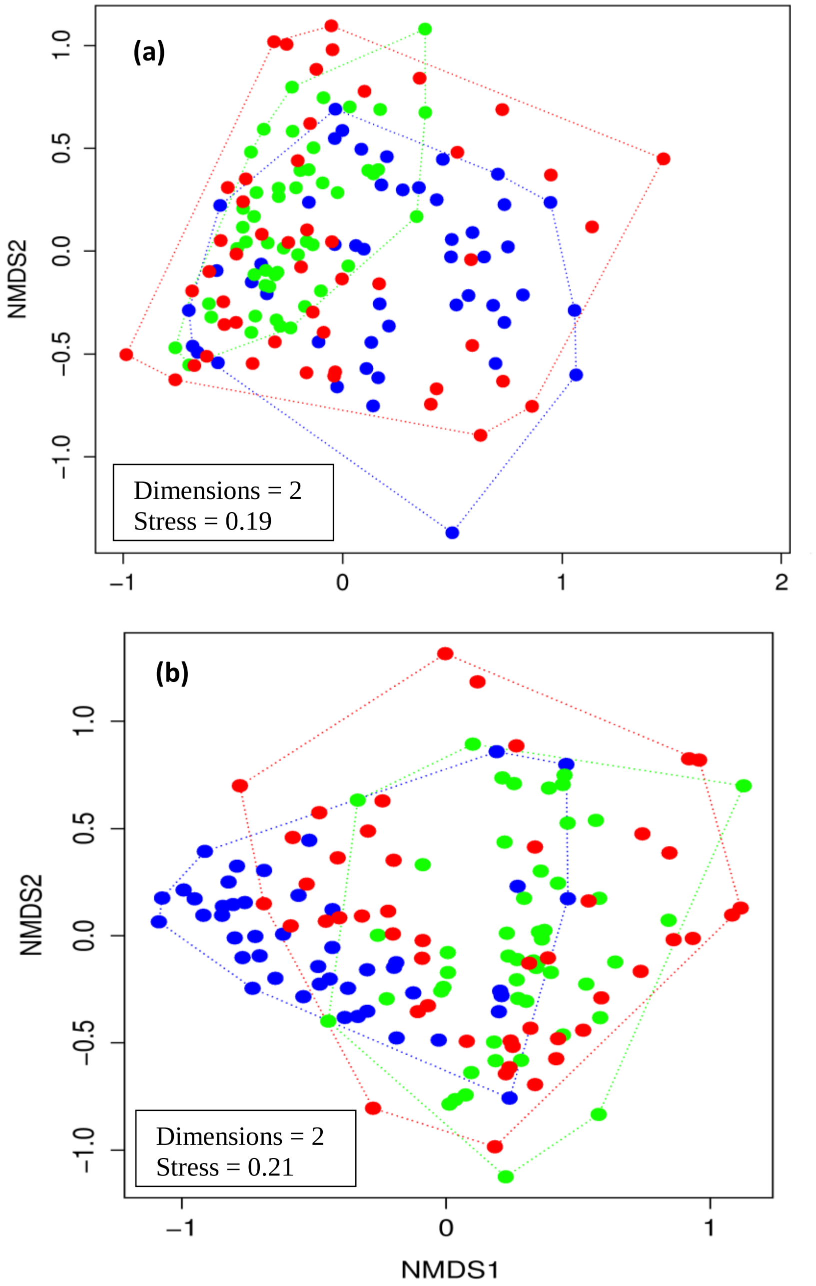


Figure 2.10 nMDS ordinations for (a) canopy and (b) subcanopy tree species. Colours and symbology as per Figure 2.8.

The multivariate form of the generalized linear models ("*mvabund"*) on tree composition indicated that the type of management had no statistically significant effect on the mean abundance of tree species in either a reduced or an additive model at the α = 0.05 level; nor did the two models differ in their explanatory power (see Appendix 1). Likewise for an analysis of canopy and subcanopy tree species mean abundance, neither the reduced nor the additive model demonstrated a significant effect of the different levels of management on the mean abundance of canopy tree species (see Appendix 1). Comparison of the two models did not show any significant differences, indicating that the additive model explains no more variation than the reduced model.

Seedlings

An nMDS analysis of the seedling presence/absence data (of both canopy and subcanopy species) from the PCQ points showed that the unfragmented forest points did not form a cluster that was clearly visually separated from the fragmented, whether fenced or unfenced, sites (Figure 2.11). As with the tree data, however, some specific fenced and unfenced fragment PCQ points were very similar to unfragmented forest composition (Figure 2.11a). All of the fenced and unfenced points falling within the unfragmented forest PCQ points cluster were from the FD1 and UD2 sites. The composition of the seedling bank in the fenced and unfenced fragments did not show any strong structure and the points are scattered across the ordination space. *B. tawa* seedlings are present throughout the ordination space, again suggesting that there is little association between *B. tawa* seedling presence and the type of management (Figure 2.11b).

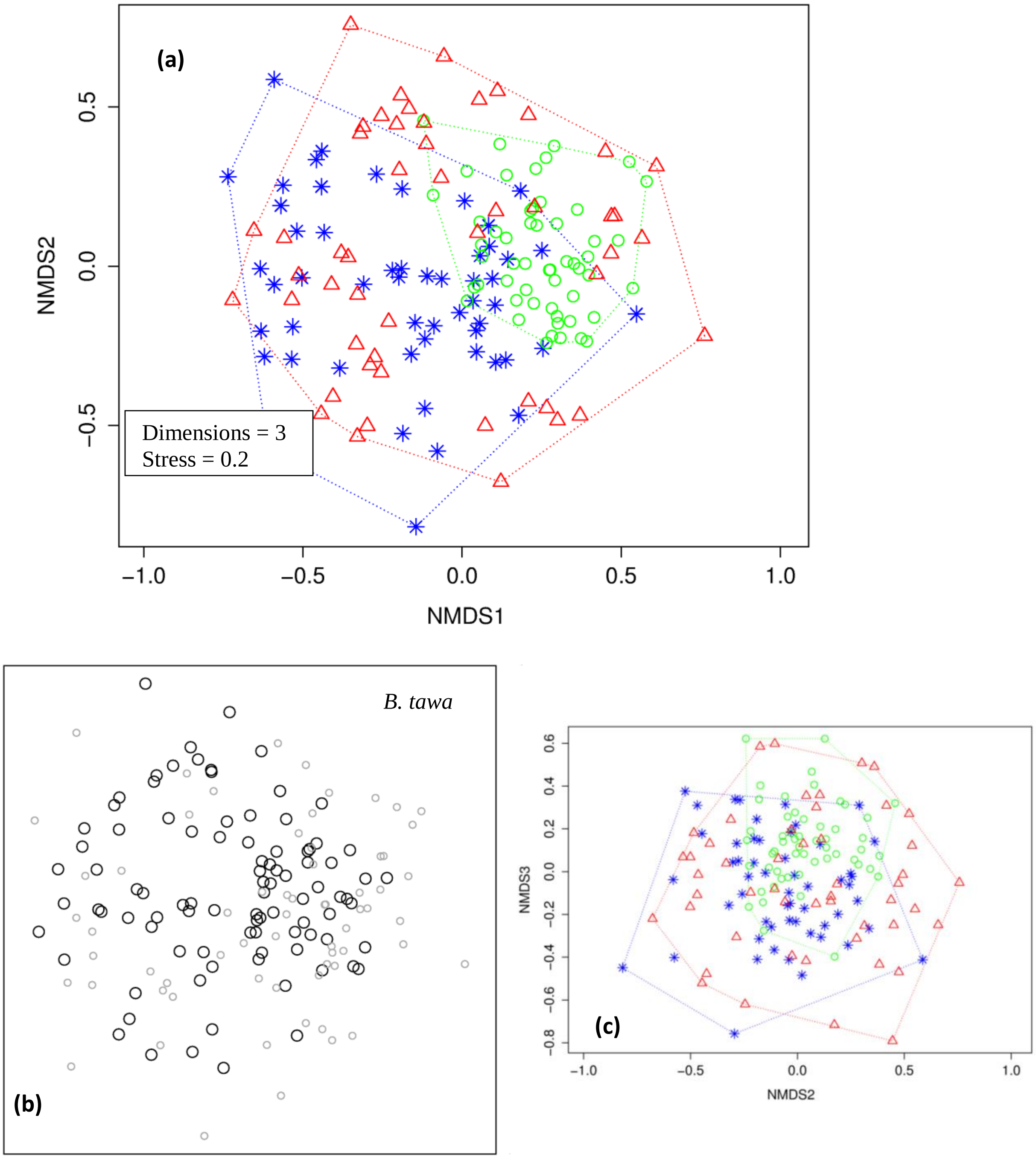


Figure 2.11 nMDS ordinations for canopy and subcanopy seedlings (dimension 1 vs. 2) (a) Green circles represent unfragmented forest, blue asterisks correspond to fenced fragments and red triangles are unfenced fragments; blue asterisk and red triangles together represent the fragmentation effect. (b) occurrence of *B. tawa* individuals. Greyed circles indicate plots where *B. tawa* was absent. Dashed lines indicate area in ordination space each management type occupies. (c) ordination of dimension 2 vs 3. Blue asterisk and red triangles represent the fragmentation effect.

Ordination (nMDS) of the presence/absence of seedlings of canopy vs. subcanopy species showed no obvious pattern or clustering of the PCQ points (Figure 2.12), with most points falling into a single diffuse group.

Neither a reduced nor an additive multivariate GLM showed a significant effect of the factors in mean abundance of seedlings at a $\alpha = 0.05$ (see Appendix 1); nor did the two models differ in their explanatory power. Analysis of the mean abundance of canopy seedlings of the reduced model and additive model found no significant effect of any of the factors on mean abundance at a $\alpha = 0.05$ (see Appendix 1). Subcanopy seedling mean abundance results from the reduced model and additive model showed that none of the factors had an effect on mean abundance of subcanopy tree seedlings at a level of significance $\alpha = 0.05$ (see Appendix 1). In both analyses (canopy and subcanopy seedlings) none of the models (reduced and additive) captured any additional variation.

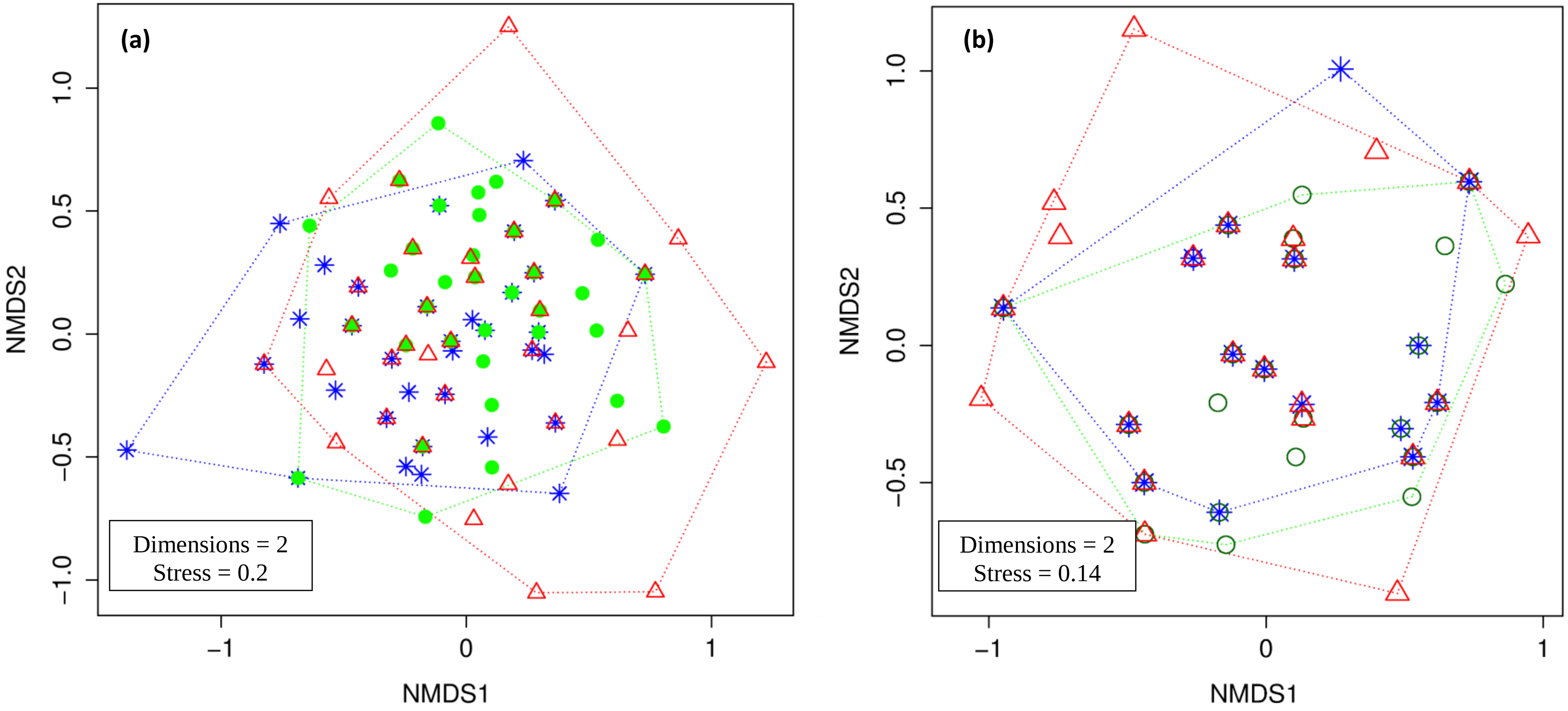


Figure 2.12 nMDS ordinations for (a) canopy and (b) subcanopy seedlings. Green circles represent unfragmented forest, blue asterisks correspond to fenced fragments and red triangles are unfenced fragments; blue asterisk and red triangles represent the fragmentation effect. Dashed lines indicate area in ordination space each management type occupies. Because I used presence/absence data many points lie directly on top of each other (i.e. have identical composition and abundance). Blue asterisk and red triangles represent the fragmentation effect.

2.3.2 Tree Coring

Across the nine sites 81 tree cores were obtained. The reliability of some of the cores was low and 18 were not considered in the final analyses, giving total $n = 63$, with dch ranged from 7 cm to 103.5 cm. The youngest individuals cored in the unfragmented forests were 45 years, 62 years in the fenced fragments and 59 years in the unfenced fragments. The average age of the youngest individuals in the unfragmented forests was 65 ± 25 years, 67 ± 7 years in the fenced fragments and 75 ± 14 years in the unfenced fragments. In the unfragmented forest the majority of the individuals were concentrated in the categories of 120 to more than 220 years (Figure 2.13). In the fenced sites most of the individuals were concentrated in two groups: 1) age categories from 80 to 120 years and 2) 160 to more than 220 years (Figure 2.13). In the unfenced fragments most of the individuals were concentrated between 60 and 160 years (Figure 2.13).

2.3.3 Soil analysis, canopy cover and litter depth

To determine whether different abiotic conditions are associated with the three management regimes I performed a principal component analysis (PCA). Just three components explained over 71 % of the total variance in the relationship between the type of management and abiotic conditions (component 1: 38.27 %, component 2: 18.08 % and component 3: 14.42 %). Nitrogen (+ve), carbon (+ve) and pH (-ve) correlate most strongly with component 1, whereas water content (+ve) and canopy density (-ve) align with component 2. Leaf litter depth (+ve) is correlated with component 3. Some variables had moderate correlations ($|r| = 0.4 - 0.6$) with component 1 and 2. As the first three components explained a relatively high proportion of the total variance of the data, following Quinn and Keough (2011), I retained those three components and repeated the analysis. The total variance explained by the first two components of this reduced PCA analysis was 57.35 %, with axis one and axis two explaining 38.27 % and 18.08 % of the total variance, respectively (Figure 2.14).

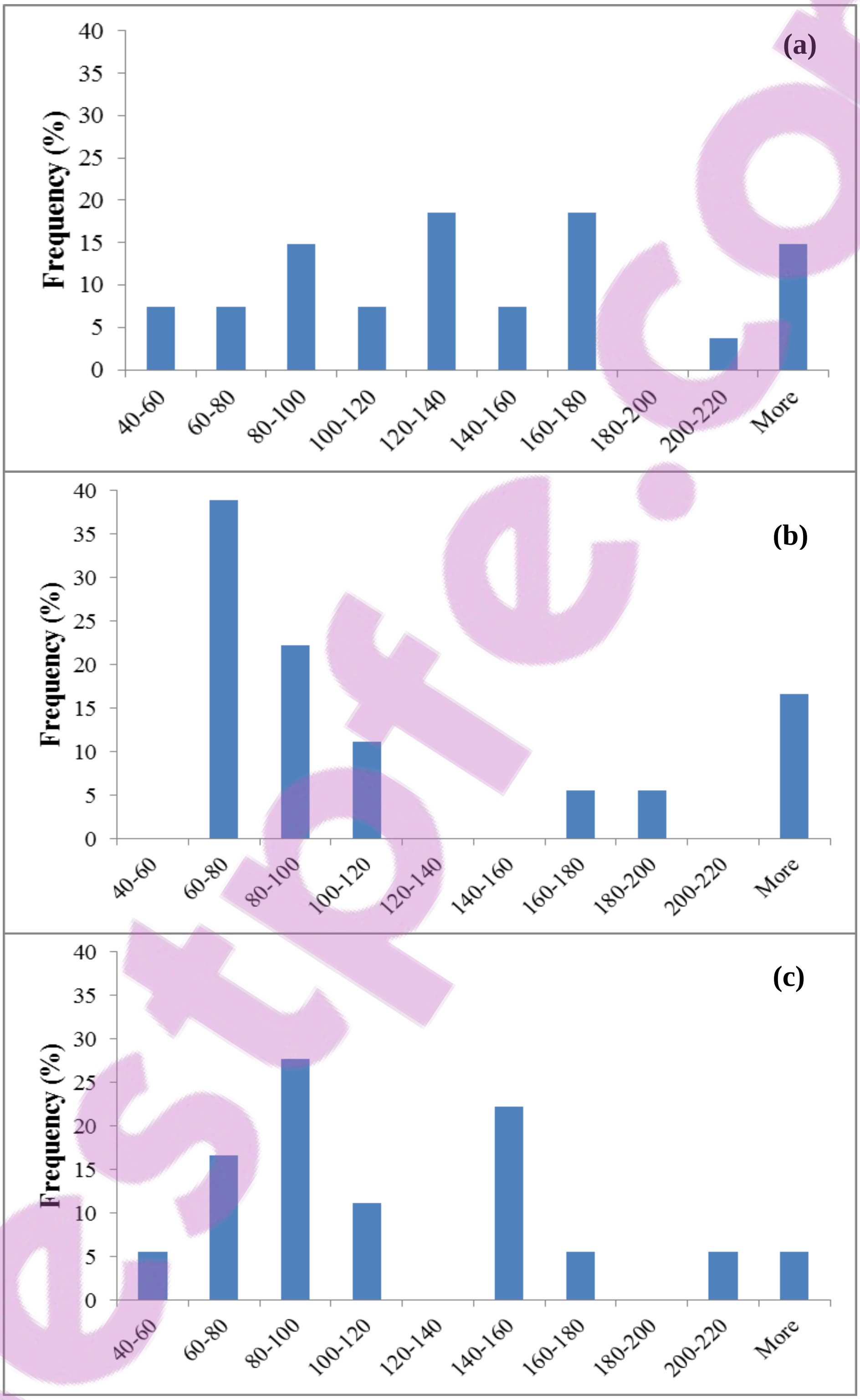


Figure 2.13 Frequencies of tree ages by type of management based on age-increment cores. (a) unfragmented forest, (b) fenced fragment and (c) unfenced fragment. Calculations are based on *n* = 27 for unfragmented forest, *n* =18 for fenced forest fragment and *n* = 18 for unfenced fragment.

With the exception of one plot at the UF1 site the unfragmented forest plots are grouped together on the PCA biplot suggesting that their abiotic characteristics are similar (green dots, Figure 2.15). The variables that appear to drive this clustering are soil water content and, to a lesser extent, soil carbon and nitrogen. Plots from fragmented sites when combined (fenced and unfenced sites) form a distinct group. The variables that seem to explain the grouping of fragmented sites are: pH, phosphorus, canopy aggregation, canopy density and bulk density.

Fenced fragments form a rather less distinct group but are still distinguishable as a cluster with the exception of two plots at the FD3 site. The variables that seem to explain this effect are, in order of importance: canopy density, phosphorus, pH and nitrogen. The samples from unfenced fragments are mostly grouped towards the left, far from the unfragmented forest sites (Figure 2.14). In general, there is a gradient from upper right to lower left, from higher water content and nitrogen (unfragmented forest) to a lower water content, lower nitrogen and higher phosphorus content (unfenced fragments).

The variables nitrogen and carbon are correlated with the first dimension, $|r| = 0.93$ and $|r| = 0.86$. Soil water content is also correlated with the first dimension ($|r| = 0.56$) and with the second dimension ($|r| = 0.67$) (Figure 2.14). The unfragmented forest has higher water content (Figure 2.14), nitrogen content and carbon content than the fenced and unfenced fragment (Figure 2.15). Litter depth did not explain the distribution of the sites and did not show any strong trend across the sites. Soil water content appears to be negatively correlated with bulk density; canopy density and canopy aggregation are also negatively correlated (Figure 2.14b). Nitrogen and carbon appear to be negatively correlated with pH and phosphorus. Canopy (canopy density) and canopy aggregation (Morisita's index) are negative correlated.

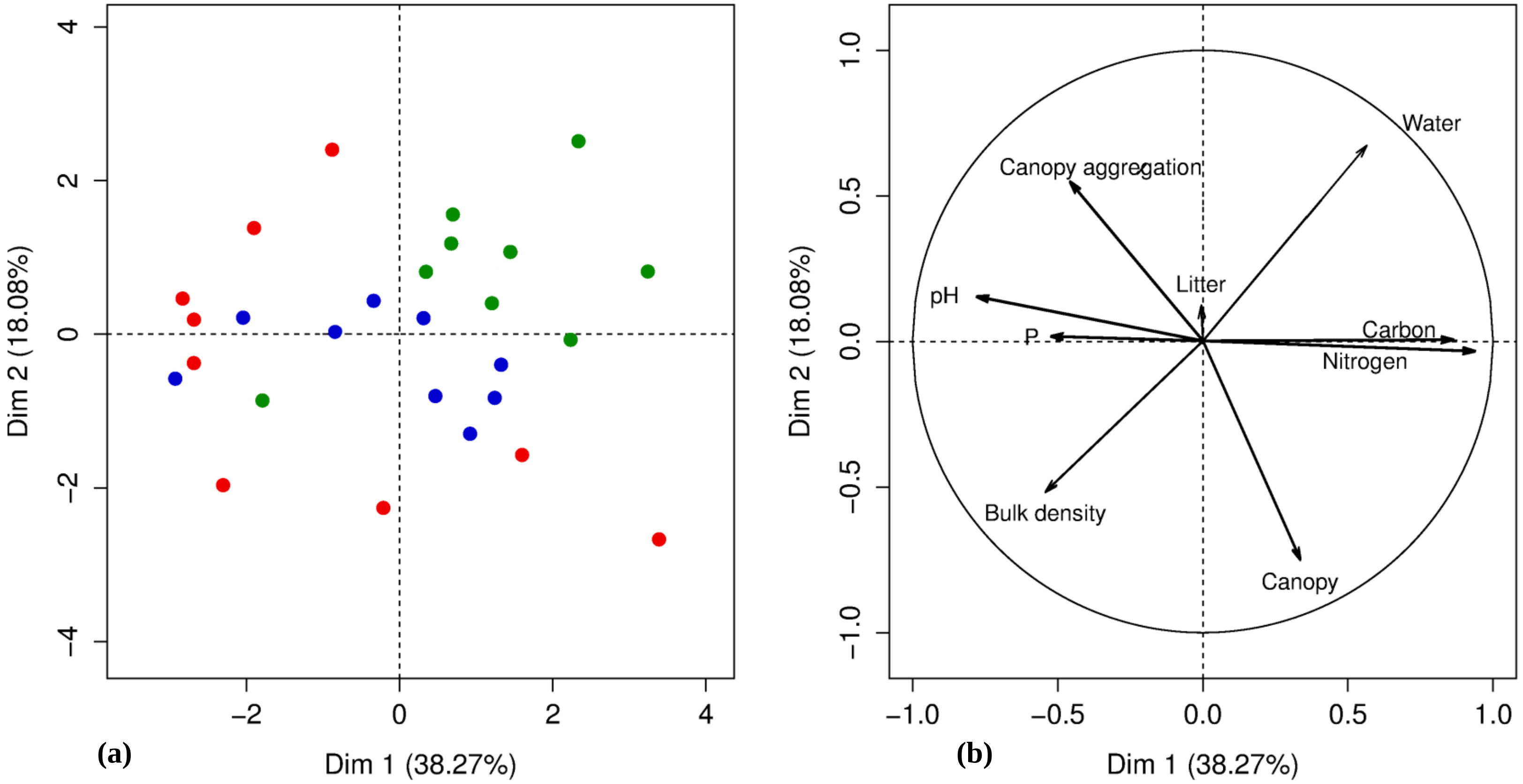


Figure 2.14 Principle components analysis (PCA) of abiotic variables (soil and canopy cover). (a) Scaling plot for sites with different levels of management (dimension 1 vs 2). Green circles correspond to unfragmented forest, blue circle to fenced fragments and red circles to unfenced fragments). (b) Representation of the variables with a correlation circle (length and direction of arrow respectively show the strength and direction of correlation). Blue and red circles represent the fragmentation effect.

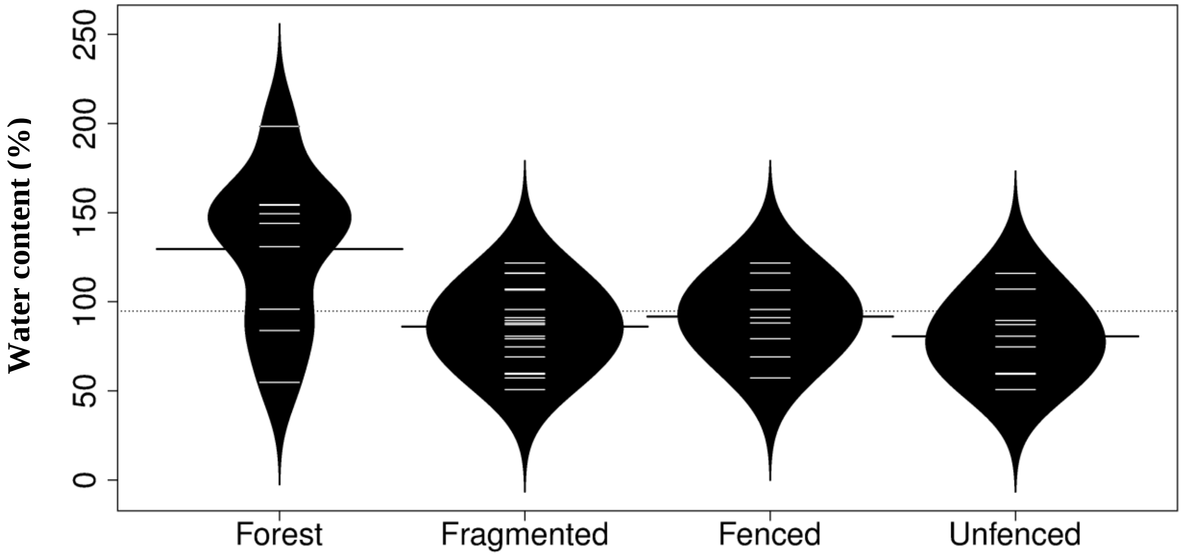


Figure 2.15 Soil water content (%) in the different types of management. Dashed lines represent the mean for all treatments. The small lines in the beans represent each sample mean, based on *n* = 9 for unfragmented forest, fenced and unfenced fragments, and fragmented is based on *n* = 18 samples (fenced and unfenced combined). The thick black line in the middle of the bean represents the mean for that particular treatment.

2.3.4 Temperature and humidity

Pearson's correlation analysis showed that mean monthly temperature was negatively correlated with humidity (r = -0.87, df = 94, $p < 0.001$) (Figure 2.16). Mean monthly maximum and mean monthly minimum temperature were also negative correlated with humidity (r = -0.87, df = 94, $p < 0.001$ and r = -0.72, df = 94, $p < 0.001$, respectively) (Figures 2.17 and 2.18). As temperature was strongly correlated with humidity, and the humidity data were patchy due to data logger failure, I only analysed the temperature dataset.

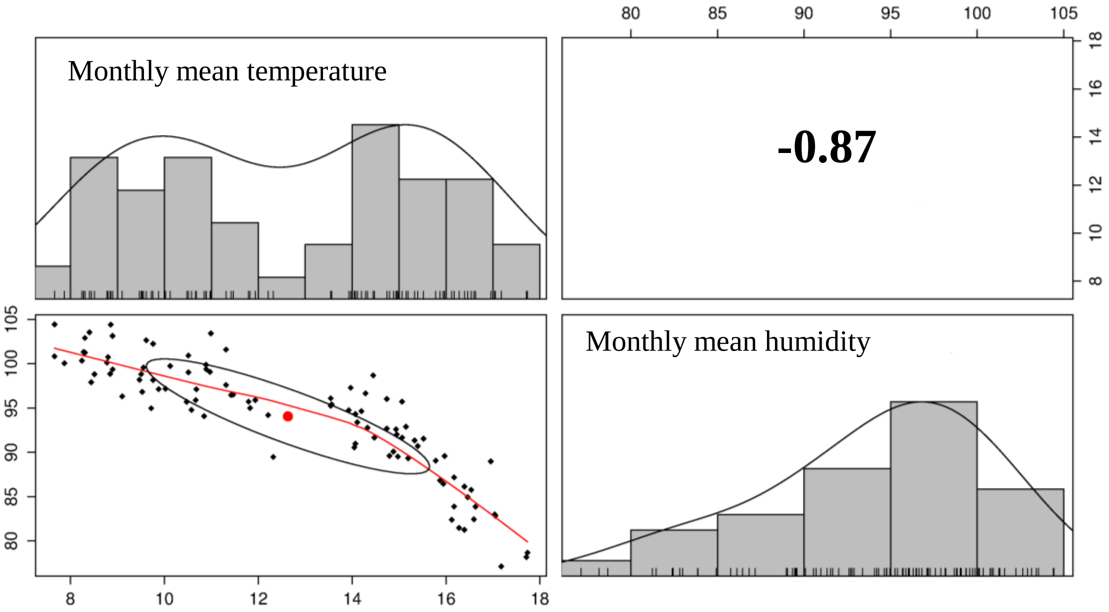


Figure 2.16 Scatterplot of matrices for monthly mean temperature and monthly mean humidity. Below the diagonal is a representation of a bivariate scatter plot with LOESS smoother, and on the diagonal are histograms (bars on x-axis show measurements) with kernel density estimates. The Pearson correlation (*r)* is shown in the upper right.

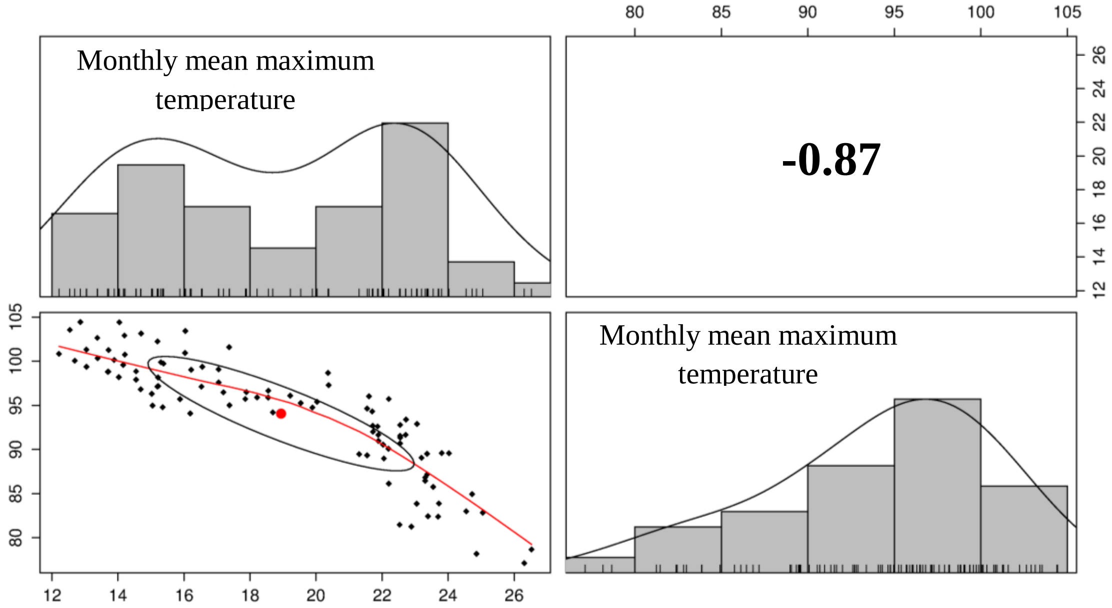


Figure 2.17 Scatter plot of matrices for monthly maximum mean temperature and monthly mean humidity. Below the diagonal is a representation of a bivariate scatter plot with LOESS smoother, and on the diagonal are histograms (bars on x-axis show measurements) with kernel density estimates. The Pearson correlation (*r)* is shown in the upper right.

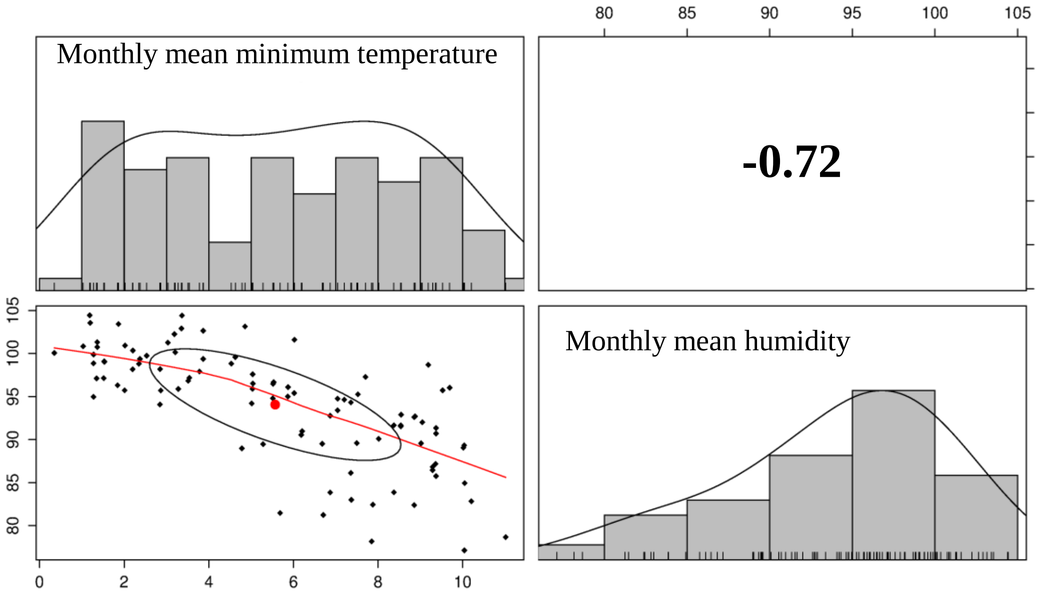


Figure 2.18 Scatter plot of matrices for monthly minimum mean temperature and monthly mean humidity. Below the diagonal is a representation of a bivariate scatter plot with LOESS smoother, and on the diagonal are histograms (bars on x-axis show measurements) with kernel density estimates. The Pearson correlation (*r)* is shown in the upper right.

Mean monthly temperatures in the fenced and unfenced fragments were similar over the measurement period, but the temperature dynamics in the unfragmented forests were rather different (Figure 2.19). In general, unfragmented forest sites experienced lower temperatures in both summer and winter than the other two site types. In autumn and spring the temperatures were similar across all sites. However, in summer 2013 (December to January 2013) temperatures in the unfragmented forest sites were 1 °C lower than at the fragmented (fenced and unfenced) sites. This period corresponded with a drought period in New Zealand, particularly in the North Island (NIWA, 2014a). Over the past decade (2002 – 2012) the monthly mean rainfall in February and March for the Maungatautari area was 78 and 75 mm, respectively (Maungatautari station; -37.96°, 175.54°). The recorded monthly mean rainfall for the same months in 2013 was 27 and 45 mm. During the same months in the Te Miro area, the mean monthly mean rainfall over the last decade was 69 and 72 mm, as compared to just 1.8 and 44 mm received in 2013 (Morrinsville Dam; -37.78°, 175.59°) (NIWA, 2014b).

Mean maximum temperature showed no clear pattern across the different management types. In general, in summer there were differences of 1 to 1.5 °C in mean maximum temperatures between the unfragmented forests and the fenced and unfenced fragments (Figure 2.20). The mean maximum temperature increased dramatically during the 2013 drought period in comparison with the same period in 2012. For example in January 2013 it increased by 3 °C for the unfragmented forest and the fenced fragments, and by 5 °C in the unfenced fragment. During the drought period a difference of 3 °C in mean maximum temperature was recorded between the unfragmented forest and the unfenced fragments. Estimating the change in humidity in this month using a regression of humidity vs. temperature showed that humidity in January 2013 dropped from 79 to 73 % in the unfragmented forest, 76 to 71 % in the fenced fragment and 77 to 68 % in the unfenced fragment when compared to January 2012 estimates.

Mean minimum temperatures were similar across the three levels of management during autumn and spring (Figure 2.21). The lowest temperature was recorded in the unfenced fragments during winter of 2012 (0 °C). During the drought period the lowest temperatures were recorded in the unfragmented forest.

The range of daily temperatures in unfragmented forest sites was lower than in the fragmented sites by on average approximately 1 °C. There was also less variation in the daily range of temperatures in the unfragmented forest than in the fragmented sites (Figure 2.22a). Fenced fragments were less variable than the unfenced fragments but the average difference among them was less than a degree (Figure 2.22b). Unfragmented forests and fenced fragments were very similar to each other in terms of the temperature range experienced. In general, during the drought period the average daily temperature range increased by 2 °C in the unfragmented forest and 3 °C in the fragmented sites (Figure 2.23a). However, the variation in the daily range of temperatures in the unfragmented forest was the same as seen outside the drought period. There was a higher variation in the daily range of temperatures in the fragmented sites. During the drought there was no difference between the fenced and unfenced fragments in terms of daily range of temperatures (Figure 2.23b).

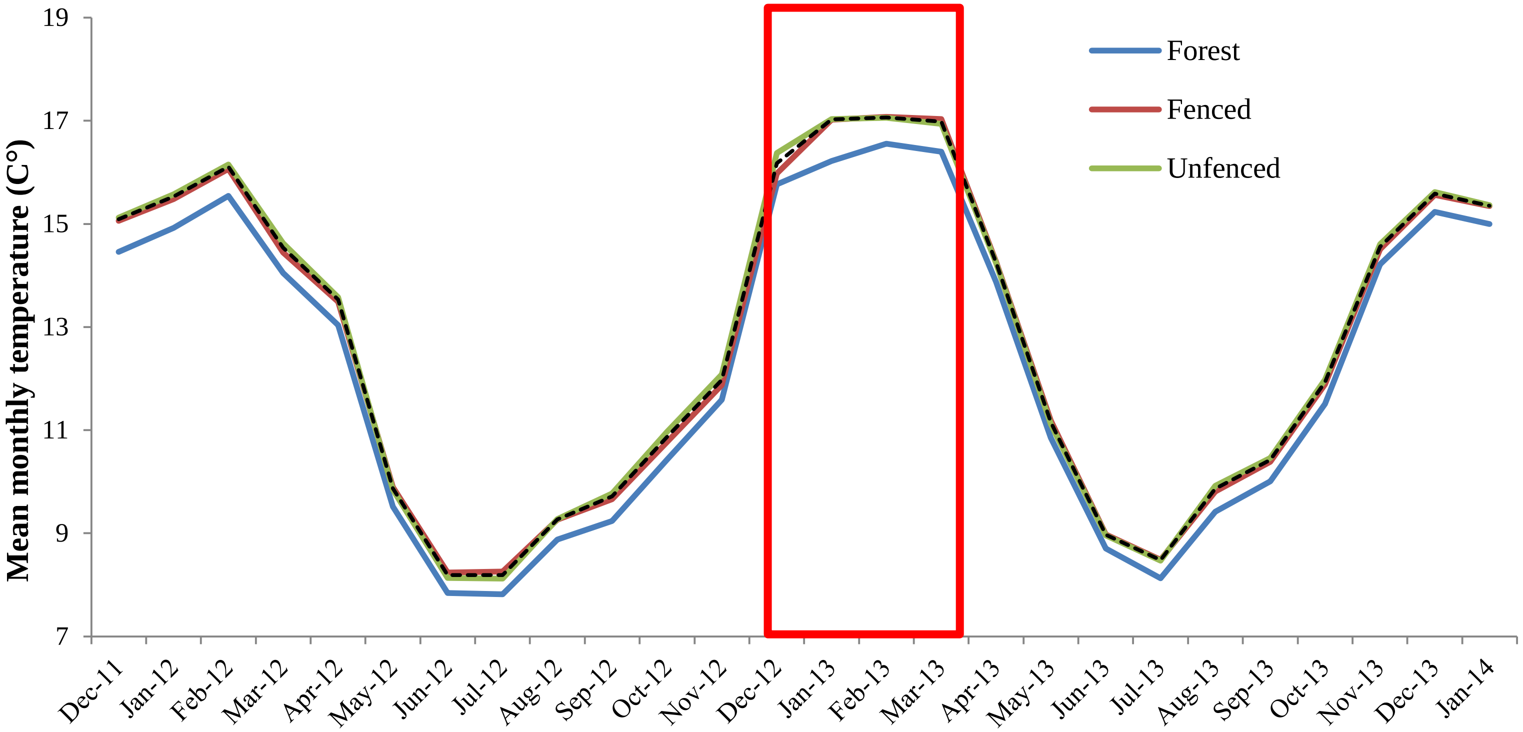


Figure 2.19 Mean monthly temperature in the study sites (*n* = 3) from December 2011 to December 2013; the red box denotes the timing and duration of the drought that occurred during the summer of 2013.

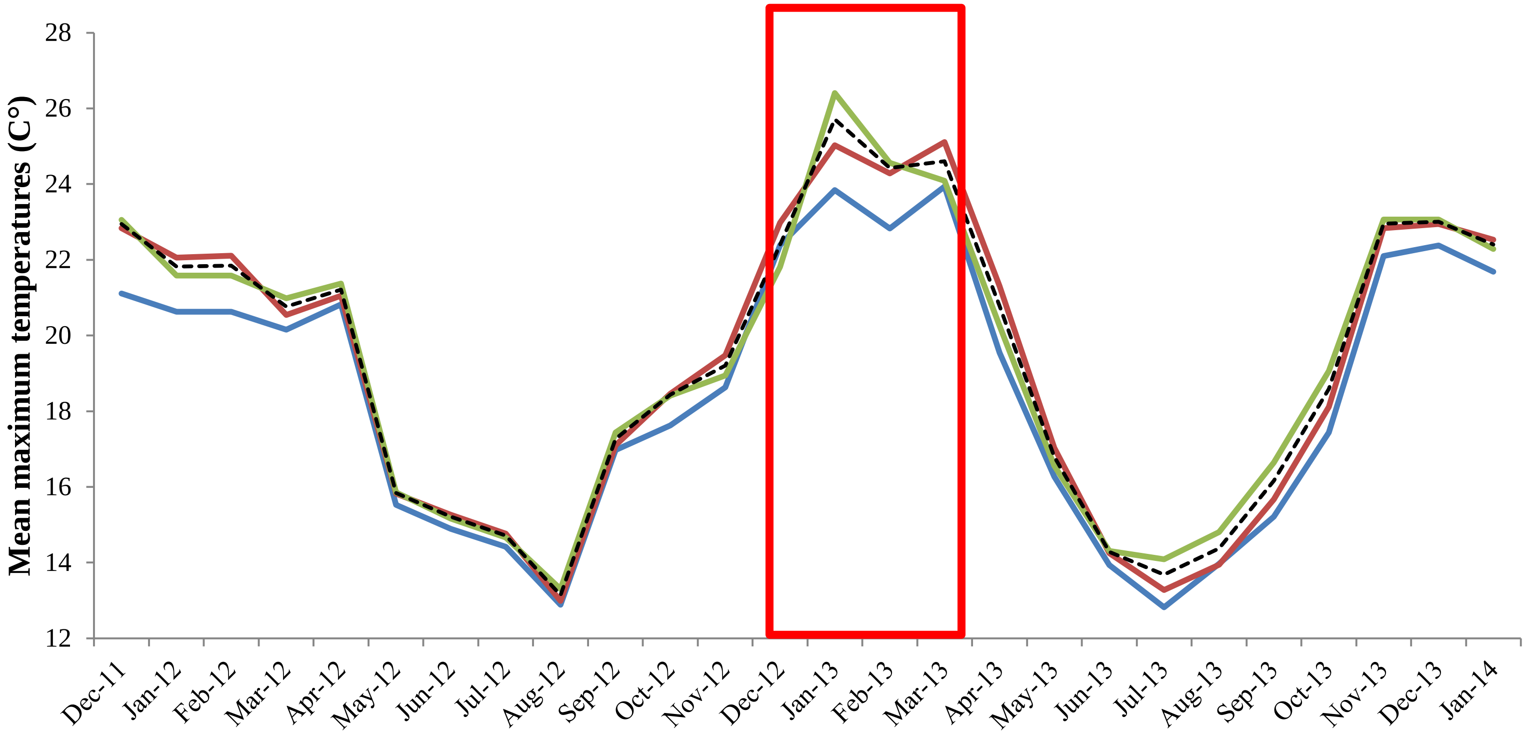


Figure 2.20 Mean maximum temperatures in the study sites (*n* = 3) from December 2011 to December 2013; the red box denotes the timing and duration of the drought that occurred during the summer of 2013. Colouring as per Figure 2.18.

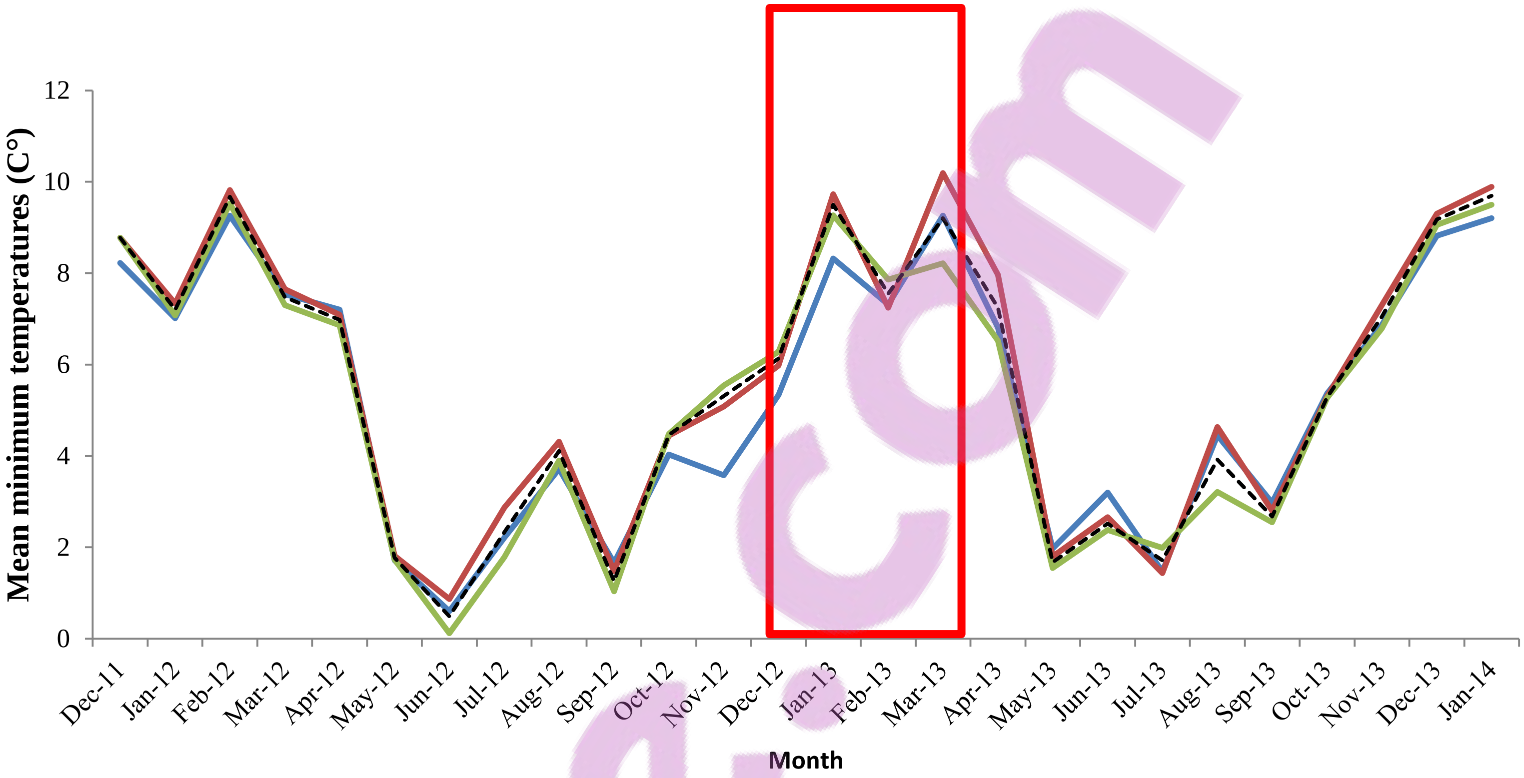


Figure 2.21 Mean minimum temperatures in the study sites (*n* = 3) from December 2011 to December 2013; the red box denotes the timing and duration of the drought that occurred during the summer of 2013.

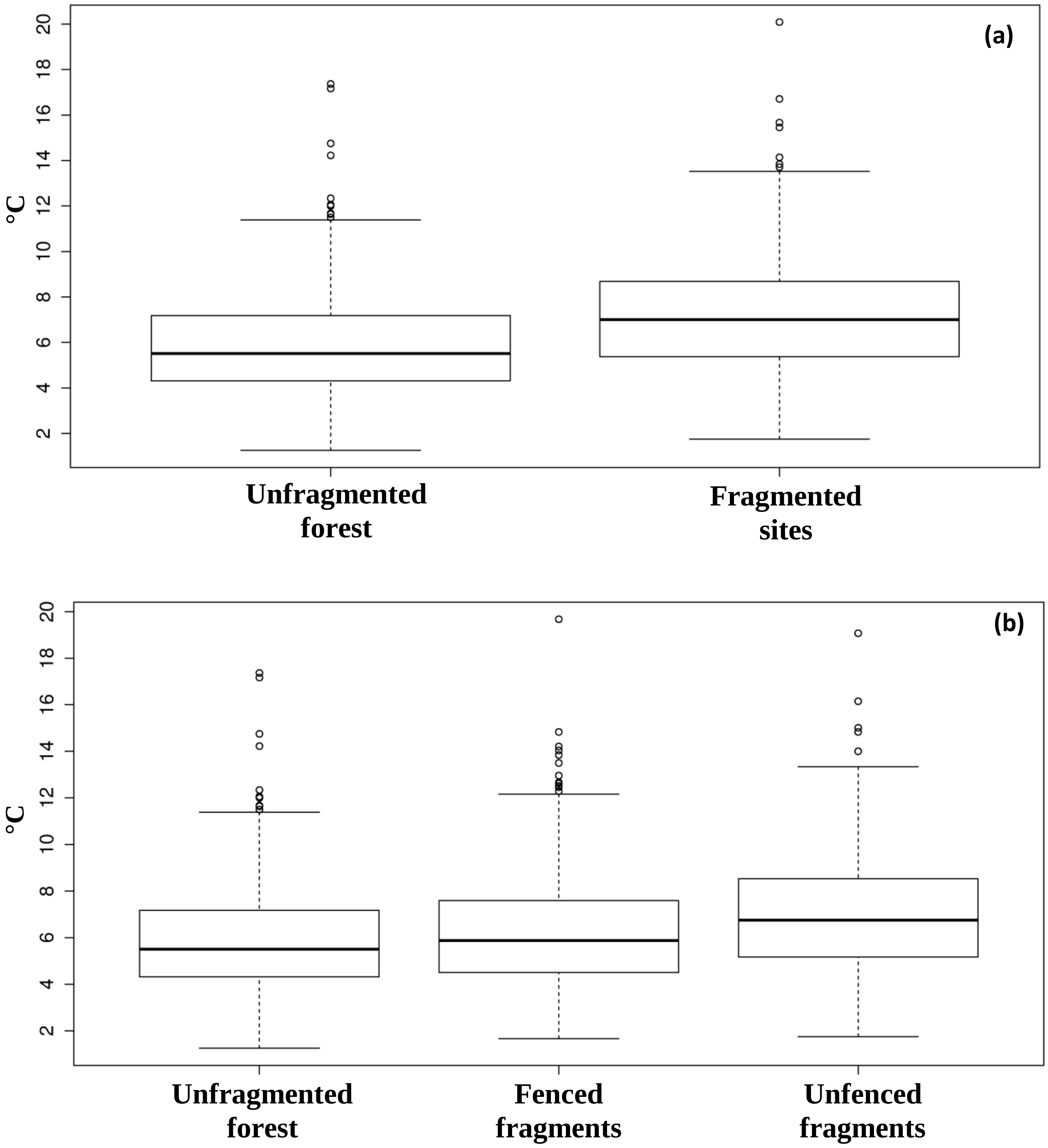


Figure 2.22 Range of daily temperatures from December 2011 to January 2014 for (a) unfragmented forest and fragmented sites and (b) unfragmented forest, fenced and unfenced fragments.

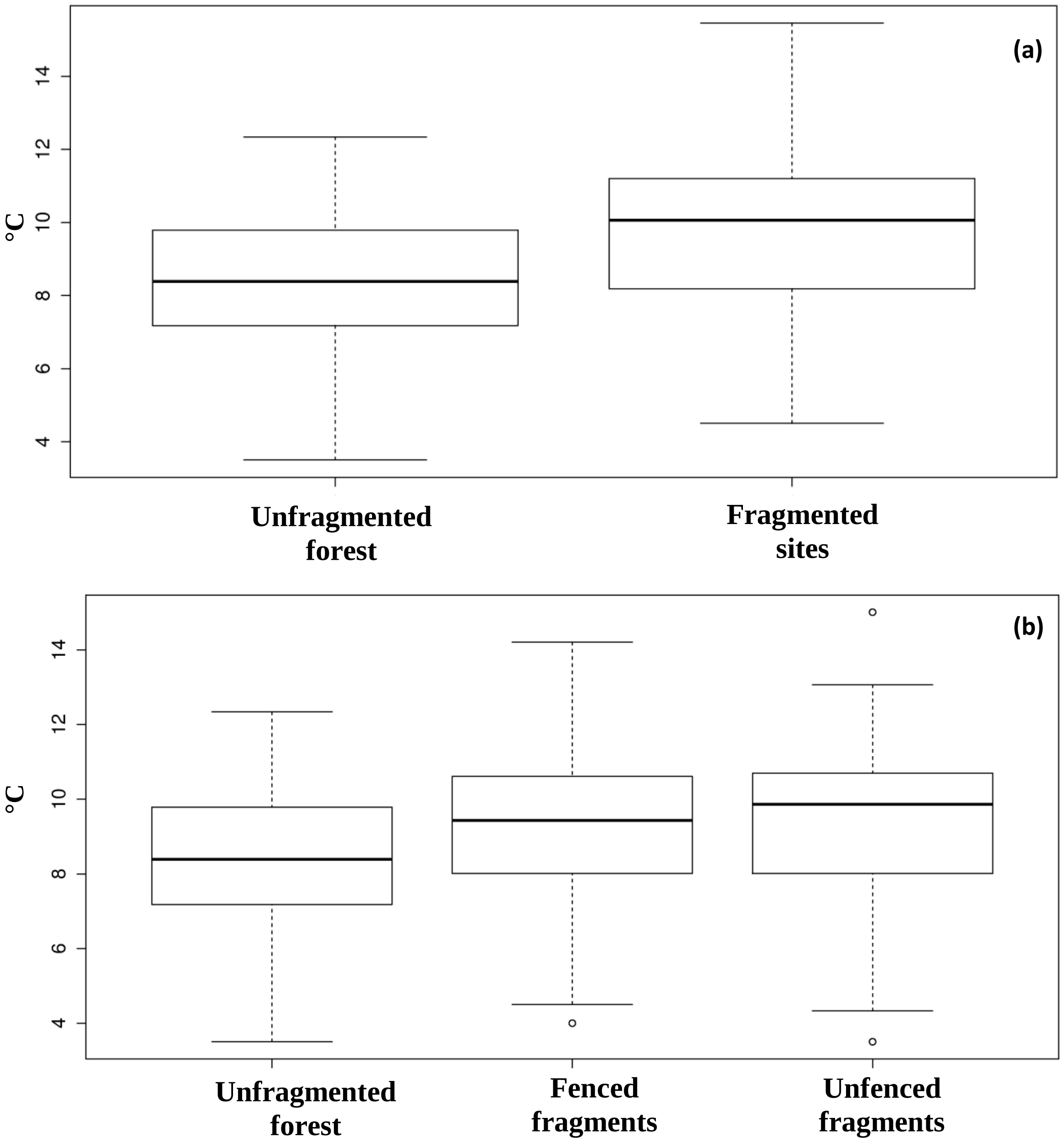


Figure 2.23 Range of daily temperatures during the drought (January to February 2013) for (a) unfragmented forest and fragmented sites and (b) unfragmented forest, fenced and unfenced fragments.

2.4 Discussion

In this chapter I have explored the potential effects of different types of management (fragmentation and fencing) on the current-day composition of podocarp-tawa forest fragments and the abiotic conditions that characterise them (soil, light and climate).

Canopy tree density (*B. tawa*, *K. excelsa*, *L. novae-zelandiae*) was higher in the unfragmented forest than in the fragmented sites (fenced and unfenced fragments). *B. tawa* and *L. novae-zelandiae* were present across all management types; however they were present at lower density in the fenced fragments. While compositional and structural similarities between the unfragmented forest and fenced forest fragments might be expected because of the effects of fencing, this was not the case. The density and basal area of *B. tawa* in the fenced fragments was low (76 ± 50 ind/ha, 15.21 ± 1.95 m^2/ha) in comparison with the unfragmented forest (164 ± 83 ind/ha, 24.07 ± 2.93 m^2/ha), however only the differences in basal area were slightly significant (p= 0.09). In the unfenced fragments, the basal area of *B. tawa* was similar than in the unfragmented forest (24.42 ± 22.99 m^2/ha and 24.07 ± 2.93m^2/ha, respectively), but in the unfenced fragments there was a high variability in the values of basal area. However, the *B. tawa* densities in the unfenced fragments were lower than in the unfragmented forest suggesting that in the unfenced fragments the trees tend to be bigger and presumably older (Table 2.3). Similarly, the basal area of *L. novae-zelandiae* was higher in fenced fragments but with fewer individuals (68 ± 41 ind/ha, 33.84 ± 32.34 m^2/ha). As with *B. tawa* they were on average larger trees in comparison with those in the unfragmented forest (140 ± 47 ind/ha, 18.8 ± 3.94 m^2/ha) and unfenced fragments (147 ± 179 ind/ha, 9.35 ± 7.10 m^2/ha).

In terms of subcanopy tree species, the abundances of the dominant species (*M. ramiflorus* and *H. arborea*) were similar across all three management types. The basal area of *M. ramiflorus* suggests that the individuals present in the different types of management were relatively large (low density and high basal area), especially in the fenced fragments. However, 35 % of the *M. ramiflorus* individuals were multi-stemmed, which could perhaps better explain the high basal area. In general, multi-stemmed individuals are evidence of past disturbance (e.g. intensive past grazing) (Bellingan and Sparrow 2009). A similar pattern was observed for *H. arborea* in the unfenced fragments, where 30 % of trees were multi-stemmed. *P. excelsum* was present in high numbers in the unfenced and fenced fragments; with a high basal area especially in the fenced fragments (1.94 ± 1.55 m^2/ha). Since only 15% of *P. excelsum* are multi-stemmed, this suggests that most of the *P. excelsum* individuals were juvenile in both sites. It is important to note that *P. excelsum* thickets were dense, especially in some of the fenced fragments (e.g. site FD3; Figure 2.8). Thickets of subcanopy species, such as *P. excelsum*, can reduce local light levels and increase competition for seedlings and saplings (Burns et al. 2011), which may explain the lack of canopy seedlings in this particular fragment.

The *B. tawa* size-frequency data showed that in both the fenced and unfenced fragments most of the individuals fell into larger diameter classes with a lack of juvenile individuals (saplings) relative to the unfragmented forest. A preliminary survey found *B. tawa* saplings (> 140 cm tall, 1 – 5 cm dbh) were present in the unfragmented forests. The size structure of the fragmented sites (fenced and unfenced fragment) suggests that small (seedling-sized) individuals are not transitioning to the sapling stage in these sites; which, ultimately, means that there will be no individuals to replace the canopy individuals, a result echoing previous studies in *B. tawa* (Burns at al. 2011) and *B. taraire* (Myers and Court 2013). The absence of saplings (1 – 5 cm dbh) was consistent across all of the fragments irrespective of fencing, which means that fencing had no effect in promoting the survival of seedlings to larger size classes.

nMDS ordination of the adult trees based on the PCQ data showed that the unfragmented forest PCQ points had comparable species abundances and composition (the PCQ points were tightly clustered in the ordination space), but I did not find a similar pattern for the fragmented sites or fenced fragments. However, when I analysed canopy and subcanopy tree species separately, the nMDS ordination of the subcanopy trees alone showed a more diffuse unfragmented forest cluster (meaning that PCQ points of unfragmented forest sites were scattered), which suggests that the relative abundances of subcanopy tree species differ amongst the different unfragmented forest PCQ points. This, again, indicates that the effects of management vary even within the same management type. Nevertheless, *a posteriori* analysis using multivariate GLM models (mvabund) did not find any effect of management type on the abundance of canopy and subcanopy trees.

B. tawa was present in almost every plot and site in the PCQ data. However, *B. tawa* weighted abundance scores were higher in the cluster formed by the unfragmented forest PCQ points, and tended to be lower towards the PCQ points from fragmented sites and fenced fragment sites. This was contrary to my expected results, as I predicted that fencing would provide the protection necessary for *B. tawa* abundances in fenced fragments to be similar to those in unfragmented forests. However, *B. tawa* trees can take up to 49 years to reach 11 cm dbh (West 1986) and therefore a fragment that was fenced 20 years ago, such as those in this study, may not yet have accumulated any *B. tawa* trees with a dbh > 5 cm (the absence of saplings notwithstanding).

We might have expected to find similarities between the unfragmented and fenced forest in the composition of subcanopy tree species because they grow faster and so the effects of fencing could be detected in a 10 to 20 year timeframe. In the case of canopy trees, changes could be less noticeable due to the length of their lifespan and their slower growth rate. We found the opposite: fenced and unfenced PCQ points were similar to each other, except for the PCQ points from the FD2 fenced fragment which were closer to the unfragmented forest PCQ points. This outcome is likely a result, at least in part, of the initial species composition when fragments were initially fenced. Burns et al. (2011) suggested that due to the past history of the fragments (e.g. past logging, prolonged herbivore action) some species were lost and that could explain the apparent divergence between the fenced fragments and the unfragmented forest.

B. tawa tree core data showed that the ages of the youngest trees in the unfragmented forests, fenced fragments and unfenced fragments were similar, 45, 62 and 59 years respectively. The average age of the youngest individuals in the unfragmented forests was 65 ± 25 years, 67 ± 7 years in the fenced fragments and 75 ± 14 years in the unfenced fragments The oldest trees in the unfragmented forests, fenced fragments and unfenced fragments were 282, 261 and 272 years, respectively. It seems that there were no age differences among the different types of management. In a study by West (1986) at Pureora Forest, the youngest individual was 49 years and the oldest was 458 years. The difference in oldest trees could be explained by the difference in past human activities in the area. The ages of these trees does, however, suggest that *B. tawa* was successfully regenerating in the 1950s. This is interesting because Gudex (1959) mentioned that domestic animals were not excluded from the forests in this area (e.g. Te Miro) at the time and other mammalian herbivores such as fallow deer (*Dama dama*) and possum were present as well. These results suggest that the lack of regeneration detected in some sites (e.g. low density of seedlings and saplings) could be caused by factors other than herbivory and has occurred in the last 60 years.

nMDS ordination of the seedlings based on the PCQ data did not identify any distinctive pattern among the PCQ points from different types of management, meaning that the type of management has little to do with the presence or absence of species. In general, *B. tawa* seedlings were present throughout the ordination space, suggesting that there is little association between *B. tawa* seedling presence and the type of management. However, although I found seedlings in all sites (Figure 2.11b) I only found saplings in the unfragmented forest and in small numbers in some of the fenced and unfenced fragments (UD3 and FD3). This pattern implies that seedlings are not transitioning to the saplings stage in most fragmented sites.

Principal components analysis (PCA) results showed that plots from fragmented sites when combined (fenced and unfenced sites) form a distinct group. In terms of fencing, the same analysis showed that although they did not form part of the same group, some of the abiotic variables in two of the fenced sites (FD1 and FD2) were quantitatively similar to the same variables in the unfragmented forest. It is interesting to note that site FD2 was visually more similar to the unfragmented forest sites in terms of these abiotic variables. The FD2 site also had a high number of *B. tawa* and *L. novae-zelandiae* seedlings. On the other hand, one fenced fragment (FD3) showed strong similarities to the unfenced fragments, especially in terms of phosphorus levels; it is surrounded by extensively grazed land, and these activities are associated with the leakage of phosphatic fertilizers from the grassland into the fragment (Stevenson 2004). Again such patterns suggest that while in some cases fencing could help to improve abiotic conditions in some sites, this will depend on the current and past activities in the surrounding landscape.

The temperature data showed that unfragmented forest had a stronger buffering effect, especially in summer, than the fragmented sites (fenced and unfenced fragments) (Figures 2.22a and 2.23a). Monthly mean temperature and mean maximum temperature were lower in the unfragmented forest in comparison with fragmented sites (Figure 2.19 and 2.20). In summer (December – March), the mean minimum temperature was lower in the unfragmented forest in comparison with the fragmented sites; especially during the drought (Figure 2.21).

Mean minimum temperature was higher in fenced fragments than in the unfenced fragments during winter (June – July). Mean minimum temperature was very similar between the fenced and unfenced fragments during the summer (December - February) and especially during the drought period (January- February 2013). The unfragmented forest and the fenced fragment had lower maximum temperature during the drought when compared to the unfenced fragment. This suggests that fencing can also contribute to buffering temperature extremes to some extent (Figure 2.21b), but during the drought that buffering effect diminished considerably (Figure 2.22b). Although I chose fenced fragments with similar characteristics for this study I did not control factors such as aspect, wind direction and speed, fragment size and adjacent land cover. These factors can have a significant effect on microclimate edge effects (Young and Mitchell 1994, Denyer et al. 2006), and therefore the differences I observed in this study may be due to one or a combination of these factors and not to the buffering effect of a fenced forest fragment.

The most important caveat of this study was the low number of site replicates, which can weaken the statistical power of these results. However, it is not rare to find studies of this type with low number of samples. For example, Schmiegelow et al. (1997) used three replicates per treatment with a total number of 12 sites. Bowers and Dooley (1993) used four samples per treatment (four treatments). Benitez-Maldivo (2008) used a variable number of replicates per treatment which ranged from two to five samples. In general, studies on fragmentation have to deal with pseudo-replication and with low number of replicates mainly due to logistical considerations and the impracticality of sampling large number of sites spread over a large area (Hargrove and Pickering 1992, Debinski and Holt 2001). In this study the main limiting factor was the difficulty in finding sites that met the study criteria and were located within a reasonably bounded area (to ensure factors such as climate were consistent). While some of the results presented in this chapter must be interpreted with appropriate caution as a whole they provide a good view of what is going on under the different management types.

In conclusion, fencing does not appear to guarantee the long-term viability of podocarp-tawa forests, but it is an important, and likely necessary, first step. In addition to fencing the past history of each fragment, the activity surrounding them (i.e. their landscape context) and one issue that was not explicitly considered in this study, the size of fragments, all need to be considered. Due to the challenge of finding similar sized patches patch area could not be controlled for during the present study. In the past, it was commonly accepted that larger patches harboured higher species abundance and so led to better and more sustained survival of forest species, (Saunders et al. 1991, Debiksnki and Holt 2000). However, the matrix surrounding remnant vegetation can have a strong influence on species occurrence and spatial dynamics and may be more important than the size and spatial arrangement of remnant patches (Young and Mitchell 1994, Driscoll et al. 2013). For seedlings, for instance, Benitez-

Malvido (1998) found that edge effects were more important than area effects *per se* in affecting seedling abundance, with the centres of larger fragments (100 ha) not having significantly higher densities of tree seedlings than smaller ones (10 and 1 ha). Future studies would do well to include fragment size as a variable to determine if it does indeed influence the long-term survival of podocarp-tawa forest species.

Our study showed that fencing by itself is not enough to drive restoration processes in fragmented forest and that the effects of fragmentation are still evident after 20 years. The negative impacts suffered by the fragment in the past could explain some of the results found in this study, as other studies have suggested (e.g. Burns et al. 2011, Myers and Court 2013, Grman et al. 2013). In most cases the impacts on these landscapes have been occurring over the past 100 years, if not longer, and so it is likely that their consequences are still present at different levels. If contingency effects and history are important then there may be multiple alternative trajectories the fragments may take, which means that any one pre-determined recipe is unlikely to be able to restore all forest fragments to their original states. We recommend that future studies take into consideration the history of forest fragments, their relative distance to unfragmented forest as well as uses of the surrounding areas.

3. EFFECT OF FRAGMENTATION AND FENCING ON THE SURVIVORSHIP OF *BEILSCHMIEDIA TAWA* SEEDLINGS AND REGENERATION TRAJECTORIES

3.1 Introduction

Habitat fragmentation is one of the main processes responsible for the reduction of natural ecosystems to scattered isolated forest remnants (Iida and Nakashizuka 1995, Laurence 2000, Echeverria et al. 2006). There is considerable evidence that fragmentation negatively affects seed dispersal and seedling establishment, so preventing species from colonizing suitable sites (Laurance et al. 2006, Cramer 2007, Herrera and Garcia 2010, Zambrano et al. 2014). The effect of fragmentation on post-dispersal processes can be due to changes in soil composition, canopy cover, patch size, forest community structure, seed and seedling predation, altered microclimates, and continued degradation of the fragment (Bruna 2002, Laurance et al. 2002, Herrera and Garcia 2010, Ismail et al. 2014). As such, fragmentation is interrupting one of the most crucial processes in the plant life cycle. Reproduction is a crucial stage of any plant's life cycle. A species must establish itself in enough numbers so as to permit the replacement of dying individuals. Any phenomenon that disrupts this replacement process over a sustained period of time can, ultimately, cause a species to become locally extinct (Sodhi et al. 2010).

Laurance et al. (2006) showed that the effect of fragmentation could be rapid (within 20 years) and could cause the population decline or extinction of tree species, especially those with large seeds. In other to avoid or mitigate the effect of fragmentation, land managers have used fencing as a strategy to help conserve forest fragments (Hayward and Kerley 2009). One of the most popular methods of fencing is the basic use of poles and wires which mainly act to exclude large herbivores. Other more sophisticated fencing methods, such as predator-proof fences, have proven to be very successful although their use is limited because of the high costs involved (Burns et al. 2012).

In general, the use of fencing is perceived as a restoration activity based on the belief that once the predators or herbivores are removed most of the post-dispersal processes will return to their pre fragmentation state (Reeves 2000, Spooner et al. 2002). However, herbivore exclusion can have variable effects (e.g. shrub recruitment, understory recovery) depending on the type of vegetation and past history of the fragment (Spooner et al. 2002, Burns et al. 2011). For example, Aronson and Handel (2011) found that in deciduous forest fragments in United Stated the exclusion of white-tailed deer (*Odocoileus virginianus*) was not enough to secure the recovery of forest fragments if invasive plant species were not eradicated too. On the other hand, Spooner et al. (2002) found that after fencing woodlands in south-eastern Australia, tree and shrub regeneration was improved together with promotion of perennial grasses and a decreased soil compaction.

In the Waikato region of the North Island of New Zealand, habitat fragmentation began at least a century ago (Gudex 1959). The Waikato region is home to some of New Zealand’s most fragmented forests, with approximately 5000 fragments each less than 25 ha (Burns et al. 2011). In general, these forest fragments are on private land (Ewers and Didham 2006), with minimal management undertaken to maintain their biodiversity (Burns et al. 2011). The most common management activity is fencing to prevent herbivory by exotic mammals (Burns 2012). Fencing can involve different approaches that range from preventing access by large exotic mammals (e.g. cattle (*Bos taurus*), sheep (*Ovis aries*) to predator-proof fences, which also exclude small mammals (e.g. rabbits (*Oryctolagus cuniculus*), ship rats (*Rattus rattus*), as is the case with the Maungatarutari Scenic Reserve (Speedy et al 2007). The former approach is the most commonly used both in New Zealand and around the world, mainly because predator-proof fencing is not economically feasible for most landowners.

In Chapter 2 I used a multivariate analysis to explore vegetation-environment relationships in a series of forest communities in the context of fragmentation and fencing. In this chapter I further assess the impact of fragmentation and fencing on podocarp-tawa forest fragments, in particular, whether fragmentation and fencing could affect *Beilschemiedia tawa* recruitment. We are particularly interested in the podocarp-tawa forest type because throughout most of its distribution this forest type is under exotic herbivore pressure, competing with exotic weeds and recruitment appears to be limited (Dodd and Power 2007, Smale et al. 2008). To accomplish these objectives I compared the survivorship and growth of natural and potted seedlings in unfragmented forests, and fenced and unfenced fragments. We also explored tree-by-tree replacement (Perry and Enright 2007) data to compare and contrast possible successional dynamics across sites.

3.2 Methods

3.2.1 Study area

The same study sites as described in Chapter 2 were used in this chapter (Section 2.2.1, Figure 2.1). They comprise nine sites near Cambridge in the Waikato region, and include three unfragmented forests, three fenced (for at least 20 years) fragments and three unfenced fragments. The vegetation at all nine sites is podocarp-tawa forest with *Beilschmiedia tawa* and *Laurelia novae-zelandiae* the dominant canopy tree species (Burns et al. 2011).

3.2.2 Data collection

Seedling survivorship and growth

At each site I randomly selected three experimental areas to carry out growth and survivorship experiments (these sites were the foci of the vegetation data collection described in Chapter 2, Section 2.2.2). Each of these experimental areas was located beneath the canopy of a mature *B. tawa* tree. A cylindrical chicken-wire enclosure (1 m diameter × 1.1 m height) was constructed at the base of the *B. tawa* tree, and 10 potted *B. tawa* seedlings were placed inside it. An additional 10 potted seedlings were placed outside the enclosure within a 1 m radius (Figure 3.1). The chicken wire excluded small mammalian herbivores (e.g. ship rats and rabbits), but other herbivores (e.g. insects) could access the plants. A total of 540 seedlings (20 individuals × three areas × nine sites) were placed across the nine experimental sites. Seedlings were procured from the Taupo Native Plant Nursery, Mission Bush, South Auckland, New Zealand. The seedlings were of the same age and ranged in height from 42 – 44 cm at the start of the experiment. Two hundred and fifty seedlings came from seeds collected from Waipahihi Reserve (Taupo) in the Central North Island and 350 seedlings came from seeds collected at Battle Hill in the Wellington region (Taupo native Plant Nursery, personal communication). We randomly distributed the seedlings among the experimental sites.

The *B. tawa* seedlings were placed at the study sites in July 2011. Due to permitting requirements at some sites, they could not be planted and so all individuals remained in their pots at all sites. We marked each seedling on its main stem at a height 10 cm below the apical bud with typing correction fluid (e.g. Twink®, Liquid paper®). We also marked the seedlings at a height 5 cm above the ground with correction fluid as a guide for all diameter measurements (as per Carswell et al. 2012). Every two months from November 2011 to January 2013 I measured the height from the stem mark to the dominant apical bud and so derived height increments. Stem diameters were measured using callipers with the aforementioned 5 cm mark acting as a reference.

Figure 3.1 Example of an enclosure, located under a large tawa tree in an unfenced fragment, showing *n* = 10 seedlings inside the enclosure and *n* = 10 outside.

At each census seedlings were classified as being ‘alive’, ‘browsed’ or ‘desiccated’. We considered a seedling to be ‘alive’ if it had at least one green leaf; this category, therefore, included those seedlings that were attacked by insects and where the terminal bud was eaten but a new lateral shoot had become dominant. Those seedlings showing evidence of herbivory-induced mortality (i.e., with the stem completely missing) were classified as ‘browsed’ and were no longer measured. We classified the seedlings as ‘desiccated’ (dead) if the stem was present, but they did not have any green leaves or shoots (Figure 3.2).

Figure 3.2 Example of *B. tawa* potted seedlings that were (a) ‘desiccated’ with no green leaves or shoots, (b) ‘browsed’, and (c) ‘alive’ although it has been browsed; note the apical bud has been eaten but the seedling still has green leaves and shoots.

Natural seedling regeneration

We assessed natural regeneration using 18 plots (1 × 1 m) per site (*n* = 162). The plots were placed near each enclosure using a randomly selected bearing and distance (Chapter 2, Figure 2.4b). Each 1 × 1 m plot was divided into four quarters within which I recorded the presence of seedlings of any subcanopy and canopy species classified into three height categories: 5 - 10 cm, 10 - 30 cm and 30 - 50 cm.

We tagged naturally occurring *B. tawa* seedlings (> 30 cm) in all of the experimental areas at each site (i.e. in each of three types of management). All seedlings within 5 m of the enclosures were tagged, checked for survival every six months, and any mortality recorded. In some plots the high density of seedlings made it impossible to tag them all, in which case I tagged and counted all individuals within randomly located 1 x 1 m sub-plots. The tagged forest individuals were all from Maungatautari north and Maungatautari south, as I could not find any natural seedlings near the study stations in Te Miro forest.

Tree replacement data

As noted in Section 2.2.2, I collected tree replacement data to construct tree-by-tree replacement tables (Horn 1975, Ogden 1983). We recorded the species most likely to replace the focal tree in the PCQ surveys described in Chapter 2. The replacement individuals were classified into different functional types (tree ferns, subcanopy trees, canopy trees and *B. tawa*). To further increase the sample size I randomly selected adult trees at each site (Table 3.1) and for each recorded the species of the two most likely replacement individuals (as per Perry and Enright 2007).

Table 3.1 Number of supplementary trees sampled per site to complement the PCQ data for tree-by-tree replacement data by management type. Site names as per Table 2.1

Treatment	Site name	N° of trees sampled
Fenced	FD1	97
	FD2	48
	FD3	64
Unfenced	UD1	61
	UD2	29
	UD3	48
Unfragmented forest	UF1	102
	UF2	96
	UF3	95

3.2.3 Data analysis

All the analyses described in this section were carried out using R-2.15.1 (R Core Team 2010), unless otherwise stated.

Seedling survivorship and growth

Tree seedling data from inside and outside the enclosures were analysed separately in order to determine the effect of this protection on herbivory. We calculated the mean height and diameter at the beginning and at the end of the study for each seedling. Survivorship was calculated from the number of individuals that fell into the alive, insect attack (but alive), desiccated (dead) or browsed (dead) categories at the end of the study. We therefore discriminated between individuals that died due to herbivory attack from those that dried out. The insect attack category was considered as part of the alive category because such attacks did not prevent the seedlings from growing (see Figure 3.2c).

We analysed seedling survivorship inside and outside the enclosures. We analysed the effect of enclosures on survivorship, without the presence of herbivory by large mammals (unfenced fragment data was not considered in this analysis). We also performed an analysis of the effect of fragmentation (unfragmented forest versus fragmented sites) and fencing (fenced versus unfenced fragments) on seedling survivorship. For this analysis I only used the survivorship inside the enclosures to avoid confounding with the effect of herbivory. In addition, I analysed the survivorship of unfragmented forest and fragmented sites using the data from inside and outside the enclosures together. We did the same to compare survivorship between fenced and unfenced fragment. These analyses were performed using a two-sided Fisher's exact test ("stats" package).

We calculated the cumulative height increment between measurement periods for all the seedlings inside the enclosures that were alive at the end of the study. We calculated the cumulative mean increment of the three plots per site with three replicates per level of management (unfragmented forest, fenced fragment and unfenced fragment; *n* = 9). We did not analyse the diameter data as it did not show major changes; the mean (± 1 SD) diameter increment across all individuals was just 0.15 ± 0.38 mm (over 29 months; 0.06 mm per yr).

We analysed the data using a linear multi-effect model as proposed by Crawley (2007) with a Satterthwaite approximation for degrees of freedom. Because the data were not normally distributed I used a log-normal transformation. We considered log-normal cumulative increment on height as the response variable with the level of management as a fixed factor and seedling identifier as a random effect. We used the "*lme4*" (Bates et al. 2014) and "*lmerTest*" packages (Kuznetsova et al. 2014) in R for these analyses.

Tree replacement data

To depict the regeneration dynamics across the different levels of management I used the "*sna*" package (Butts 2014) to construct schematic diagrams (network graphs) of the different regeneration dynamics for each site based on transitions between the canopy species, subcanopy species and tree ferns. The main objective of this exploratory visual analysis was to determine which species were characterising the regeneration bank and which canopy species were enabling this process. We used the same species classification as described in Chapter 2, Section 2.2.3.

3.3 RESULTS

3.3.1 Seedling survivorship and growth

Of the 540 seedlings initially placed across the nine sites, 326 (60 %) were still alive at the end of the experiment 26 months later (Table 3.2). Of the 214 dead seedlings, 51 were eaten and 163 were desiccated, representing 24 % and 76 % of the dead seedlings, respectively. Irrespective of the type of management, survivorship inside the enclosures was higher than it was outside the enclosures (Table 3.2). We did not find a significant effect of the enclosures on the survivorship of the seedlings in the absence of herbivory by large mammals ($p = 0.27$). We did not find a significant difference in survivorship between unfragmented sites and fragmented sites (using survivorship inside the enclosure) ($p = 0.45$) but I found a significant difference between the fenced and unfenced fragments ($p = 0.04$) (using survivorship inside the enclosure). When I ran the analysis including survivorship inside and outside the enclosure I found significant differences between the unfragmented forest and the fragmented sites (p = 0.001), but we did not find a significant effect between fenced and unfenced fragments (p = 0.9).

Table 3.2 Counts and fate of potted individual *B. tawa* seedlings across each management type and their placement inside or outside an enclosure.

Enclosure	Categories	Forest N° ind (%)	Fragmented N° ind (%)	Fenced N° ind (%)	Unfenced N° ind (%)
Inside	Alive	71 (79%)	133 (74%)	60 (67%)	73 (81%)
	Insect attack*	0	23 (13%)	7 (8%)	16 (18%)
	Desiccated	19 (21%)	47 (26%)	30 (33%)	17 (19%)
	Browsed	0	0	0	0
Outside	Alive	60 (67%)	61 (36%)	37 (41%)	24 (26%)
	Insect attack*	1 (1%)	8 (4%)	4 (4%)	4 (4%)
	Desiccated	24 (27%)	74 (41%)	47 (52%)	27 (30%)
	Browsed	6 (7%)	45 (25%)	6 (7%)	39 (43%)

*'Insect attack' is considered as part of the alive category.

Table 3.2 shows that mortality was higher in fragmented sites compared with unfragmented forest, especially in seedlings outside the enclosures. Enclosures had the effect of stopping mortality by herbivory and therefore mortality was reduced inside enclosures. Outside the enclosures, however, desiccation and vertebrate browsing were much higher. Herbivory was relatively unimportant for the seedlings that were outside the enclosures in the unfragmented forest (herbivory was reported only at the UF1 site, where fallow deer (*Dama dama*) are present at low densities (DoC 2014) and fenced fragments; herbivory-induced mortality accounted for 6 % of deaths in both cases. In the unfenced fragments mortality from herbivory was more frequent than desiccation (43 vs. 30 %, respectively). Fenced fragments had a higher rate of desiccation-induced mortality (See section 2.3.4) than did the two other levels of management.

The height growth of seedlings inside the enclosures was lower than outside the enclosures, except for the unfragmented forest sites where the growth was almost identical inside and outside the enclosures (Table 3.3).

Table 3.3 Numbers of potted tawa seedlings, mean (± 1 SD) height increment and diameter at the beginning and end of the experiment (July 2011 to December 2013). In parenthesis annual mean (± 1 SD) height increment is presented.

Site	**Enclosure**	**Final number of seedlings**	**Mean height increment (cm)**	**Initial mean diameter (cm)**	**Final mean diameter (cm)**
Forest	Inside	71 (79%)	6.3 ± 2.5 (2.6 ± 0.8)	3.5 ±0.7	3.4 ± 0.6
	Outside	60 (67%)	6.8 ± 2.9 (2.8 ± 1.2)	3.4 ±0.8	3.4 ± 0.8
Fenced	Inside	60 (67%)	4.4 ± 0.9 (1.8 ± 0.4)	3.4 ±0.8	3.2 ± 1.1
	Outside	37 (41%)	5.6 ± 0.7 (2.3 ± 0.3)	3.3 ±0.8	3.5 ± 0.7
Unfenced	Inside	73 (81%)	6.6 ± 1.5 (2.7 ± 0.6)	3.4 ±0.9	3.6 ± 0.7
	Outside	24 (26%)	6.4 ± 2 (2.6 ± 0.9)	3.3 ±0.8	3.5 ± 1.2

The mean height increment inside the enclosures in the unfragmented forest was higher than the fragmented sites, 2.6 ± 0.8 cm and 2.4 ± 0.7 cm per year respectively. The mean height increment of the fenced fragments was lower than the unfenced fragments (Table 3.3). Seedlings grew throughout the entire year (Figure 3.3), but the growth in both the fenced and unfenced fragments slowed between January 2013 and March 2013. This period corresponded to a severe drought across northern New Zealand (see Section 2.3.4). In the unfragmented forest growth was initially more rapid than at the other sites (November 2011 to May 2012), with the fenced fragment having the lowest initial growth. The growth in the fenced fragments was more consistent over time than in the unfragmented forest and unfenced fragments (Figure 3.3).

Over the unfragmented forests, fenced and unfenced fragments the lowest height growth was recorded at the Maungatautari south, FD2 and UD1 sites, respectively (see Chapter 2, Figure 2.1). The highest total mean growth recorded in an unfenced fragment was at the UD2 site (3.5 ± 0.75 cm annual increment). There was no change in the diameter of the seedlings over the course of the study (Table 3.3). Individuals in the fenced fragments had the lowest mean height increment rates of 2.3 ± 0.3 cm per year.

A linear multi-effect (LME) model showed no significant differences (at $\alpha = 0.05$) in growth between the unfragmented forest and the fragmented sites ($F_{2,7} = 4.26$, MSE = 1.39, $p = 0.07$). Despite this result, the LME model suggested that seedlings in fragmented sites grew less than those in the unfragmented forest: 1.5 cm (log = 0.43) on average across the 29 months measurement period (Table 3.4). A second analysis did not find any significant differences (at $\alpha = 0.05$) in growth between the fenced and unfenced fragments ($F_{2,4} = 1.3$, MSE = 0.5, $p = 0.31$) (Table 3.4).

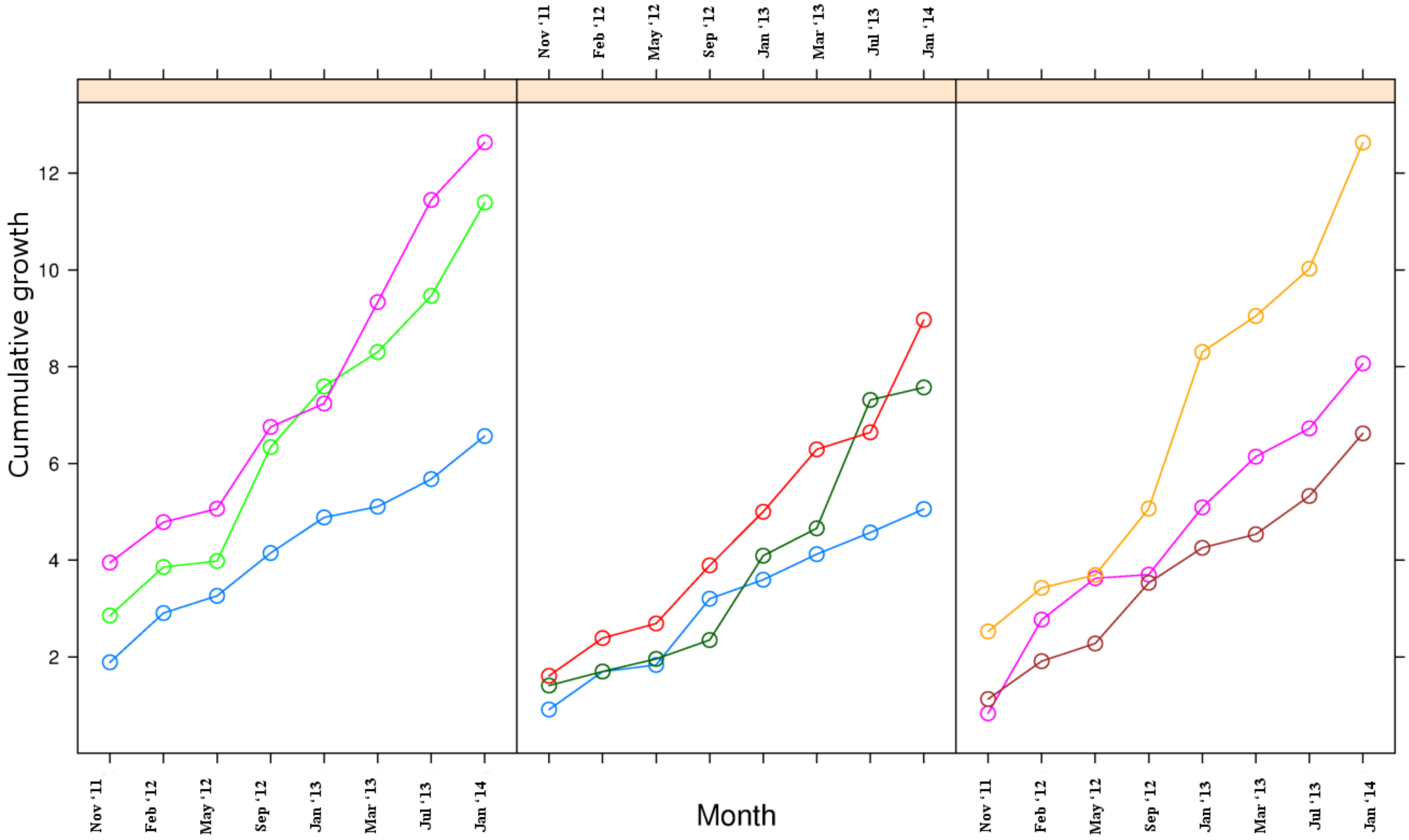


Figure 3.3 Mean cumulative growth of seedlings inside the enclosures per time and type of management. The colours denote the mean cumulative growth of the potted *B. tawa* seedlings over the three experimental areas (beneath the canopy of a mature *B. tawa*) located at each site.

Table 3.4 Fixed effect parameters in a linear mixed model of cumulative growth (cm) of *B. tawa* seedlings across three management levels. Parameters are in log units (accumulated increment in cm). Exponential of the parameter is presented for ease of interpretation. Negative values represent a decrease in cumulative growth (cm).

Model parameter	**Estimate (log)**	**Estimate (exp) (cm)**	**Standard error**	***Pr (>|t|)***
Fragmented sites (compared unfragmented forest)	-0.43	-1.5	0.19	0.07
Unfenced fragment (compared fenced fragment)	0.24	1.27	0.21	0.31

Natural Seedling Regeneration

Based on the 1 × 1 m regeneration plots the most abundant canopy tree species in the seedling bank at most of the sites was *L. novae-zelandiae*, other than at the FD1 and FD3 fenced fragments (Fig. 3.4). where, respectively, *Knightia excelsa* and *Litsea calicaris* were most abundant. In general, seedlings of *B. tawa* were present in low numbers throughout the unfragmented forest. *B. tawa* seedlings were absent from two of the fenced fragments (FD1 and FD3) and one unfenced fragment (UD2). In one fenced fragment (FD2) the density of *B. tawa* seedlings was exceptionally high (18888 ± 14369 ind/ha), as was seedling density in general in this fragment (Figure 3.4). The most abundant subcanopy species were *H. arborea* and *P. excelsum* (Figure 3.4). *H. arborea* was present at all of the sites, but in one fenced fragment (FD2) was particularly abundant (65000 ± 29627 ind/ha) (Figure 3.4). Mean survivorship of tagged natural *B. tawa* seedlings was higher in the unfragmented forest (46.6 %) than in the fragmented sites (28 %). The fenced fragments had a lower mean survivorship (24.7 %) than the unfenced fragments (31.3 %) (Table 3.5). Mean survivorship (%) was significantly different between unfragmented forest and the fragmented sites ($\chi^2 = 4.37$, $p = 0.04$). However, the effect of fencing on survival was not significant ($\chi^2 = 0.89$, $p = 0.42$).

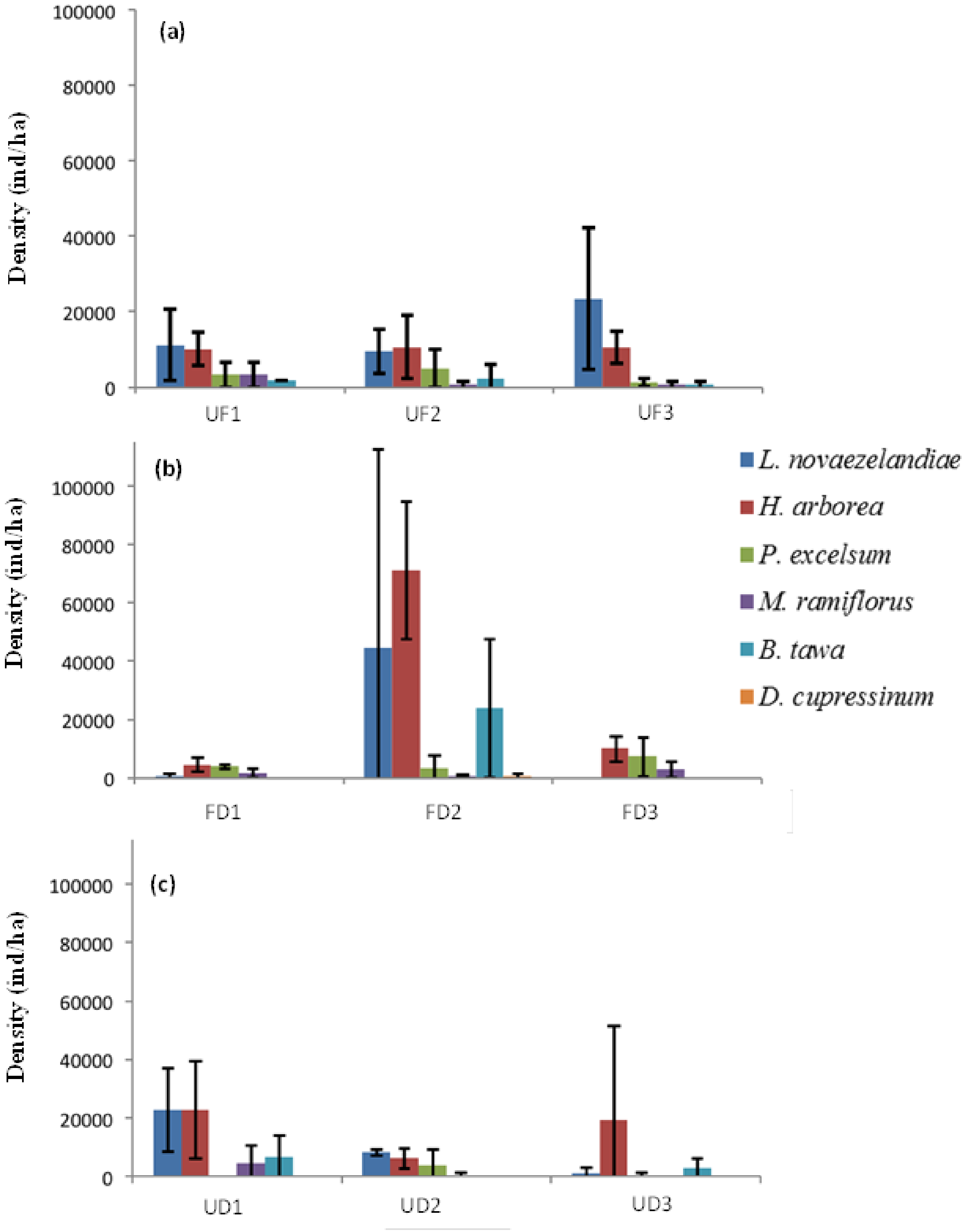


Figure 3.4 Density of seedlings (per ha) per species, site and level of management; seedlings are individuals of 5 - 50 cm height. (a) unfragmented forest sites, (b) fenced fragments and (c) unfenced fragments.

Table 3.5 Number, mean (1 ± SD) and percentage of natural seedlings by survivorship and level of management. Initial and final number corresponds to the total number of individuals in the three experimental areas per site at beginning and the end of the study. Mean survivorship is the average percentage of individuals surviving per site.

Categories	Initial N° ind	Final N° ind	Mean survivorship (%)
Forest	143	46	7.7 ± 3.8 (46.6%)
Fragmented	302	112	10 ± 7.2 (28%)
Fenced	169	55	9.2 ± 12 (24.7%)
Unfenced	133	57	9.5 ± 3.1 (31.3%)

3.3.2 Tree replacement data

Graphical analysis of the tree-by-tree replacement data suggests that the unfragmented forests have similar replacement relationships across the various functional types (tree ferns, subcanopy trees, canopy trees and *B. tawa*) as the fragmented sites (Figures 3.5a, 3.5b). However, the recruitment of tree ferns (*Cyathea dealbata*, *C. medullaris* and *Dicksonia squarrosa*) under parent tree ferns was absent from the fragmented sites. Although, the unfragmented forests and fragmented sites shared most of these replacement relationships, these relationships are weaker in the fragmented sites, meaning few individuals are recruiting (Figures 3.5a and 3.5b). The unfenced fragments had a larger number of relationships between the different functional types when compared to fenced fragments (Figures 3.5c and 3.5d). However, the relationships that exist in the fenced fragments have a higher number of recruiting individuals than in the unfenced fragment.

In unfragmented forests, the relationships between *B. tawa* recruiting under canopy trees (other than *B. tawa*) and subcanopy trees are the most important (Figure 3.4a). Even though this is the most frequently observed successional relationship, recruitment under canopy trees by other canopy trees species is also common. Subcanopy trees tend to recruit under canopy trees and, to a lesser extent under *B. tawa* trees.

The majority of the replacement pathways in the sites under other types of management (fenced and unfenced fragments) show that fewer individuals are recruiting under trees (dbh > 5) (Figures 3.5c and 3.5d). For example, recruitment of *B. tawa* under canopy trees decreases by 15 % in the fenced fragments and 17 % in the unfenced fragments, when compared to the unfragmented forest.

In the unfragmented forest the tree ferns (*Cyathea dealbata, C. medullaris* and *Dicksonia squarrosa*) are recruiting under all the functional groups but this relationship is completely absent from the fenced fragments. These results would suggest that there would be fewer or even no tree ferns present in the fenced fragments, but I found 47 tree fern individuals distributed in two of the fenced fragments (FD1 and FD3), which is comparable to the 46 tree fern individuals in the unfragmented forest over the three sites I considered.

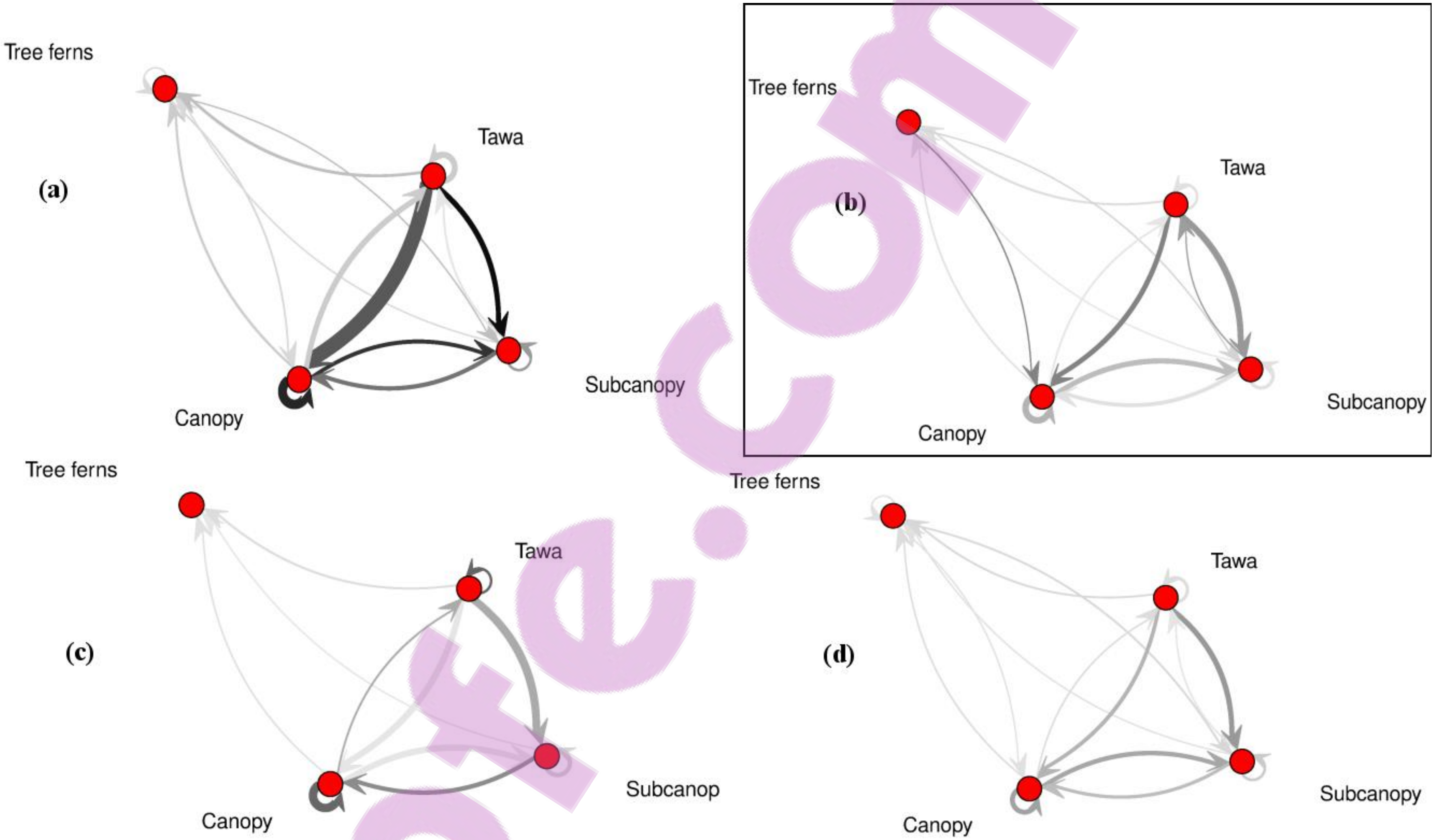


Figure 3.5 Tree replacement diagrams. (a) unfragmented forest, (b) fenced and unfenced fragment combined, (c) fenced forest fragments and (d) unfenced fragment. Arrows represent the presence of a relationship between the different groups, with the thickness and grey-scaling of the arrow indicating the relative importance of the relationship (number of times observed).

3.4 Discussion

The goal of this chapter was to determine the role of fragmentation and fencing in the survivorship of podocarp-tawa forest fragments. In particular, I wanted to determine whether fencing could help buffer the effects of recruitment problems faced by *B. tawa*.

The main factors that affected *B. tawa* seedling survivorship were desiccation and herbivory; and seedlings were more likely to die of these factors in fragments. Although I cannot be completely certain that the potted seedlings in the experimental areas died because of water stress, most of them started to die or had evidence of drought-stress after March 2013, which was just after a prolonged and intense drought period (NIWA, 2014a). This pattern suggests that protection against large herbivores (i.e. fencing) is not in itself sufficient to improve seedling survival, as water stress may have as large or even a larger negative impact than herbivory does (Table 3.2). PCA analysis of soil samples from the fragmented sites (see Chapter 2, Section 2.3.3) showed lower soil water content than in the unfragmented forests. Similarly, Zambrano et al. (2014) found that soil from forest fragments had significantly less nitrogen and water available to plants.

We did find a significant difference in the survivorship of the experimental *B. tawa* potted seedlings in the unfragmented forest when compared with fragmented sites. However, the single act of fencing fragments had no effect on survivorship. It is worth mentioning that seedlings in the unfragmented forest had a higher percentage of survival than those in the fenced forest fragments which was statistically significant, regardless of whether they were inside or outside the enclosures. The main cause of death in the fenced fragments was desiccation, which was higher than in the unfragmented forest or unfenced fragment. We would have expected to find evidence of lower desiccation mortality in the fenced fragments as I found evidence of a potential climate buffering effect of fencing in the analyses from Chapter 2 (Section 2.3.4).

Rates of death by desiccation in the unfragmented forest were lower than the unfenced fragments. The fact that survivorship was lower in the fenced fragments contradicts my initial expectation that seedlings in a fenced fragment would experience similar survival rates to those in unfragmented forest. On the other hand, the experimental enclosures did make a difference to the survival of the potted seedlings in the unfenced forest fragments where survivorship of seedlings outside the enclosures was greatly reduced due to herbivory, mainly by cows and rabbits. This was an expected result in an unfenced fragment. Burns et al. (2012) and Smale et al. (2005) suggest that pest-proof fencing can isolate ecosystems from exotic pests and allow landowners to make significant conservation gains.

Our data suggest that in terms of improving *B. tawa* seedling survival odds, unfragmented forests represent the ‘best’ management strategy and that fencing alone, without considering other abiotic stresses such as dehydration, may not suffice. The LME showed that *B. tawa* seedlings had a higher growth rate in the unfragmented forest in comparison with the fragmented sites, however these results were only marginally significant. Fencing did not have an effect on growth in comparison with the unfenced fragments (Table 3.4). In addition the potted *B. tawa* seedlings in the unfragmented forest grew faster than those in the other types of management (Table 3.3 and Figure 3.3).

However, at one unfenced site, UD2, seedlings grew at the same rate as in the unfragmented forest. This similarity in growth could be due to a variety of factors, including the local geography. The unfenced UD2 site was a natural gully formed by running water, which, in addition, provided some protection from wind exposure. Wind exposure was a difficult factor to control for, and although not always possible I strived to place all experimental areas as far from the edges of the fragments as possible. Also, due to the small size of the fragment, enclosures had to be placed near the centre of the fragment, i.e. near the gully and source of water. These seedlings were likely exposed to higher humidity due to these topographic effects. Unfortunately, the humidity data of this site was incomplete due to the loss of the sensors and I could not analyse this further.

In some, but certainly not all, fenced fragments naturally established seedlings, including *B. tawa, L. novae-zelandiae* and *D. cupressinum* seedlings were present in low numbers (Figure 3.4). In a similar study Burns et al. (2011) also found low numbers of *B. tawa* and *L. novae-zelandiae* in fenced fragments. Thus, the results obtained from the fenced fragments suggest that they are more similar to unfenced fragments than was initially expected. It is interesting to note, however, that at least one fenced site had very high numbers of seedlings of these late-successional species. The FD2 fenced fragment contained a relatively high number of *B. tawa* and *L. novae-zelandiae* seedlings, 23888 and 44444 individuals per ha, respectively. These high densities may indicate that factors other than the fencing itself may be at play, in contrast to what Smale et al. (2005) found for *Dacrycarpus dacrydioides* (kahikatea) forests where fencing itself was enough to increase the density of native species. Burns et al. (2011) suggested that a site's history can be just as important or even more so, than protection against large herbivores, and the inconsistent response of fragments to fencing that I observed also suggests that site-level effects and contingencies are important.

While regeneration plots did not detect the presence of *B. tawa* in all the sites, seedling presence/absence data from PCQ plots from Chapter 2 (Section 2.3.1) showed that *B. tawa* was present in all types of management (unfragmented forest, fenced fragments and unfenced fragments). This discrepancy is expected as, when species densities are too low, abundance methods (regeneration plots) may not detect them (Joseph et al. 2006). Basically PCQ plots covered a bigger overall area, at a lower resolution, than the regeneration plots and the chances of detecting any one individual were higher. When I started this study I did not have any *a priori* information to guide the study design so I decided to apply both methods to detect the presence of the different species, especially *B. tawa.* In summary, the species that were not detected in the regeneration plots were not present or were present in low densities and were detected by the PCQ plots.

Survivorship of tagged natural seedlings was higher in the unfragmented forest than in the fragmented sites, which is consistent with the potted seedling survivorship results. In the fenced fragments survivorship was lower than in the unfenced fragments. However, the fenced fragments had the highest number of tagged individuals (169 ind. in total) in comparison with the unfragmented forest (143 ind. in total) and unfenced fragment (133 ind. in total), and all those seedlings came from the same fenced site (FD2) that had high numbers of other canopy species seedlings too (i.e. *L. novae-zelandiae*) (Figure 3.4).

Tree replacement data showed that most of the successional relationships between the functional types are present in the unfragmented forest and in the fragmented sites. However the relationships in the fragmented sites are weaker than in the unfragmented forest. In the fenced fragments some relationships are missing in comparison with the unfenced fragment. Even though fencing is not helping to improve the relationships among the different functional types (tree ferns, subcanopy trees, canopy trees and *B. tawa*) it is helping to improve the ones that are present when compared with the unfenced fragments. For example, the relationship that exists between *B tawa* recruitment and the parent trees and subcanopy trees is stronger in the fenced than in the unfenced fragments.

Based on the tree replacement data, it seems that canopy species and *B. tawa* will continue to dominate in the unfragmented forest. In the fragmented sites, dominance of canopy species and *B. tawa* will decrease; potentially favouring subcanopy species and tree ferns. In the fenced fragments canopy species will still dominate but *B. tawa* will become less prevalent; subcanopy trees will become more prevalent. In the unfenced fragment all canopy species, *B. tawa* and subcanopy species will become less prevalent potentially due the effect of herbivory.

In chapter 2 I discussed that the major caveat of this study was the low number of replication ($n = 3$). In addition to the reasons argued in the previous chapter (e.g. lack of suitable sites), we also faced logistical problems. Distributing more seedlings among more sites would have required more human resources than were available. Furthermore, it proved very difficult to procure a higher number of seedlings and the experiment as conducted involved purchasing the entire production of the only nursery that had sufficient seedlings to fulfil the specifications outlined for this experiment (e.g. age). Despite these limitations, I believe that the significant effects that I found in terms of survivorship showed that that effect was strong even with a small number of samples. In the case of *B. tawa* seedlings growth among the different management types had a marginal effect ($p = 0.07$) that would probably strengthen with a higher level of replication. In short, I believe that despite the small number of replications my results showed some trends that can help to better understand the factors affecting recruitment in forest fragments.

In conclusion, fragmentation appears to have a negative effect on survivorship, growth of potted *B. tawa* and on survivorship of natural *B. tawa* seedlings. In general, my results show that fencing does not appear to be an overwhelmingly important factor in survivorship and growth of *B. tawa*, although fencing did improve the abundance of seedlings of some species in some cases (FD2 site). Also, the potential climate buffer effect that was described in Chapter 2 seems to have little effect on the survivorship of *B. tawa*, especially under stressful conditions (i.e. drought). Clearly, the most important effect of fencing was diminishing herbivory by large mammals. As suggested by Burns et al. (2011) and Ewers (2006), and discussed in Chapter 2, it seems that the past history and the particular circumstances of each fragment are as important as fencing itself. We recommend future studies to research the importance of the past history and the current state of the fragments.

4. IS THE LACK OF RECRUITMENT OF *BEILSCHMIEDIA TAWA* CAUSED BY AUTOTOXICITY?

4.1 Introduction

Plants produce a large number of secondary chemical compounds that are not part of their primary physiological processes. Some of these compounds have inhibitory or stimulatory effects and may have significant effects on both conspecific and heterospecific individuals. As such chemical compounds do not target specific species; they could also have a negative effect on individuals of the same species, particularly on their growth, a process called autotoxicity (Friedman and Waller 1985, Inderjit and Weiner 2001, Fernandez et al. 2008).

Many studies have considered this sometimes dramatic allelopathic effect across a wide range of species (Rice 1995, Cummings et al. 2012). Studies on *Beilschmiedia* Lauraceae have identified several allelopathic compounds, but fewer than 5 % of the species in this genus have been assessed for the presence of potentially allelopathic chemical compounds (Banfield et al. 1994, Chouna 2009, Chaverri and Ciccio 2010). A suite of phytochemicals such as bio-active lignans, flavonoids, triterpenoids, tetracyclic endiandric acids and alkaloids have been reported in *B. miersii*, *B. elliptica*, *B. oligandra*; many of these compounds are known to have allelopathic properties (Banfield et al. 1994, Chouna 2009, Chaverri and Ciccio 2010).

In New Zealand, few studies have dealt with allelopathy in native species and most of them are more than 20 years old (e.g. June 1976, Froude 1980, Wyse and Burns 2013). Russell and Fraser (1969) found alkaloids in *B. tawa* fruits. Cambie et al. (1961) did not find any alkaloids in the leaves, wood or bark of *B. tawa*, but found leucoanthocyanins in the leaves. Leucoanthocyanins or proanthocyanidins have been described as germination and growth inhibitors in some plant species (e.g. *Prunus armeniaca*) (Rawat et al. 1998). One of the most important attempts to determine allelopathic interactions in New Zealand is that of Froude (1980) who studied the potential allelopathic effect of 36 plant species, including *B. tawa*. Froude (1980) determined that *B. tawa* had a moderate inhibitory effect in cress (*Lepidium sativum*) and *Weinmania racemosa* radicle growth.

B. tawa is affected by a lack of recruitment in many areas across New Zealand (Burns et al. 2011). As a New Zealand endemic species, this regeneration failure is cause for concern. In sites impacted by introduced mammals germination rates are poor as low as 4 % (Knowles and Beveridge 1982), and germination rates are low even when herbivores are excluded; on the other hand in virgin forest mass germination has been reported (Knowles and Beveridge 1982). West (1986) reported that the density of tawa seedlings is higher in previously logged sites than in virgin forest. These observations suggest that there may be a range of factors that could be responsible for the low germination rates observed in fragmented sites. In fragmented forests, edge effects could potentially alter conditions such as air temperature and soil moisture that can cause stress in plants (Young and Mitchell 1994, Hobbs and Yates 2003; See chapter 2). Nowadays, the main biotic factors affecting podocarp-tawa forest are the pressure exerted by exotic seed and seedling predators such as deer and possums, and the reduced seed dispersal services provided by the native wood pigeon (*Hemiphaga novaeseelandiae*) (Knowles and Beveridge 1982, Mander et al. 1998, Burns et al. 2011). *H. novaeseelandiae* plays an important role in *B. tawa* regeneration as it provides long distance dispersal and seeds that pass through its digestive system germinate at a faster rate (West 1986, Burrows 1999, Robertson et al. 2006). This means that having the mesocarp removed could have an impact in germination and growth of new seedlings.

Under stressful conditions such as those seen in fragments, chemical inhibition (allelopathy) can play an important role in plant community dynamics (Anaya 1999). Muller (1969) suggests that chemical inhibition is strongly influenced by the physical (e.g. soil type) and/or biotic (e.g. herbivory) environment, a theory that is supported by many other authors (e.g. Gawronska and Golisz 2006 and references therein). Einhellig (1987) suggests that plants growing in stressful environments with non-optimal soil nutrient, moisture and temperature conditions are more likely to be affected by allelopathical chemicals than plants growing in optimal conditions.

I performed a preliminary study on a sensitive species to answer,

- Is there any effect of *B. tawa* leaves on germination and growth on lettuce (*Lactuca sativa*)?

And as allelopathic compounds can leach into the soil,

- Could soil from different sites under different types of have an effect on germination and growth of *L. sativa*?

And if there is a negative effect on this sensitive species (*L. sativa*),

- Could leachate from the leaves of *B. tawa* have a significant allelopathic effect on the germination and growth of *B. tawa*?

And if the mesocarp removal of *B. tawa* seeds,

- Could it have an effect on germination and potentially on *B. tawa* seedlings growth?

4.2 Methods

4.2.1 Leachate experiments on *L. sativa* seeds

To determine the potential allelopathic effects of *B. tawa* leaves on germination, I used a randomised design with three leachate treatments and one control with three replicates per treatment (*n* = 12). *B. tawa* leaves were collected randomly from different individuals from the Te Miro Scenic Reserve, Waikato region (37º47'35" S, 175º33'15"). We chopped up 20 grams of dried *B. tawa* leaves and left them to macerate in distilled water for 24 hours at room temperature. We then prepared three different concentrations of this leachate: a) 1:1 (dis1:1), b) 1:20 (dis1:20) and c) 1:50 (dis1:50). We used distilled water as a control. The experiment was repeated twice.

We randomly assigned each treatment to one of 12 petri dishes lined with filter paper. We placed 60 *L. sativa* seeds in each dish. I chose to use *L. sativa* as the trial species because it is frequently used as a bio-indicator and as a monitor of contamination (Charles et al. 2011). All of the seeds were part of the same lot with a germination rate of 99% (Yates Seeds ®, pers. comm.). Seeds were given water from the assigned treatment every 24 hours. The petri dishes were placed under a 12-hour light cycle for 10 days (first experiment) or seven days (second experiment; shorter time due to faster sprout growth) and were monitored daily. At the completion of the experiment I randomly selected 30 sprouts from each petri dish, and measured the length of their hypocotyls and radicles.

4.2.2 Soil experiment on *L. sativa* seeds

To determine if the allelopathic chemicals present in the *B. tawa* leaves can influence soil properties I collected soil from three different sites under varying levels of management: unfragmented forest, fenced and unfenced forest fragments (Chapter 2). Te Miro Reserve and

Maungatautari Ecological Island (north and south enclosures) were considered an unfragmented forest; fenced and unfenced sites were forest remnants surrounded by pastureland (e.g. cattle, sheep). The fencing consisted of barbed wire, installed at least 20 years ago, to remove the impact of large mammals such as cattle and horses. These sites all also had some form of pest control for smaller mammals such as rats and possums, mainly baiting with poison.

We used a randomised design with three treatments and nine replicates per treatment (*n* = 27) plus a control replicated three times. We collected three soil samples from nine sites under different levels of management (fencing and pest control) where *B. tawa* was present (*n* = 27; Table 4.1). The soil samples were classified as coming from the unfragmented forest, fenced fragments and unfenced fragments. Soil samples coming from the same site were mixed into one sample. A seed raising mix (Yates®) was used as a control. Seeds were watered with distilled water every 24 hours or when the soil was dry. As the pH of the soil samples was too low (pH = 3.6 - 5.9) for *L. sativa* to grow I mixed the soil with lime (1:2) to raise the pH to an optimal range (pH = 6.0 - 7.0; Table 4.2) following Wyse and Burns (2013).

Soil chemical analyses were performed to discard differences within the sites. Levels of nitrogen and carbon were estimated using the dry combustion method (Bisutti et al. 2004) with an elemental analyzer (LECO TRUSPEC CN, St. Joseph, MI, US). We used the Bray and Kurtz N°1 method as an index of available phosphorus (Bray and Kurtz 1945). The pH of the soil was measured in a supernatant liquid with a digital pH meter (Kalra and Maynard 1991). The water content was estimated using the gravimetric method (Kalra and Maynard 1991). Bulk density was calculated by weighing dry soil divided by the total soil volume.

Table 4.1 Locations of sites where soils samples were taken, ordered by treatment and area.

Treatment	**Site name**	**Location**	**Area (ha)**
Fenced	FD1	37°47'47"S, 175°34'13"E	8
	FD2	38° 3'35"S, 175°32'12"E	5
	FD3	37°59'60" S, 175°32'53" E	2
Unfenced	UD1	38° 3'30"S, 175°33'46"E	5
	UD2	37°47'46" S, 175°34'17" E	2
	UD3	37°59'58"S, 175°32'47"E	2
Unfragmented forest	UF1	37º47'35" S, 175º33'15" E	>350
	UF2	38° 0'19"S, 175°34'38"E	>700
	UF3	38° 3'13"S, 175°34'0.62"E	>700

Table 4.2 pH values for soil without and with lime used in the germination and growth trials by treatment and site. Results are from a composite sample using three samples per site.

Treatment	Site name	Soil (pH)	Soil + lime (pH)
Fenced	FD1	5.2	6.5
	FD2	5.1	6.5
	FD3	4.8	6.7
Unfenced	UD1	4.8	6.4
	UD2	5.7	7.5
	UD3	4.9	6.7
Unfragmented forest	UF1	3.4	6.2
	UF2	4.6	6.2
	UF3	3.7	6.1

Each soil treatment was assigned to a petri dish and replicated nine times. We used 10 g of soil in each of the petri dishes. We placed 30 *L. sativa* seeds in each dish. The seed lot had a 99 % germination rate (Yates Seeds ®, pers. comm.). The dishes were checked every 24 hours and watered as necessary. The petri dishes were placed under a 12-hour light cycle for seven days. The experiment was visually inspected every day. At the end of the experiment I randomly selected 15 sprouts from each petri dish, and measured the hypocotyls and radicle length of the sprouts.

4.2.3 Leachate experiments on *B. tawa* seeds

Leachate preparation

B. tawa leaves were collected at random from different trees in the Te Miro Scenic Reserve, Waikato region (37º47'35" S, 175º33'15"). We chopped up 100 grams of dried *B. tawa* leaves and left them to macerate in 1 L of distilled water for 24 hours at room temperature. We then prepared two different concentrations of this leachate: a) 1:1 and b) 1:50. We used distilled water to dilute the leachates to the appropriate concentration. Distilled water was used as a control treatment.

Seed collection and viability

Our main collection site for *B. tawa* seeds was the Pureroa Forest Park *(*38º30'57" S, 175º33'35" E) where I collected approximately 220 *B. tawa* seeds during the first week of May 2012. Tawa failed to produce seeds in northern New Zealand during the summers of 2011 and 2012 making the collection process difficult. I visited a number of sites, including Maungatautari ecological reserve, in the Waikato region, but there were no seeds for collection.

Seeds with heavy fungal attack or with evident insect attack were purged. The remaining c. 200 seeds were mixed and 56 seeds were randomly selected (approximately 28% of the seeds) to perform a viability test using the cutting test. This method was preferred over the tretrazolium test because of its simplicity and immediate results (Ooi et al. 2004). As fleshy seeds tend to loose viability quickly and as I did not know how long the seeds had been on the ground at the time of collection, I processed them all within 24 hours of collection. The seeds were recorded as viable if firm, moist and white-yellow endosperm was present. Dry, black/dark brown or “squishy” seeds were recorded as unviable (following Ooi et al. 2004). Furthermore, seeds with evident brown/black holes were categorized as having suffered “insect attack” and were discarded because of the probability that the insect continued to feed from the cotyledon, thus making the seed unviable.

Experimental design

To determine the potential allelopathic effects of *B. tawa* leaves on germination, eight seeds with mesocarp were randomly chosen and put into a seed tray. As mentioned in Chapter 1, the kererū (*Hemiphaga novaeseelandiae*) is a common disperser of *B. tawa* seeds (Campbell and Atkinson 2002). In order to simulate passage through the pigeon’s digestive tract, an additional eight seeds were randomly chosen and the mesocarp was removed before they were put into a seed tray. The seeds were placed in seed trays with a seed raising mix. We randomly assigned a leachate treatment (control, 1:50, 1:1) to each seed tray. Each of the treatments was replicated three times. Over the first three weeks all the seeds were watered with filtered water to avoid initial stress. Then, seeds were watered with the assigned treatment every four days or if the soil was dry. After 30 days I started to water them only once a week. Every time I watered the seeds I recorded whether or not germination had occurred. Germination was deemed to have occurred on plumule emergence. At the completion of the experiment all the seeds that did not germinate were dissected and the hypocotyl and radicle length of all seedlings measured.

4.2.4 Data Analysis

Leachate experiment on *L. sativa* seeds

Because the leachate and soil experiment data were not normally distributed I used non-parametric statistics in all analyses. Kruskal-Wallis rank sum tests were used to evaluate differences among the different treatments (1:1, 1:20, 1:50, and control) on median change in hypocotyls and radicle length, with an *a posteriori* Conover-Iman test using the package "*agricolae*" (de Mendiburu 2012) in R-2.15.1 *(*R Core Team, 2010). The same analyses were used to evaluate differences among the soil treatments on median change in germination.

Because of the small sample size the results from the soil analysis (nitrogen, carbon, phosphorus, water content, bulk density and pH) were analyzed using a Friedman test based on 9999 Monte-Carlo resamplings to evaluate differences among the different treatments (forest, unfenced, fenced). For this analysis I used the package "*coin*" (Hothorn et al. 2008) in *R-2.15.1 (*R Core Team 2010).

Statistical analysis leachate experiment on *B. tawa* seeds

The percentage of the total number of seeds (Gt) corresponding to each treatment (leachate plus seed treatment), which germinated during the experiment, was calculated (the experiment lasted 153 days). Gt (percentage) was calculated as the number of germinated seeds divided by the total initial number of seeds with no evidence of insect attack after been dissected. Gt was computed only for exploratory purposes, and no statistical analyses were performed on it. A germination speed index (S) was calculated following Chiapusio et al. (1997):

$$S = (N_1 * 1) + (N_2 - N_1)\frac{1}{2} + (N_3 - N_2)\frac{1}{3} + \cdots + (N_n - N_{n-1})\frac{1}{n} \tag{4.1}$$

$N_1, N_2 N_3, .., N_n$, are the proportion of germinated seeds obtained the first (1), second (2), third (3),…, (n-1), (n) days or hours.

We chose the S index, as it is the preferred method used in allelopathy germination trials

(Wardle et al. 1991, Haugland and Brandsaeter 1996, Chiapusio et al. 1997, Ranal and Santana 2006). A Shapiro-Wilk test of normality was performed on the S index. The test was not significant so I assumed normality of the data. A two-way ANOVA was used to evaluate the effect of two factors (leachate and seed treatment) on the germination speed indexes, with a *post hoc* pairwise comparison of treatment group means using Tukey's HSD. The analysis was carried out using the package *"stats"* (R Core Team 2010) and "*agricolae*" (de Mendiburu 2012) in *R-2.15.1* (R Core Team 2010).

For hypocotyl and radicle length, I used non-parametric statistics in all analyses, as the data were not normally distributed. It was decided not to consider the mesocarp treatment in the analysis, as *a priori* exploratory analysis of the data (using a boxplot) suggested that this treatment did not have any effect in the hypocotyl or radicle length. I used the same statistical test as for the leachate and soil experiment data to evaluate differences among the different treatments (1:1, 1:50, and control) on median change in hypocotyls and radicle length.

4.3 Results

4.3.1 Leachate experiments on *L. sativa* seeds

In the first experiment the seeds started to germinate after five days. The final germination rate for the control, dis1:50 and dis1:20 ranged between 99% and 100%. The final percentage of germination for the dis1:1 was 79%. A Kruskal-Wallis test showed significant differences in germination between the treatments ($\chi^2 = 9.3$, df = 3, $p < 0.02$). A *post hoc* pairwise test using a Conover-Inman test with Holm correction indicated significant differences between the dis1:1 treatment and all other treatments (Table 4.3). When the experiment was repeated the seeds germinated faster than in the first experiment (after two days) and no difference in germination across treatments could be discerned. The final germination percentage across all treatments was similar to that seen in first experiment (99 – 100 %).

Table 4.3 Inhibitory effect of different concentrations of *B. tawa* leachate on seed germination of *L. sativa*. [1]Mean of the ranks not sharing the same letter are significantly different ($p < 0.05$).

Treatment	Ranks mean[1]	Means
Control	8.5 ^{a}	60
dis 1:50	7 ^{a}	59.6
dis 1:20	8.5 ^{a}	60
dis 1:1	2 ^{b}	47.6

The first time I carried out the experiment, hypocotyl and radicle length were significantly different between treatments (hypocotyl: χ^2 = 8.95, df = 3, p = 0.02; and radicle length: χ^2 = 8.4, df = 3, p = 0.03; Figure 4.1). The second time the experiment was carried out hypocotyl and radicle length were again significantly different between treatments, although the results were slightly weaker for radicle length (hypocotyl length: χ^2 = 8.43, df = 3, $p < 0.03$; radicle length: χ^2= 6.4, df = 3, $p < 0.09$; Figure 4.1).

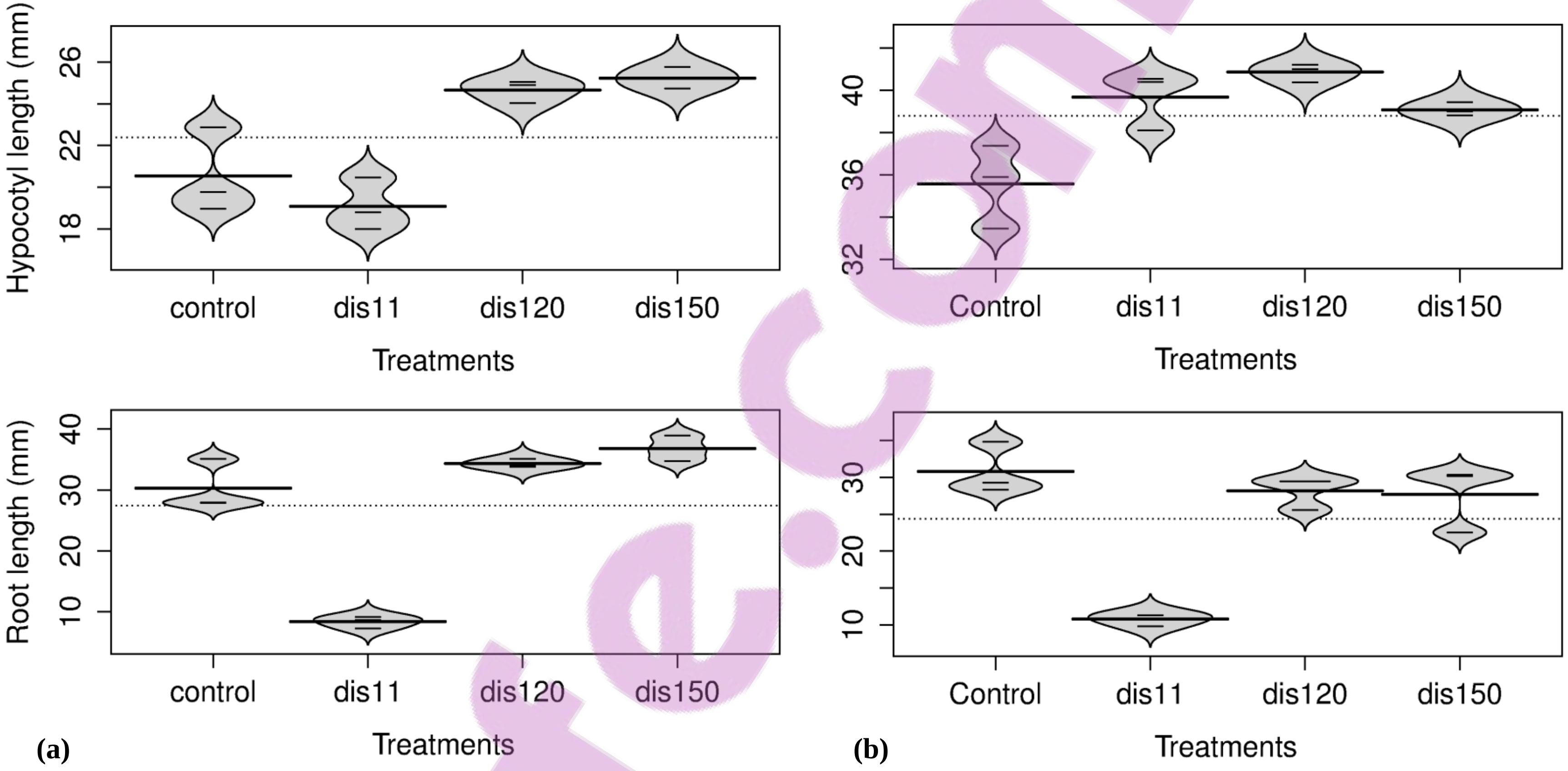


Figure 4.1 Effect of different *B. tawa* leachate concentrations in hypocotyl and radicle lengths (mm) of *L. sativa*, (a) for the first time the experiment was carried out and (b) for the second time the experiment was carried out. Dashed lines represent the mean for all four treatments. The small lines in the beans represent each sample mean. The thick black line in the middle of the bean represents the mean for that particular treatment. dis11, dis120 and dis150 correspond to different concentrations of *B. tawa* leachate 1:1, 1:20 and 1:50, respectively.

In both trials there were significant differences in hypocotyl length between the control and the 1:20 and 1:50 treatments (*post hoc* pairwise tests using a Conover-Iman test with Holm correction). Only in the second trial did I find differences between the control and the 1:1 treatment. The first time I performed the experiment I found significant differences between the 1:1 treatment and the 1:20 and 1:50 treatments. The second time the experiment was run I did not find these differences (Table 4.4). For radicle lengths, I found differences between the 1:1 and the 1:20, 1:50 and control treatment in both experiments (Table 4.4). A significant difference between the control and the 1:50 treatment was only evident the first time I ran the experiment.

Table 4.4 Inhibitory effect of different concentrations of *B. tawa* leachate on hypocotyl and radicle lengths of *L. sativa*; (a) first and (b) second experiment [1]Mean of the ranks not sharing the same letter are significantly different ($p < 0.05$).

(a)

Hypocotyls		**Radicles**	
Treatment	**Ranks mean[1]**	**Treatment**	**Ranks mean[1]**
dis150	10.3 ^{a}	dis150	10.3 ^{a}
dis120	8.7 ^{a}	dis120	7.7 $^{a\ b}$
Control	4.3 ^{b}	Control	6 ^{b}
dis11	2.7 ^{b}	dis11	2 ^{c}

Table 4.4 **(continued)** Inhibitory effect of different concentrations of *B. tawa* leachate on hypocotyl and radicle lengths of *L. sativa*; (a) first and (b) second experiment. ^{1}Mean of the ranks not sharing the same letter are significantly different *($p < 0.05$).*

(b)

Hypocotyls		**Radicles**	
Treatment	**Ranks mean^{1}**	**Treatment**	**Ranks mean^{1}**
dis150	6 ^{b}	dis150	8.3 ^{a}
dis120	10.3 ^{a}	dis120	7.3 ^{a}
Control	2 ^{c}	Control	8.3 ^{a}
dis11	7.6 $^{a\,b}$	dis11	2 ^{b}

4.3.2 Soil experiments on *L. sativa* seeds

After one day the lettuce seeds started to germinate. The percentages of germination for the control, natural forest, fenced and unfenced varied between 96% and 99%. A Kruskal-Wallis test showed no significant differences in germination between the soil treatments (χ^2= 5.9, df = 3, p = 0.11).

A Kruskal-Wallis test found significant differences in hypocotyl length (hypocotyl length: χ^2 = 8.3, df = 3, p = 0.04) (Figure 4.2), but not in radicle length (χ^2 = 6.4, df = 3, p < 0.1) (Figure 4.2). A *post hoc* paired comparison test for hypocotyl length using a Conover-Inman test with Holm correction showed significant differences between the control and the forest and the fenced treatment. There were no differences between the different sites (Table 4.5).

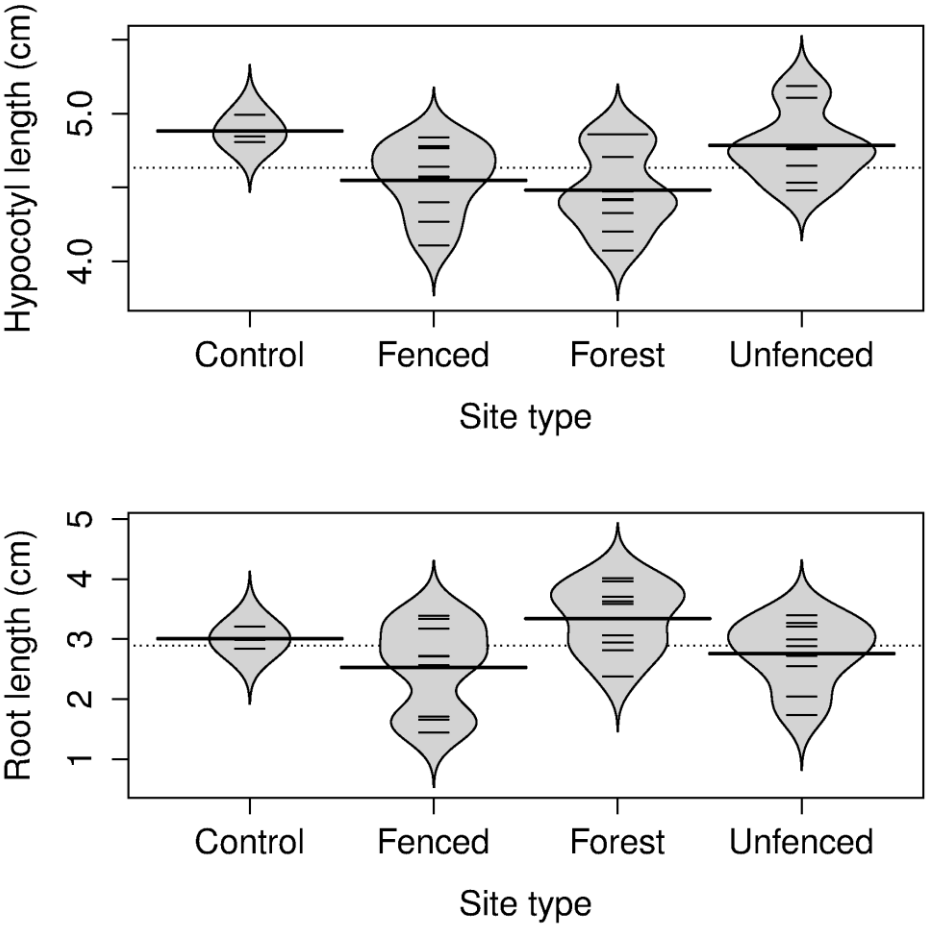


Figure 4.2 Effect of soils from different management levels on *L. sativa* hypocotyl and radicle length (cm).

Table 4.5 Effect of soil from sites with different levels of management on *hypocotyl of L. sativa*. [1]Mean of the ranks not sharing the same letter are significantly different *(hypocotyl: $p < 0.05$)*

Hypocotyls		
Treatment	**Ranks mean[1]**	**Mean**
Control	25.3 ^{a}	4.88
Unfenced	19.2 $^{a\ b}$	4.78
Fenced	12.7 ^{b}	4.54
Unfragmented forest	11.3 ^{b}	4.48

Soil analysis

We statically analyzed the soil nutrient data described in Chapter 2 (Section 2.2.2). We did not find any significant difference in nutrient conditions between the soil samples from the different sites, but I present them here as a general guide to the differences between them (Table 4.6, Figure 4.3). Nitrogen levels are similar between unfragmented forest and fenced fragments; except for one sample, the unfenced sites all had lower levels of nitrogen. The same general pattern could be observed in soil carbon levels. However, phosphorus tended to be lower than nitrogen and carbon in most sites except for one sample each in the fenced and the unfenced fragments. Soil water content is higher in most of the unfragmented forest sites. Bulk density is lower in the unfragmented forest but higher in most of the fenced fragments. Also, bulk density in unfenced fragments levels are in the middle between unfragmented forest and fenced fragments. In general, pH values are higher in the unfenced fragment except for one sample. The lowest pH values were found in the unfragmented forest. The pH values in the fenced fragments are very consistent among them and closer to the unfragmented forest than the unfenced fragments.

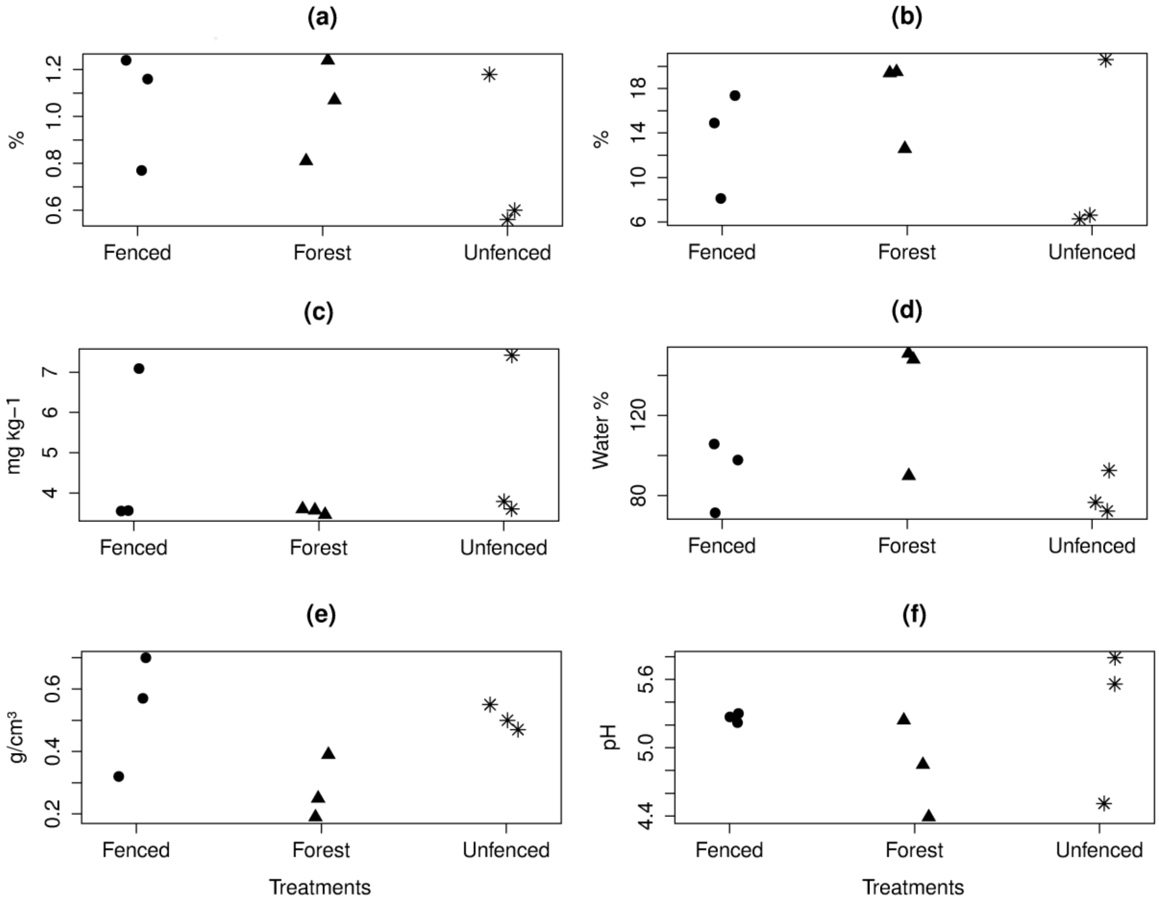


Figure 4.3 Soil properties across the study sites: (a) nitrogen, (b) carbon, (c) phosphorus, (d) water content, (e) bulk density and (f) pH. Forest, fenced and unfenced refers to different levels of management.

Table 4.6 Soil characteristics across the three site types; values represent the mean plus standard deviation (SD) of three independent samples from the nine different sites per level of management.

Site	Nitrogen (%)	Carbon (%)	P in soil (mg kg-1)	Water % by mass	Bulk density	pH
Fenced	1.1 ± 0.25	13.5 ± 4.80	4.7 ± 2.04	91.7 ± 17.92	0.53 ± 0.19	5.3 ± 0.1
Unfenced	0.78 ± 0.35	11.2 ± 8.18	4.9 ± 2.15	80.6 ± 10.64	0.51 ± 0.04	5.3 ± 0.7
Unfragmented forest	1.04 ± 0.22	17.2 ± 3.96	3.5 ± 0.07	129.6 ± 34.4	0.28 ± 0.11	4.8 ± 0.4

4.3.3 Leachate experiments on *B. tawa* seeds

Viability test

61 % of the seeds were viable, 32 % had suffered insect attack and 7 % were unviable.

Germination

The first tawa germination occurred after 45 days. At the end of 153 days, of a total of 144 seeds planted, 83 seeds had germinated (57.6%), 33 were attacked by insects (22.9%) and 28 had failed to germinate (19.4%). The causal insect was captured and identified as a tortricid moth *Cryptaspasma querula*. The larvae of this moth are described as feeding on fresh cotyledons of *B. tawa* by Beveridge (1964) and Knowles and Beveridge (1982). The Gt was 37 % and 61 % for the treatment leachate 1:1 with and without mesocarp, respectively. The Gt for the treatment leachate 1:50 with mesocarp was 82 % and 73 % without it. For the control the Gt was 63 % with mesocarp and 50 % without mesocarp (Figure 4.4).

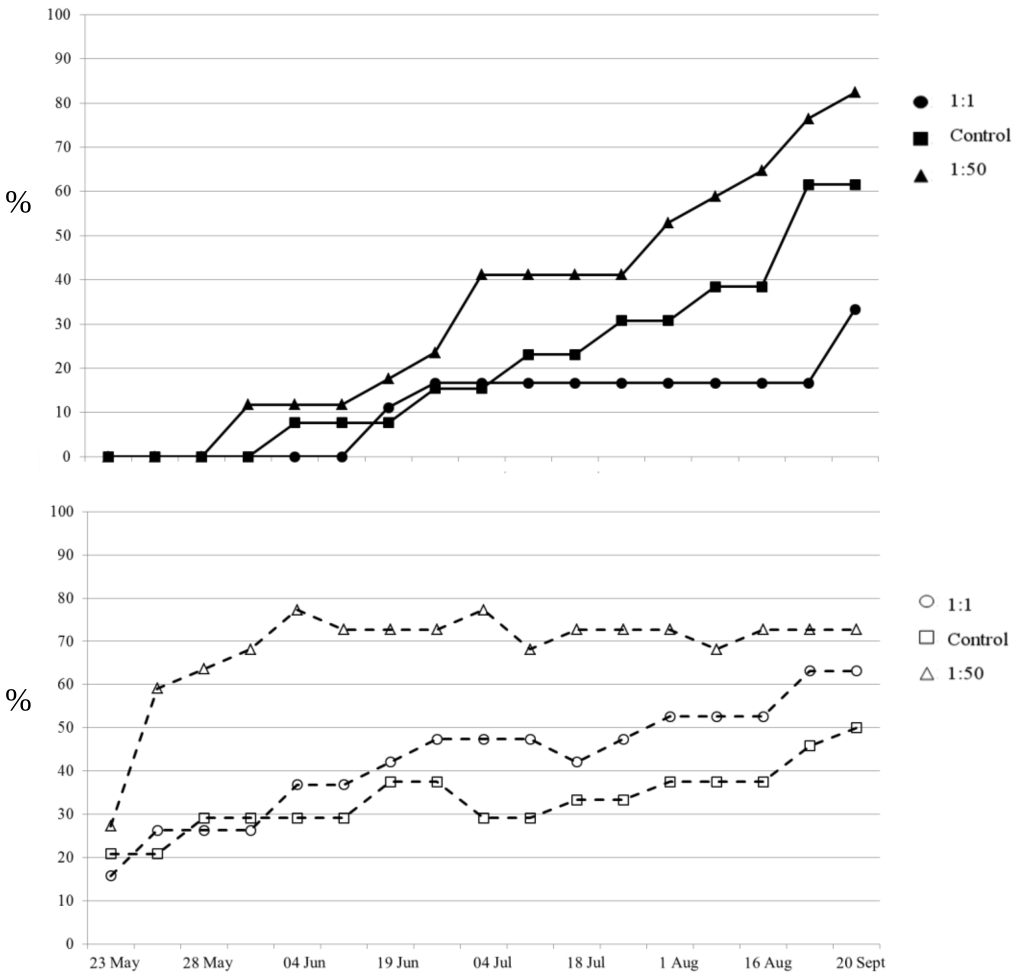


Figure 4.4 Percentage of seed germinated under the different treatments. The dashed line represents the no mesocarp treatment and the solid line represents the mesocarp treatment.

A two-way ANOVA test conducted on the germination speed index (S) data, showed that the main effect of leachate was significant, $F_{2,12}$ = 5.42, MSE = 0.50, p = 0.02, η^2=0.30 with CI = [0.007,0.62], as was the main effect of seed treatment, $F_{1,12}$ = 10.67, MSE = 1.00, p = 0.006, η^2 = 0.29 with CI = [0.04,0.63] . The interaction of these two factors was not significant $F_{2,12}$ = 1.09, MSE = 0.10, p = 0.36. A *post hoc* paired comparison test using Tukey's HSD for different leachate concentration showed that there were significant differences between the 1:50 and the rest of the treatments (control and 1:1). All other comparisons were not significant. For the seed treatment there were significant differences between the mesocarp and without mesocarp treatment (Figure 4.5, Table 4.7).

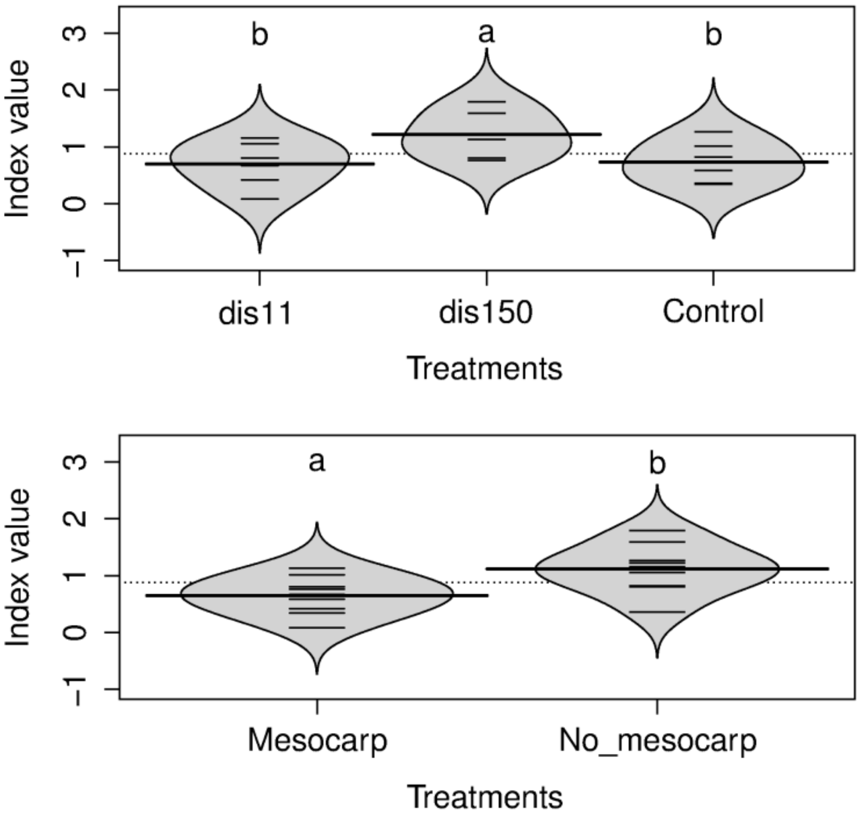


Figure 4.5 Effect of different *B. tawa* leachate concentrations and seed treatment on germination index (S). Letters represents a *post hoc* pairwise comparison of treatment group means leachate and seed treatment using Tukey's HSD. Means not sharing the same letter are significantly different.

Table 4.7 *Post hoc* pairwise comparison of treatment group means (a) leachate and (b) seed treatment using Tukey's HSD, $p < 0.05$. [1] Means not sharing the same letter are significantly different.

a)

Treatment	**Mean**[1]
dis1:50	1.21^{a}
Control	0.73^{b}
dis1:1	0.69^{b}

(b)

Treatment	**Mean**
Mesocarp	1.21^{a}
No mesocarp	0.73^{b}

Hypocotyl and radicle

Hypocotyl and radicle length were significantly different between leachate treatments (hypocotyl: $\chi^2 = 5.63$, df = 2, $p = 0.059$; and radicle length: $\chi^2 = 6.06$, $df = 2$, $p = 0.04$) (Figure 4.6). The boxplot showed evidence of a difference that could be small but significant. A *post hoc* pairwise test using a Conover-Iman test with Holm correction for hypocotyl length indicated significant differences between the 1:1 and the control treatment ($p < 0.05$, r = 0.44) and 1:50 treatment ($p < 0.05$, r = 0.55). There were no differences between the control and the 1:50 treatment (Figure 4.6 Table 4.8). For radicle lengths, *post hoc* paired comparison tests showed differences for radicles length indicated significant differences between the 1:1 and the 1:50 treatment ($p < 0.05$, r = 0.55). There were no differences between the control and the 1:50 treatment (Figure 4.6, Table 4.8).

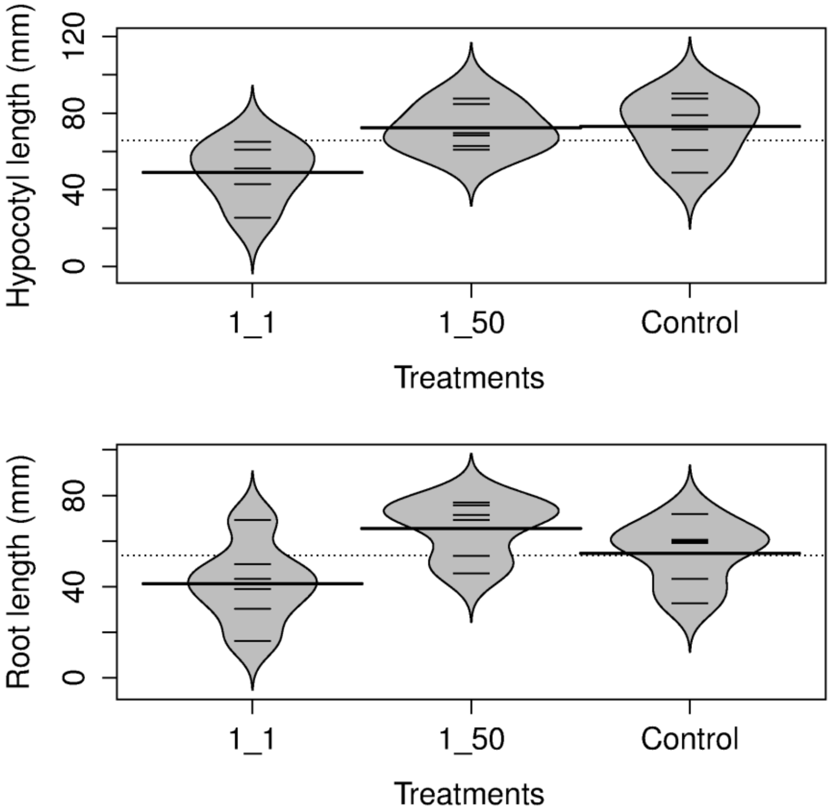


Figure 4.6 Effect of different *B. tawa* leachate concentrations on hypocotyl and radicle lengths of *B. tawa* seedlings (mm).

Table 4.8 Inhibitory effect of different concentrations of *B. tawa* leachate on hypocotyl and radicle lengths of *B. tawa*. *= significant differences ($p = 0.05$).

Hypocotyls		**Radicles**	
Comparisons	**Observed difference***	**Comparisons**	**Observed difference***
dis1:50	10.83^{a}	dis1:50	13.25^{a}
control	10.92^{a}	control	9.58^{ab}
dis1:1	4.5^{b}	dis1:1	5.66^{b}

4.4 Discussion

4.4.1 Leachate experiments on *L. sativa* seeds

There are a substantial number of studies on the allelopathic effect in different species (e.g. Rice 1995), especially when negative impacts are suspected (Reigosa et al. 2006). However in New Zealand the number of allelopathic studies is limited, particularly in the *Beilschimedia* (Froude 1980). Nonetheless, a few studies have found chemical compounds with proven allelopathic properties in *B. tawa* fruits (alkaloids) and leaves (leucoanthocyanins) (Cambie et al. 1961, Russell and Fraser 1969). Some authors suggest that when plants are stressed, allelopathic effects could be more significant and negatively affect otherwise healthy individuals (e.g. Gawronska and Golisz 2006 and references therein). Thus allelopathy may be playing a role in the germination and growth of *B. tawa*, particularly in disturbed sites where other stresses are also acting.

4.4.2 Germination rate of *L. sativa* seeds

The first time the experiment was carried out there was a negative effect on germination rate at high concentrations of the leachate (dis1:1), which could be explained because tannins (e.g. leucoanthocyanins) inactivate β-glucosidases, which may cause inhibition of seed germination and growth of plants (Fritz 2007). We did not observe any negative effect in the germination the second time I ran the experiment. This difference may be due to different initial leachate concentrations, as I cannot be certain that the initial leachate had the same chemical concentration in both experiments. We did not find any effect of the soil on germination, which suggests that there is no allelopathic effect on germination caused by compounds present in the soil or at least they are not present at a concentration that could have a negative impact.

4.4.3 Radicle and hypocotyl elongation of *L. sativa* seeds

We found a negative effect of leaf leachate at high concentrations (dis1:1) and a positive effect at low concentrations (dis1:20 and dis1:50) on radicle elongation in both experiments. On the other hand, there was a positive effect on hypocotyl elongation at low leachate concentrations (dis1:20, dis1:50) and a negative (first experiment) or positive effect (second experiment) at high concentrations (dis1:1).

In general, allelopathic compounds have a threshold of activity below which they might have zero or even positive effects on growth (Chon and Nelson 2010). This type of threshold behavior might explain the positive effects that I found in the hypocotyl with treatment dis1:20 and dis1:50. Alternatively, a concentration threshold could explain the negative effect on radicle growth observed at concentrated doses (dis1:1). The differences in hypocotyls length between experiments could be explained by differences in chemical concentration in the leachates despite the fact that I used the same amount of leaves.

The germination and growth inhibitory effects of the leaf leachate of *B. tawa* on *L. sativa* could be related to the presence of leucoanthocyanins described by Cambie et al. (1961).

Even though, these results could reflect a phytotoxic effect rather than an allelopathic effect of the leachates. In any case, it seems that germination rate and hypocotyl length are not sensitive to the concentration of the chemicals in the leachates. This is not the case for radicle length because in both experiments radicle growth was significantly hindered. Despite the fact that I found a significant effect of the soil on hypocotyl length I could not find differences between the different site types except when compared to the control.

Even though I cannot determine what kind of chemical(s) or what concentration of this/these chemical(s) is responsible for the negative or positive effect on elongation of hypocotyls or radicles, previous studies by Cambie et al. (1961) and Russell and Fraser (1969) showed that leaves of *B. tawa* contain chemicals with proved allelopathic properties. Because there will be inter-individual and seasonal variation in the concentration of the active chemicals in the leaves, I do not know the exact concentration of chemical(s) in the leachates used to prepare the dissolutions. The random sampling of leaves means I did not control for these variables, but nor should there be any systematic bias.

Our study demonstrates that *B. tawa* leachate could potentially have an allelopathic effect (both harmful and beneficial), depending on the concentrations of leachate and the part of the germinating seedling exposed to it. We could not match these results to field conditions (soil) as I did not observe different soils from different site types affecting either germination or growth. We recommend future studies focus on analyzing the chemical composition of leachates and soil, as well as carry out germination tests with more resistant species, including germination test with *B. tawa* itself to discard autotoxicity.

4.4.4 Leachate experiment on *B. tawa* seeds

Germination

The first germination in this experiment occurred 45 days after sowing, which is outside the range that has been documented for this species (27 - 40 days; Burrows 1999), but West (1986) showed that germination time could vary due to temperature fluctuations from 2 weeks to 15 weeks.

Both the leachate and the presence/absence of mesocarp had an effect on germination. The leachate at low concentrations (1:50) has a positive effect on germination speed. The effect size and confidence interval for this effect suggest that the effect not only exists but that it is quite large. The results also showed that high concentrated leachate (1:1) has no effect on germination. As the effect of this treatment did not differ from control, is unlikely that the leachate could have any negative effect on germination at high concentrations; this contrasts with the outcomes of a previous study in the perhaps more sensitive *L. sativa* (Section 4.3.1). The removal of mesocarp proved to have a positive effect on the speed of germination, as previous studies have suggested (West 1986, Burrows 1999). The effect of accelerated germination due to the removal of the mesocarp supports the hypothesis that passage through the digestive system of New Zealand pigeon or kererū (*Hemiphaga novaeseelandiae*) have a beneficial effect on seeds as they will germinate faster, giving them a higher probability of establishment success.

Hypocotyl and radicle length

High concentrations (dis1:1) of the leaf leachate had a negative effect on hypocotyl and radicle elongation of *B. tawa* seedlings. The effect size suggests that this negative effect might be large. The treatment dis1:50 and control did not have any effects on the hypocotyl elongation. However radicle length was affected positively by the dis1:50 treatment. These results are similar to a previous study using *B. tawa* leachate on *L. sativa* seeds (Section 4.4.4), which showed that leachate at low concentrations had a positive effect on hypocotyl and radicle elongation. In both studies I found that dis1:1 had a negative effect hypocotyl and radicle elongation.

The results of this study show that *B. tawa* leaf leachate can have a detrimental effect on its own seeds and on the early development stages of its seedlings depending on the concentration of leave leachate. Seeds that fall near or directly below the parent tree on soil that is littered with *B. tawa* leaves, could potentially germinate more slowly and potentially at a lower rate, although this is going to depend on the amount of *B. tawa* litter present on the understory. In addition, if these seeds still contain their mesocarp, i.e. have not passed through the digestive tract of the *H. novaeseelandiae*, their chances of survival or establishment diminish even further. While, the effect of pH of *B. tawa* leachate on germination and growth was not tested, it seemed unncessesary as Froude (1980) previously discarded this effect. Furthermore, the tree replacement data presented in Chapter 3 showed that most of the tree species seedlings, including *B. tawa* seedlings, can grow under adult *B. tawa*, even in sites with a pH as low as 4.4 again suggesting that pH does not have an effect on germination or growth. Given these points, it seems unlikely that the pH of the leachate played a significant role in the differences in growth that I found. Future studies should focus instead on determining if the chemicals present in *B. tawa* leaves could be transferred to the soil and remain there to cause a similar effect as seen under laboratory conditions.

5. MODELLING THE SPATIAL DYNAMICS OF PODOCARP-TAWA FOREST FRAGMENTS

5.1 Introduction

Environmental models provide tools to help research by simulating and predicting a system's behaviours, with the aims of learning and prediction (Mulligan and Wainwright 2013). Many different types of ecological models have been developed and used to consider vegetation dynamics across a wide range of ecosystem types (Hall and Hollinger 2000, Perry and Millington 2008. One of the most widely used types of model are the so-called individual based models (IBM; Grimm and Railsback 2005). An IBM is basically a representation of a collection of single organisms, often known as agents (e.g. a tree), their environment and the interactions between them (Reuter et al 2011). Forest gap models started being developed in the late 1960s to study forest succession under the environmental conditions present at the time (Botkin et al. 1975).

Individual-based models are bottom-up and are designed to explore how aggregate system properties arise from individual-level processes and interactions (Stillman et al. 2014). IBM's consist of an environment in which interactions between the different organisms occur. The individual organisms or agents are defined by a set of behaviours and parameters that regulate their interaction(s) with each other and their environment. The interactions individual- environment interactions are specific to each organism (i.e. depend on each individuals spatio-temporcal context) and are tracked over time; if the model incorporates spatially explicit dynamics they are classified as spatially explicit individually-based model (SEIBM) (Grimm and Railsback 2005, Deangelis and Mooij 2005). IBM models have been used in a range of different research contexts such as global change biology, long-term forest dynamics and within-generation dynamics of forest ecosystems (Bugmann 2001, Grimm et al. 1999). In general, although models of vegetation dynamics have been developed across a wide range of different scales many of them have been developed as research rather than as explicit management tools.

Many existing individual-based forest gap models are derived from the JABOWA model, which was designed as a community level forest dynamics simulator by Botkin et al (1972). A second gap model called FORET (Shugart 1984) was developed based on JABOWA and formed the base for the 80% of the gap models developed until 1995 (Liu and Ashton 1995). Widely used examples of modern gap models based on FORET are LINKAGES and SORTIE. IBM models have been criticized on a range of methodological and theoretical grounds (Bugmann 2001). For example, the processes that the models are dealing with are in general very complex and this can translate into complex models that are difficult to implement, analyse and interpret. Other issues are that some models do not account for uniqueness of individuals, meaning, for example, that individuals of the same age are considered to share the same characteristics, effectively discarding individual variability (Grimm et al 1999).

In New Zealand, models derivations from JABOWA, LINKAGES and SORTIE have been developed. For example, DeVelice (1988) developed a new model called FORENZ, derived from JABOWA-FORET, but without including temperature and light limitation on growth, to predict forest dynamics on slip-faces in Fiordland. Hall and Hollinger (2000) used a model called LINKNZ adapted from the model LINKAGES to simulate conifer–hardwood and beech species forest succession. LINKNZ has also successfully been used to explore vegetation and climate shifts in the early Holocene (McGlone et al. 2011).Kunstler et al (2009) used a model derived from SORTIE named SORTIE/NZ to simulate the dynamics of lowland temperate rain forests on the southern island. However, when compared to, for example, North America the use of individual-based indigenous forest models in New Zealand has been limited (Shugart and Smith 1996; although see Thrippleton et al. 2014).

Simulation models capable of representing the long-term dynamics of forest fragments are useful tools for supporting managers in making decisions regarding the conservation of such ecosystems. Models can potentially help in the conservation and restoration of degraded systems both by improving the fundamental understanding of their dynamics and by providing predictions for the development of management actions (e.g. Xi et al. 2008)

Because ecological modelling can help to focus limited resources and can guide management actions, it is of particular importance in developing and evaluating effective restoration strategies for threatened endemic tree species. Such is the case of podocarp-tawa forests and of tawa (*Beilschmiedia tawa*) in particular, which has shown signs of recruitment stress (see Chapters 2 and 3).

The spatially explicit individually-based model (SEIBM) described in this Chapter represents the long-term dynamics and viability of podocarp-tawa forest fragments under different types of management (unfragmented forest, fenced and unfenced fragments) and, in particular, the fate of tawa (*Beilschmiedia tawa*) in these settings. The model considers six forest canopy and subcanopy species that typify these environments: *Beilschmiedia tawa, Hedycarya arborea, Laurelia novae-zelandiae, Piper excelsum, Melicytus ramiflorus* and *Dacrydium* *cupressinum*. The model design is by intention reasonably generic and could be adapted to model other types of forests if needed.

5.2 Model description

The model description below follows the Overview, Design concepts, and Details (ODD) protocol described by Grimm et al. (2006, 2010); this approach is designed to support comprehensive and transparent model description and communication.

5.2.1 Purpose

The main purpose of the model is to: (i) explore the long-term viability of podocarp-tawa forest fragments under different types of management activities (including no management), (ii) assess the ability of forest fragments to persist in the absence of any management intervention and (iii) evaluate whether the use of fencing and planting as interventionist management strategies affect the long-term survival of these forest remnants.

5.2.2 Entities, state variables, and scales

The basic unit represented in the model is an individual tree, with individuals divided into three distinct life-stages: seedlings, saplings and adult trees. Each individual adult tree is characterized by the following state variables: spatial location (on a discrete-space grid or lattice), species, diameter at breast height (dbh), height and age. Seedlings and saplings do not have an explicit spatial location, beyond their abundance in a given grid cell. Each species is characterized by the following parameters: shade tolerance, reproduction age, regeneration height, seed production, dispersal, gap maker, suppression tolerance, suppression mortality rate, palatability (herbivory), edge response and long-distance dispersal (each explained further below). Seedlings and saplings are characterized by their survival, and seedlings have an additional parameter called seedling transition, which represents the rate at which they transition to the sapling class (see Appendix 2). The parameters shown in Appendix 2 are those whose values differ across the six species represented in the model.

The model was initialized and parameterized using data collected from study sites categorized as unfragmented forest, fenced forest fragments and unfenced forest fragments (for a full description see Chapter 2) (Figure 5.1). The model was initialized with a fixed number of seedlings, saplings and trees distributed across the six species as appropriate for each site category (unfragmented forest, fenced, unfenced fragments). The age of the individual trees was estimated from empirical diameter at breast height (dbh) data (Section 4.2.5), and the same dbh data were used to calculate the height of the trees. The initial distribution of dbh values was simulated from a distribution function conditioned on size-frequency information from each site. Thus, the initial size-frequency structure of the forest will differ each time the model is run, but the composition and structure of the forest will be similar each time.

One ‘tick’ (the fundamental temporal unit in the model) represents one year and, unless otherwise noted, all simulations were run for 2000 years. The model is grid-based with only one adult tree able to occupy any one grid cell, with the grid cells 10 × 10 m in size. We choose this grid size because it is the approximate canopy size of an individual *B. tawa* tree. The model is spatially-explicit and capable of simulating the dynamics of each individual adult tree in forest areas up to a size of ca. 25 ha; larger areas can be simulated but computational cost becomes prohibitive.

Figure 5.1 Understory of the (a) unfragmented forest, (b) unfenced forest fragment, and an image from a fenced forest fragment as seen from the outside (c).

5.2.3 Process overview and scheduling

In each tick the model sequentially processes a series of ecological routines as follows: restoration planting, seed dispersal (both from within and beyond the fragment), herbivory, mortality, gap formation, regeneration (recruitment), growth and seedling/sapling demography (Figure 5.2).

Before running the model the user can define different parameterisations and management scenarios. The scenarios can be easily set-up by adjusting boolean (on-off) switches for herbivory (seedlings and saplings), edge effect and the nature of any long-distance dispersal (Figure 5.3). For example, to simulate the dynamics of an unfenced fragment the herbivory and edge effect would be 'on', in the case of fenced fragments only the edge effect would be on, and for forest fragments both switches would likely be off. The model can also represent landscape-level disturbance and density-dependent mortality processes, but these were not simulated in the analyses presented here and so are not further considered.

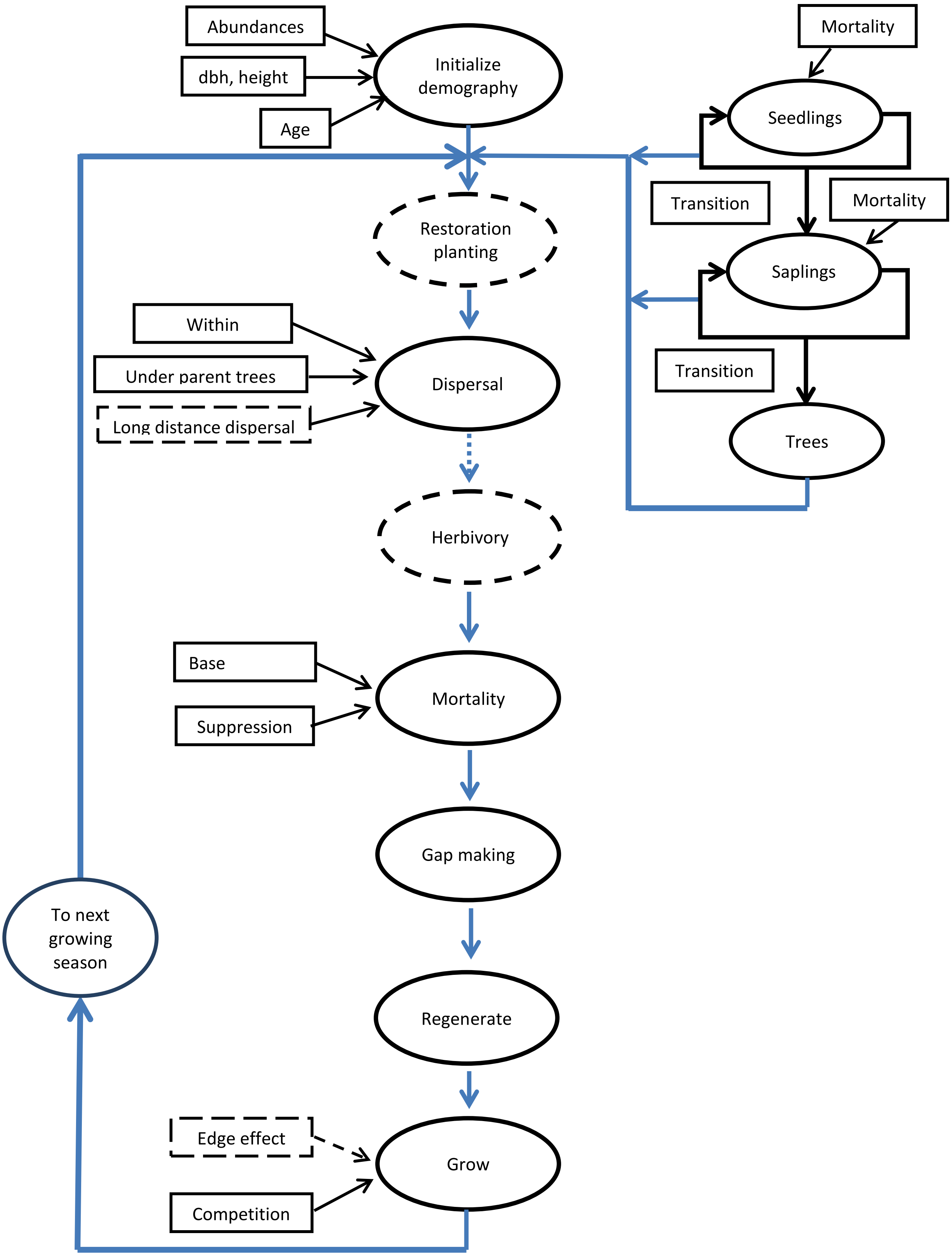
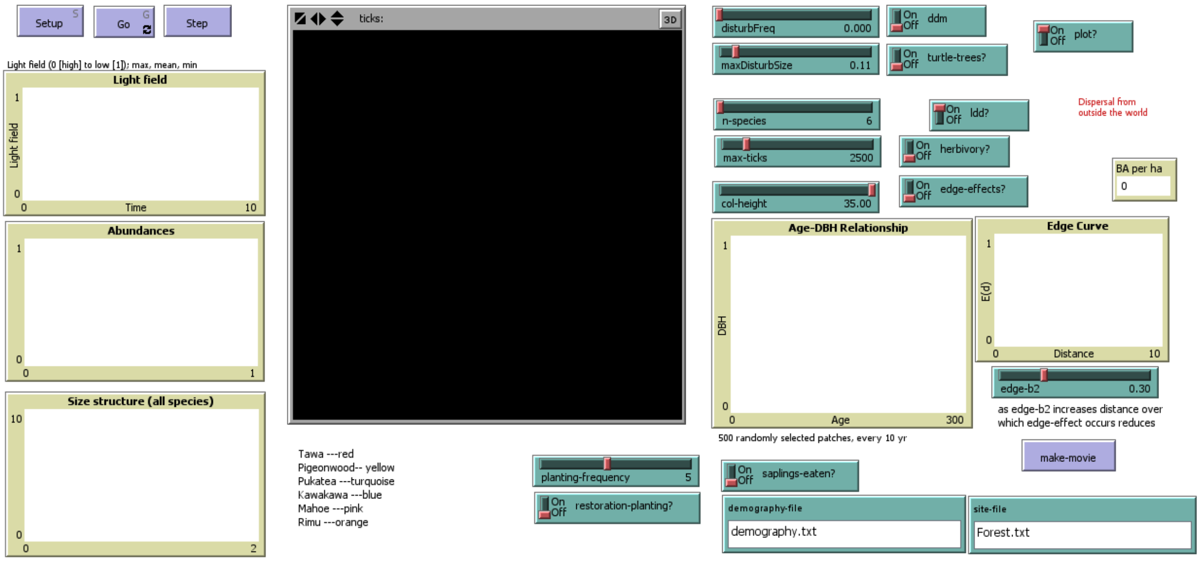


Figure 5.2 Flow-chart representing the sequence of the different ecological processes represented in the SEIBM; dashed lines represent processes that can be turned on and off.



disturbFreq 0.000
maxDisturbSize 0.11
n-species 6
max-ticks 2500
col-height 35.00
edge-b2 0.30
planting-frequency 5
ddm Off
turtle-trees? Off
plot? On
ldd? On
herbivory? Off
edge-effects? Off
saplings-eaten? Off
restoration-planting? Off
BA per ha 0
demography-file demography.txt
site-file Forest.txt

Figure 5.3 Illustration of the model interface (the model is implemented in Netlogo 5.0.4; Wilensky 1999).

At initialization the adult tree abundances, dbh and age of each individual will depend on the scenario being considered (unfragmented forest, fenced and unfenced fragment). The model starts with a forest with the same number of seedlings (10 seedlings [individuals < approximately 50 cm in height] per species per grid cell) regardless of the scenario (up to 50 cm in height) and saplings (1 sapling [individuals > approximately 50 cm in height) per species per grid cell).

The transition to an adult tree has two stages. The first stage corresponds to seedlings that form the seedling bank. A species-specific proportion of seedlings move to the second stage of sapling each year. Each year individuals in the sapling stage can transition (via a lottery process weighted by the light levels in each grid cell) to adult trees if there is not already an adult tree present in the grid cell.

In both life-history stages, if the individuals survive but do not transition to the next stage they remain as part of the seedling or sapling bank until they either successfully move to the next stage or they die. A species-specific proportion of individuals is removed each year, representing the mortality of seedlings and saplings.

Natural regeneration, as simulated, starts with three dispersal processes: neighbourhood dispersal ('under parent tree' dispersal), local dispersal (within landscape dispersal), and long-distance dispersal. In order to reduce the computation burden, and as is common in forest models, the fate of individual seeds is not modelled, and instead established seedlings are dispersed. Both local and long-distance dispersal processes depend on the ability of each species to disperse by vectors such as wind and birds. If restoration is active, planting of saplings is simulated by adding a fixed (user-determined) number of saplings of each species to the sapling bank.

After natural regeneration and restoration have occurred, the herbivory routine starts. The effects of herbivory on regeneration are represented by reducing the seedling and sapling banks by a species-specific fraction (i.e., herbivory-related mortality) based on their palatability as estimated from information in Wallis and James (1972), Allen et al. (1997), Husheer (2005) and Landcare Research (2005).

Mortality consists of an annual background mortality rate and suppression arising from slow growth or competition (due to neighbouring individuals competing for light). The annual background mortality rate is calculated using the equation provided by Shugart (1984) and is age-independent; individuals have around a 2% chance of surviving to their maximum possible age. If an individual's growth (averaged over the previous five years) is less than the species critical growth (a proportion of the optimal growth for an individual at a given age, with lower values indicating increasing shade-tolerance or ability to persist through long periods of suppression) the model assumes that the individual is suppressed and hence suffering elevated stress. Suppressed individuals die at a species-specific rate. If the dead tree is a ‘gap-maker’ species, a gap is formed shaped as a 45° degree cone of a length proportional to the height of the dead tree in a random direction from the tree. All adult individuals in patches falling under that cone are assumed to have been hit and damaged by the falling tree and also die.

Each canopy-dominant tree grows following the basic equations described by Botkin et al. (1972) in the JABOWA gap model. This approach calculates the optimal diameter growth rate for an individual of a given species and size and then down-weights it based on competitive interactions and environmental conditions. An individual tree’s height is calculated following the allometric approach described by Botkin et al. (1972) and Botkin (1993); full details are provided below. The calculated dbh increment is reduced by competition and an edge effect; environmental conditions such as soils are assumed to be uniform within the modelled area. The competitive effect occurs if a tree’s height is less than any of the neighbouring trees’ heights. If edge effects are represented then a penalty is applied to the dbh increment depending on the location and how well the species can tolerate the edge environment. This effect is represented by the edge-effect parameter, which is specific for each species and is based on literature that indicates how the species included in the model respond to edge environments (see Appendix 2).

5.2.4 Design concepts

Basic principles: The guiding objective of this model was to simulate the vegetation dynamics of native forest fragments. We were specifically interested in the long-term dynamics of native podocarp-tawa forest fragments in northern New Zealand and the fate of specific tree species, especially *B. tawa*, in them. In order to simulate different management activities such as fencing and herbivore control, several boolean switches were added: seedling and sapling herbivory, edge effects and the active planting of seedlings (restoration activity). The model represents fundamental demographic processes such as seed dispersal, reproduction, and mortality. Spatio-temporal variability in soils and climatic conditions were not included, and they were assumed to be constant across the entire fragment. Individual species demographies are parameterized using data collected specifically for the purpose (Chapters 2 and 3), supplemented by empirical data from other studies; for example, maximum height, shade tolerance and maximum age were determined based on the available literature.

Emergence: Forest dynamics and population structures emerge from the interaction of different individuals and species across the three life-stages considered (seedling, sapling and adult tree).

Sensing. Trees "know" their life cycle stage (seedling, sapling, and adult tree) and what species they belong to; they also "know" their age, height and their dbh.

Interaction. Competition for light is the fundamental interaction represented in the model. When the amount of light being received by a given individual (i.e. grid cell) is insufficient to sustain growth the individual is considered to be suppressed. The point at which this suppression occurs depends on each species shade-tolerance. The period over which a suppressed individual can remain in this state before suffering mortality is species-specific. Also, regeneration replacement is influenced by local light conditions.

Stochasticity: Nearly all of the components in the model are stochastic.

5.2.5 Initialization

Species are initially randomly assigned to each of the grid cells. The initial number of seedlings and saplings present in each cell was defined using empirical data collected from each of the study sites. Adult trees' dbh are generated randomly using a log-normal distribution with mean and standard deviation estimated from field data (Table 5.1). The data used in this initialization process depend on the scenario being modelled (forest, fenced fragment and unfenced fragment). Tree heights are calculated using the initial dbh and via equation 5.4 (Section 5.2.7). The age at initialization of each tree is estimated from their dbh and height using equations 5.1 and 5.4 in Section 5.2.7. By consequence, the forest generated is different each time the model is set up, although its overall statistical properties are the same from run-to-run. The remainder of the parameters that comprise the species demography, such as shade tolerance, maximum height, among others, are fixed across a species lifetime and are the same over all simulations.

Table 5.1 Mean (m) and standard deviation dbh for each species used in the initialization.

Species	Mean dbh (m)	dbh standard deviation
B. tawa	0.369	0.10
L. novae-zelandiae	0.11	0.01
H. arborea	0.227	0.20
P. excelsum	0.01	0.01
M. ramiflorus	0.284	0.10
D. cupressinum	0.01	0.01

The herbivory effect is spatially heterogeneous but it will affect a given species with a consistent intensity when it is in place, so the overall effect will be similar each time it is represented. The pervasiveness of the edge effect is controlled by the parameter *b2* (see eq. 5.2), which was always set to 0.3.

5.2.6 Input data

The model does not use input data to represent exogenous time-varying processes (e.g. climate or hydrology).

5.2.7 Submodels

Initial demographics

Patches are initialized as described in Section 5.2.5 using empirical data collected for this purpose.

Diameter

Each species growth is represented by an annual diameter increment (ΔD; m/yr), which is calculated using the formula provided by Botkin et al. (1972) for the JABOWA gap model. The gap model approach has not been used frequently in New Zealand (DeVelice 1988, Hall and Hollinger 2000). However, the standard approach allows us to generate an optimal growth curve for a given species (Figure 5.4):

$$\Delta D = \frac{(dbh \times g \times (1 - (dbh \times H)/(D_{\max} \times H_{\max}))}{(2.74 + 3 \times \mathrm{b}_2 \times dbh - 4 \times \mathrm{b}_3 \times dbh^2)} \tag{5.1}$$

where: *dbh* is diameter at breast height (m), H is tree height in meters (from equation 5.1), H_{max} is maximum height (m) and D_{max} is maximum diameter (dbh), which are species-specific. b_2 and b_3 are species-specific allometric constants. Two-thirds of the maximum dbh (D_{max}) is reached at 50 % of the maximum age.

b_2 and b_3 are calculated using the formulae (equation 5.2) given by Botkin et al. (1972):

$$b_2 = 2(H_{max} - 1.37)/D_{max}$$

$$b_3 = (H_{max} - 1.37)/{D_{max}}^2 \tag{5.2}$$

where: 1.37 is the height (m) of the smallest adult trees represented in the model, H_{max} is maximum height and D_{max} is the maximum diameter (dbh) a given species can attain.

Diameter increment (ΔD_c) is corrected by the neighbour effect (value from 0 to 1) and edge effect (value from 0 to 1) as follows (assuming edge and neighbour effects are multiplicative):

$$\Delta D_c = D \times CP \times EP \tag{5.3}$$

where: ΔD_c is the current diameter increment after the correction, *CP* is the competitive penalty and *EP* is edge penalty (see Section 5.2.7).

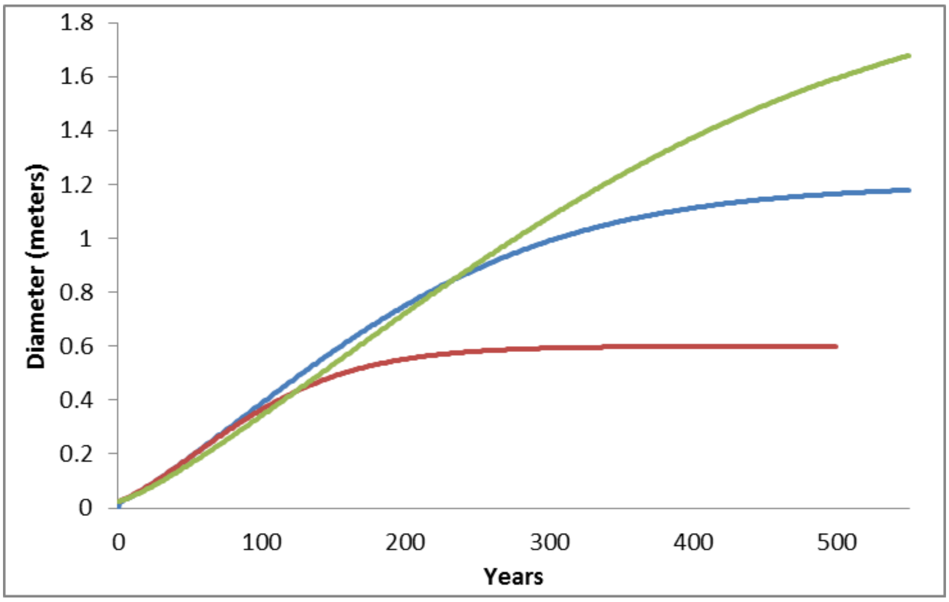


Figure 5.4 Optimal growth curves (diameter) for three tree species: (i) *B. tawa* (blue) with maximum height 35 m, maximum dbh 1.2 m, maximum age 450 years, (ii) *M. ramiflorous* (red) with maximum height 12 m, maximum dbh 0.6 m, maximum age 250 years and (iii) *D. cupressinum* (green) with maximum height 35 m, maximum dbh 2 m, maximum age 800 years. *B. tawa* and *M. ramiflorous* growth curves are shown up to the maximum age those species can reach.

Height

The height (in meters) of a tree with a dbh is calculated using the following formula provided by Kerr and Smith (1955), which is the standard approach for gap models and their derivatives:

$$H = 1.37 + (b_2 \times \mathrm{dbh}) - (b_3 \times \mathrm{dbh}^2) \tag{5.4}$$

where 1.37 represents the dbh in meters of saplings when they transition to adults.

Restoration planting

Restoration planting is simulated by adding saplings to the sapling bank at a species-specific amount at a specific frequency (e.g. yearly, every five years, etc.) (Figure 5.5)

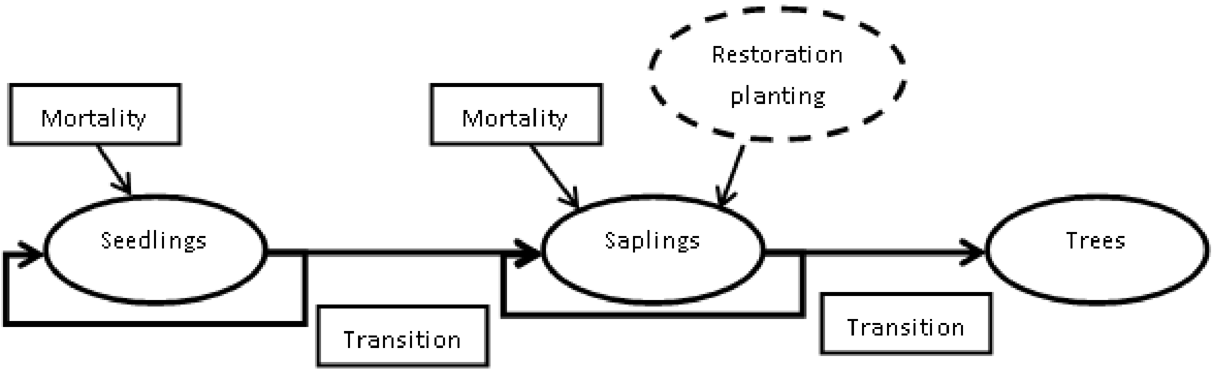


Figure 5.5 Detailed schematic of the representation of the plant individual's life cycle (seedling/sapling/tree) in the model. The restoration planting circle shows where in the cycle the saplings are added. The dashed line denotes that this process can be switched on and off.

Dispersal

Dispersal is comprised of three separate processes: neighbourhood dispersal, local dispersal and long-distance dispersal.

1. Neighbourhood dispersal

A seedling is added to each of the focal grid cell's neighbours (see Section 5.2.7 for a description of this parameter; Figure 5.6b).

2. Local dispersal

A number of seedlings, based on the seed production parameter (seed production is set to the same value for all the species), are dispersed in a random direction to a specific distance *d* (where *d* is drawn from a negative exponential distribution controlled by the species-specific mean dispersal distance). The dispersed individual will be added to the seedling bank in the appropriate grid cell.

3. Long distance dispersal

The total long-distance seed rain is calculated using a binomial distribution based on each species abundance and the proportion of seeds actively dispersed by each species (parameter *ldd-species*). This approach makes the assumption that the composition of the modelled area represents that of the broader landscape. Once the aggregate seed rain is calculated, the seeds are dispersed at random across the simulated landscape by adding a seedling to the seedling bank or by establishing a new seedling if there is none (Figure 5.6c).

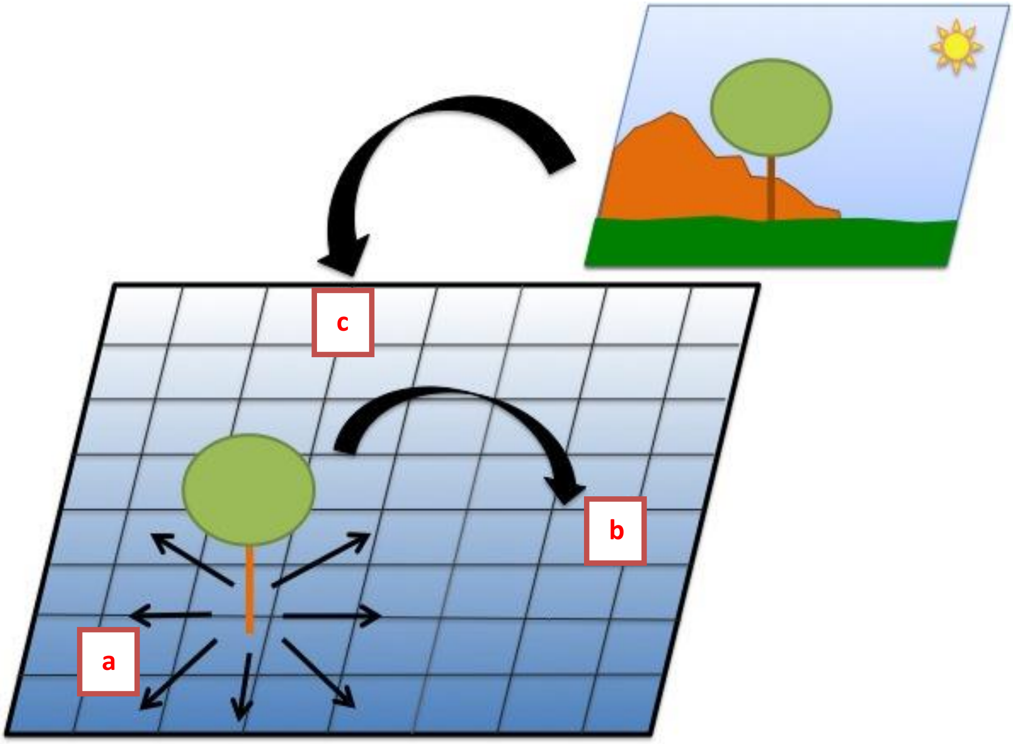


Figure 5.6 Description of the dispersal processes: (a) neighbourhood dispersal, (b) local (within fragment) dispersal and (c) long-distance dispersal (from beyond the fragment).

Herbivory

We considered herbivory as a component of juvenile mortality as described in the Mortality Section below. We mention it here to preserve the sequential order of process scheduling in the model. The seedling and sapling banks are reduced in a species-specific proportion due to predation by herbivores (Figure 5.7).

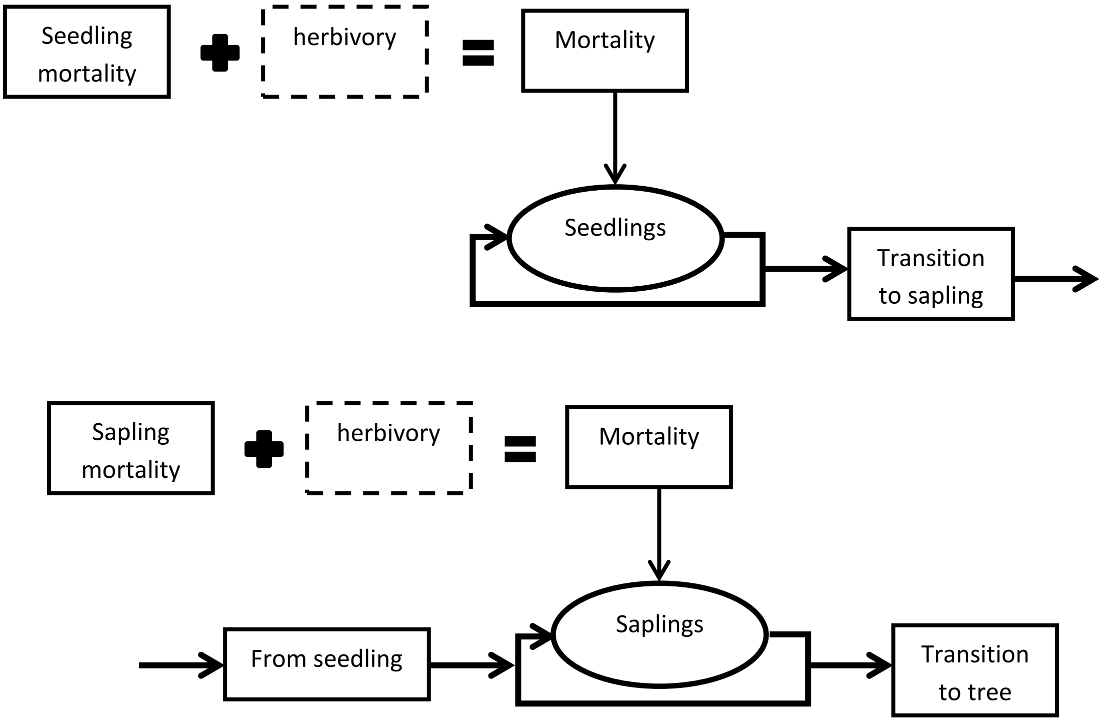


Figure 5.7 Description of seedling and sapling mortality. Dashed lines represent a process that can be turned on and off.

Mortality

Juvenile mortality

Seedlings and saplings suffer annual mortality at a species-specific rate, with the number of individuals in each class dying drawn from a binomial distribution (Figure 5.7). Total seedling mortality is given by the total individuals minus the proportion of individuals that survive minus the individuals that make the transition to the next life-stage (sapling). Sapling mortality is represented by the total number of saplings minus the proportion surviving.

Mortality rate

Annual tree (adult) mortality follows the formula of Shugart (1984); this process is age-independent:

$$M_{rate} = \left(\frac{4}{m_{age}}\right) \tag{5.5}$$

M_{rate} yield a background mortality rate such that 98% of individuals die before reaching the species maximum age (m_{age}).

Gap making

If the dying individual is a gap-maker species then it will create a canopy gap extending beyond its own grid cell on its death. The newly generated gap will have a conic shape (length given by tree height and 45° arc), with all individuals in affected grid cells suffering mortality.

Regeneration

New seedlings are added to each grid cell's seedling bank each year as described above. Seedlings transition to the sapling bank either by "growing" from a seedling or by the restoration planting process.

Edge effect

The edge effect (E_{eff}) is represented by the following non-linear function:

$$E_{eff} = b_1 \times \exp(-b_2 \times d) \tag{5.6}$$

where: $b_1 = 1$, and b_2 controls the distance over which the edge effect extends into the forest fragment.

As b_2 increases, the distance over which the edge has an effect reduces and *vice versa*. As edge effect is calculated for each patch, distance (*d*) represents the distance from the edge to a given patch (Figure 5.8). The edge effect is symmetrical.

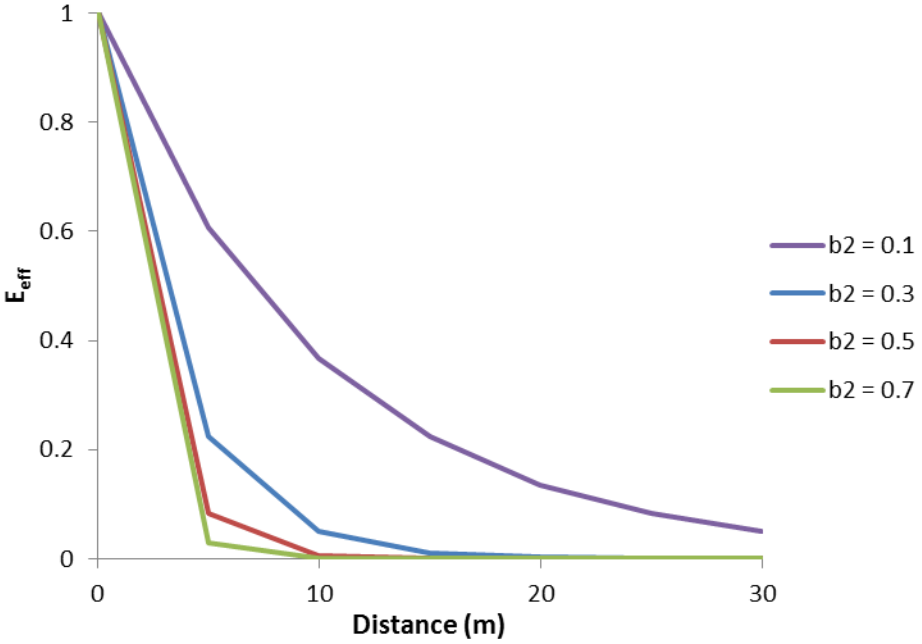


Figure 5.8 Representation of the effect of *b2* on the edge effect curve. Distance (*d*) is the distance from the edge (0 m) to the centre of the patch or where the edge effect ends it impact. Although cell size in the model is 10 m, the function was calculated using a 5 m step for ease of interpretation.

Edge penalty

The edge penalty ranges from 0 to 1 (i.e. the effect of the edge on a species growth-rate increasing mortality risk) and is calculated by multiplying the edge effect relative to distance by the ability of the species to persist in edge environments:

$$EP = (1 - (E_{eff} \times (1 - E_{resp}))$$

(5.7)

where: edge effect (E_{eff}) is the edge effect relative to the distance from the edge from equation (5.7), E_{resp} ranges from 0 to 1 and represents how well a species is adapted to edge environments.

Competition

The strength of competition (scaled from 0 to 1) that each individual is experiencing is based on its height relative to those of its neighbours, which is a proxy for local light availability [based on Dislich et al. (2009)]:

$$CP = (\frac{H}{H_{nhb}})^2$$

(5.8)

where: CP is the competitive penalty, H is height from equation 5.1 and H_{nhb} is the height of the surrounding trees.

5.3 Baseline analysis

We explored the ‘baseline’ dynamics of an unfragmented forest of 25 ha (i.e. a 50 × 50 grid of 10 × 10 m cells) by running the model 30 times for 2000 years. We graphically analysed three of the model’s key output variables: the abundance of the dominant late successional species (*B. tawa*, *L. novae-zelandiae* and *D. cupressinum*) included in the model, their mean dbh and mean basal area. We did not use inferential statistics to evaluate the model’s dynamics and behaviours. Simulation-based analyses can be highly replicated, which leads to very small *p* values regardless of the effects size and ultimately rejection of null hypotheses of no difference between treatments, which are known *a priori* to be false invalidating the premise of the test (White et al. 2014).

For most of the six species, adult abundance is very similar from run-to-run. However, this is not the case for *B. tawa* and *L. novae-zelandiae* where there were differences in the number of individuals of up to 22% between runs. This dynamic is unsurprising because *B. tawa* and *L. novae-zelandiae* have similar habitat requirements so they are constantly competing for resources and tend to dominate late-successional (low light) environments (Figures 5.10 and 5.11). The dynamic of these two species shows path-dependent effects; when a species starts to do well it will capture more grid cells, increase in abundance and so capture more cells, and so forth.

West (1986) showed that *B. tawa* has higher canopy cover and tends to be the dominant species in unfragmented podocarp-tawa forest, and, conversely, that *D. cupressinum* has a lower canopy cover and is under-represented in the unfragmented forest. At first, *B. tawa* and *L. novae-zelandiae* are randomly distributed across the modelled forest but they then slowly shift to a more aggregated pattern. *D. cupressinum* develops a scattered pattern comprising few, large individuals as proposed by the lozenge model (Ogden and Stewart 1995) (Figure 5.9, Digital Appendix 1).

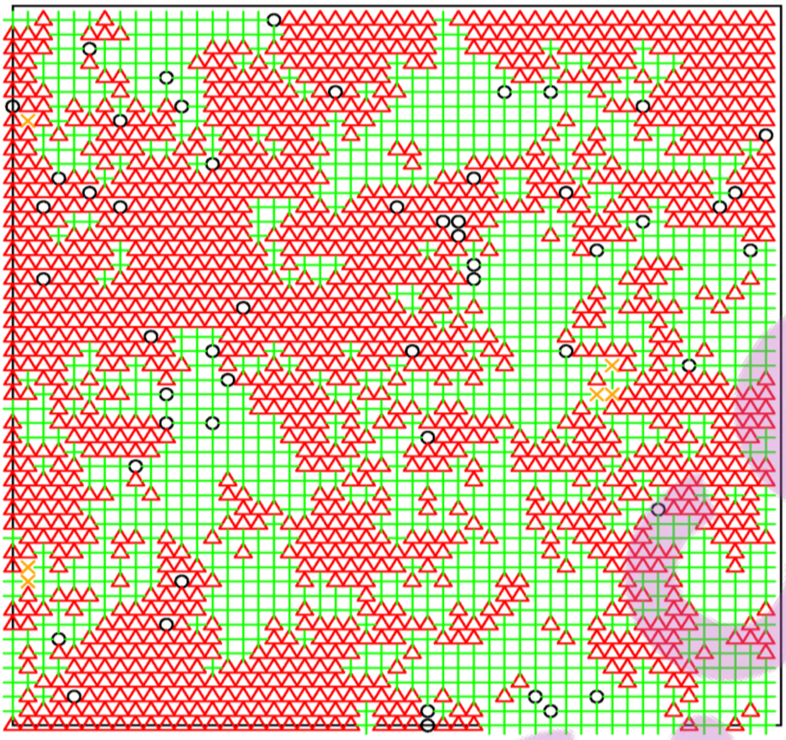


Figure 5.9 Image of a modelled unfragmented forest at 2000 years. Black colour represents gaps in the forest, red *B. tawa* individuals, green *L. novae-zelandiae* and orange *D. cupressinum*.

We compared the densities of *B. tawa, L. novae-zelandiae* and *D. cupressinum* at the end of 2000 simulation years with field data obtained from the PCQ analyses (see Chapter 2, Section 2.3.1). For *B. tawa* the model yielded a mean density of 50 individuals per ha (95% CI [48.5, 51.6]) while the PCQ data yielded 154 individuals per ha (95% CI [135, 176.4]). *L. novae-zelandiae* mean density were 47 individuals per ha (95% CI [45.9, 49.1]) and 134 individuals per ha (95% CI [117.6, 153.6]) for the model and PCQ data, respectively. For *D. cupressinum* the model gave mean density of 0.08 individuals per ha (95% CI [0.01, 0.14]) while the PCQ data estimates two individuals per ha (95% CI [2.1, 2.8]). The discrepancy in abundances between what was obtained in the model and the field data gathered from the PCQ analyses is, at least in part, due to the fact that the maximum number of trees the model can simulate is approximately 100 individuals per ha (grid cells are 10 × 10 m and only one adult tree can occupy any given grid cell). Nevertheless, the proportional abundances of the different species in the model are very similar to the data obtained in the field (Figure 5.10).

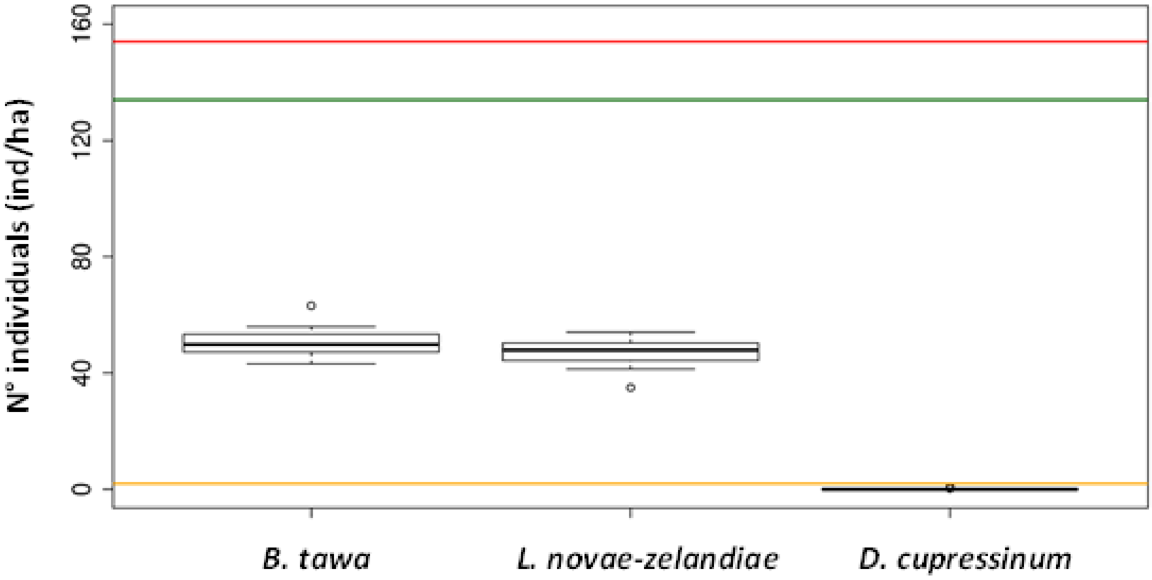


Figure 5.10 Boxplot of species density after 2000 years (n = 30 model realizations). Coloured lines represent abundances of species using field data obtained from the unfragmented forest (Chapter 2). Red line represents *B. tawa*, green *L. novae-zelandiae* and orange *D. cupressinum*.

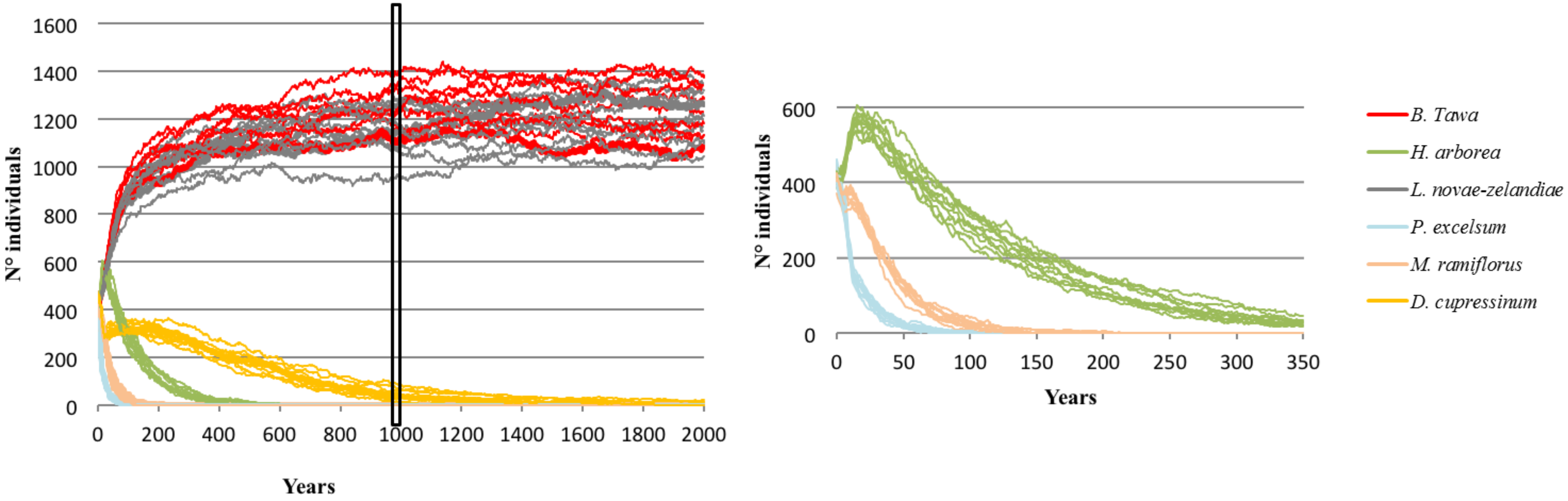


Figure 5.11 Species abundances in n = 10 randomly selected model realizations under baseline conditions, each of 2000 years. The black box represents the point where the abundances of the dominant late-successional species stabilized (based on visual assessment). The graph on the right shows detail of the early successional species (*H. arborea*, *P.excelsum* and *M. ramiflorus*) dynamics.

Mean dbh for both *B. tawa* and *L. novae-zelandiae* are stable during each run and show little variation between simulations, which is consistent with the fact that abundances maintain a constant pattern within any given run (Figures 5.12 and 5.13).

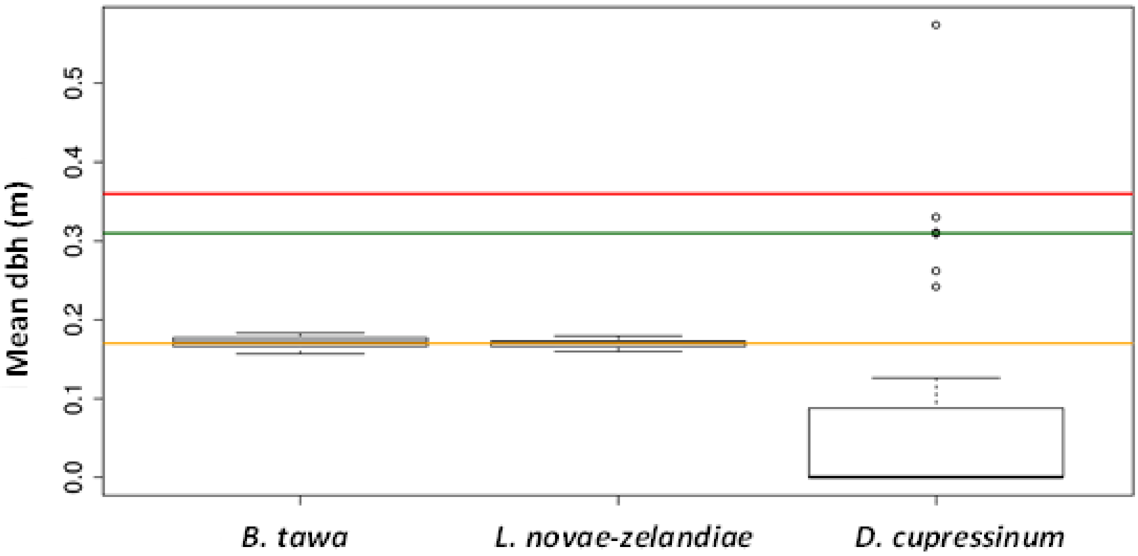


Figure 5.12 Boxplot of species mean dbh (m) after 2000 years (n = 30 model realizations). Coloured lines represent mean dbh of species for *B. tawa* and *L. novae-zelandiae* using field data obtained from the unfragmented forest (Chapter 2) and using Chavasse and Travers (1966) mean dhb for *D. cupressinum*. Colours as per Figure 5.10.

For *B. tawa* the model estimated a mean dhb of 17.1 cm (95 % CI [16.8, 17.3]) while I obtained a dbh of 36.1 cm (95 % CI [29.4, 42.6]) from the PCQ results. For *L. novae-zelandiae* the model estimated a mean dhb of 16.9 cm (95 % CI [16.7, 17.1]) while a dbh of 31.1 cm (95 % CI [23.8, 38.3]) was obtained from the PCQ results. Although the results from the model and the PCQ differ, the results from the model do not seem implausible as mean dbh from the field data is fairly variable and lower mean dbh values for *B. tawa* of 26.3 ± 2.3 cm have been reported in other studies (Smale et al. 2008). They do suggest, however, that mortality rates in the model are too high for smaller individuals. For *D. cupressinum* the model gave an estimated mean dbh of 7 cm (95 % CI [2, 13]). We could not compare the model results for *D. cupressinum* with the PCQ data from the unfragmented forests as I recorded only one individual with a diameter of 1.7 m; previous studies have reported mean dbh values of 17 to 55 cm (Chavasse and Travers 1966).

We also analysed the size-frequency distribution for *B. tawa* and *L. novae-zelandiae*, and the graphs of frequencies versus dbh followed a “reverse-J” distribution. This means that most individuals fall in the smaller diameter class, with fewer and fewer in the larger diameter classes (Figure 5.14). We compared the percentage of individuals per size-class generated by the model with the observed data (Table 5.2).

Table 5.2 Comparison of the percentage of individuals per size-class given by the model and the observed data for *B. tawa* and *L. novae-zelandiae*. Model data is based on *n* = 30 model realizations and observed data is based on *n* = 62 for *B. tawa* and *n* = 54 for *L. novae-zelandiae.*

	B. tawa		*L. novae-zelandiae*	
	Model	Observed	Model	Observed
Size-class (dbh)	Individuals (%)	Individuals (%)	Individuals (%)	Individuals (%)
0-20 cm	74	35	72	43
20-40 cm	14	29	15	30
40-60 cm	6	19	7	19
60-80 cm	2	5	2	4
80-100 cm	2	10	2	4
100-120 cm	2	0	2	0
>120 cm	0	2	0	2

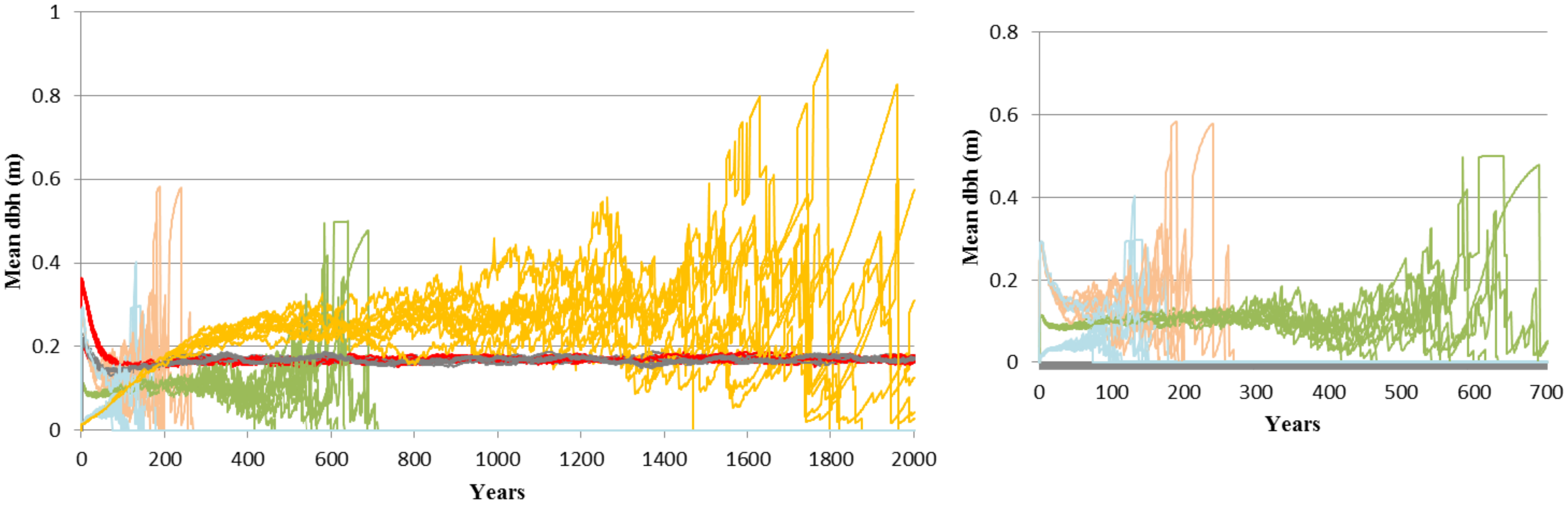


Figure 5.13 Mean dbh for each of the six species in n = 10 randomly selected model realizations under baseline conditions, across 2000 years; colouring as per Figure 5.11. The graph on the right shows detail of the early successional species (*H. arborea*, *P.excelsum* and *M. ramiflorus*). The erratic trajectories correspond to a few large individuals that produce a sharp drop in the mean dbh when they die.

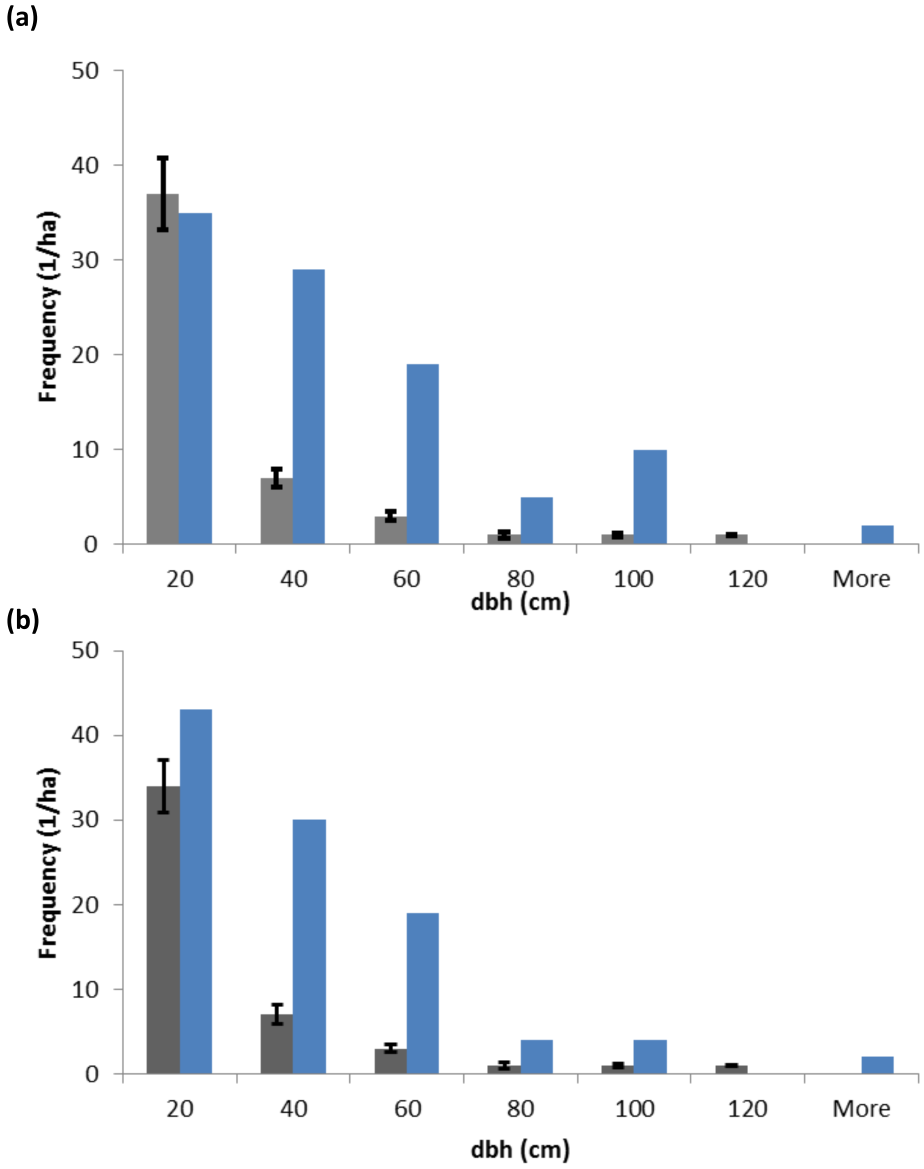


Figure 5.14 Size-class frequency distribution of $n = 30$ model realizations for (a) *B. tawa* and (b) *L. novae-zelandiae*. Blue bars correspond to the field data for each species from Chapter 2 (Table 2.5).

For *B. tawa*, the model generates a higher number of small individuals (0 - 20 cm) than is seen in the field and, commensurately, a smaller number of medium (20 - 40 cm) and large individuals (> 40 cm) (Table 5.2). This again suggests that mortality, especially in the smaller size classes, is more intense in the model than in the field. The frequency of the smaller size-class (0 - 20 cm) and large size-class (< 40 cm) produced by the model are, however, similar to those reported by West (1986) (n = 641). Despite the discrepancy between the model and the observed data from the sites considered, the model produces reasonable predictions in most size classes and estimates similar to those of West (1986).

We compared the mean basal area results from the model after 2000 years with those estimated in the field (Section 2.3.1) (Figures 5.15 and 5.16). For *B. tawa* the model estimated mean basal area of 2.8 m^2/ha (95 % CI [2.6, 2.9]) while the PCQ results yielded 24 m^2/ha (95 % CI [21.1, 27.5]). In the case of *L. novae-zelandiae* the estimated mean basal area was 2.5 m^2/ha (95 % CI [2.4, 2.6]) while the PCQ data yielded 17.9 m^2/ha (95 % CI [15.6, 20.4]). *D. cupressinum* estimated mean basal area was 0.01 m^2/ha (95 % CI [0.008, 0.025]) as compared to 6.1 m^2/ha (95 % CI [5.3, 6.9]) for the PCQ data. As the model can only simulate a maximum of 100 individuals per ha, basal areas are going to be smaller in comparison with the PCQ data. To reduce that effect I extrapolated the densities from the PCQ using the model's basal areas (i.e. the tree sizes produced by the model were multiplied by the densities estimated in the field). For *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* the estimated basal area were 8.1 m^2/ha, 6.27 m^2/ha and 0.244 m^2/ha, respectively, which are still lower than the field-based values.

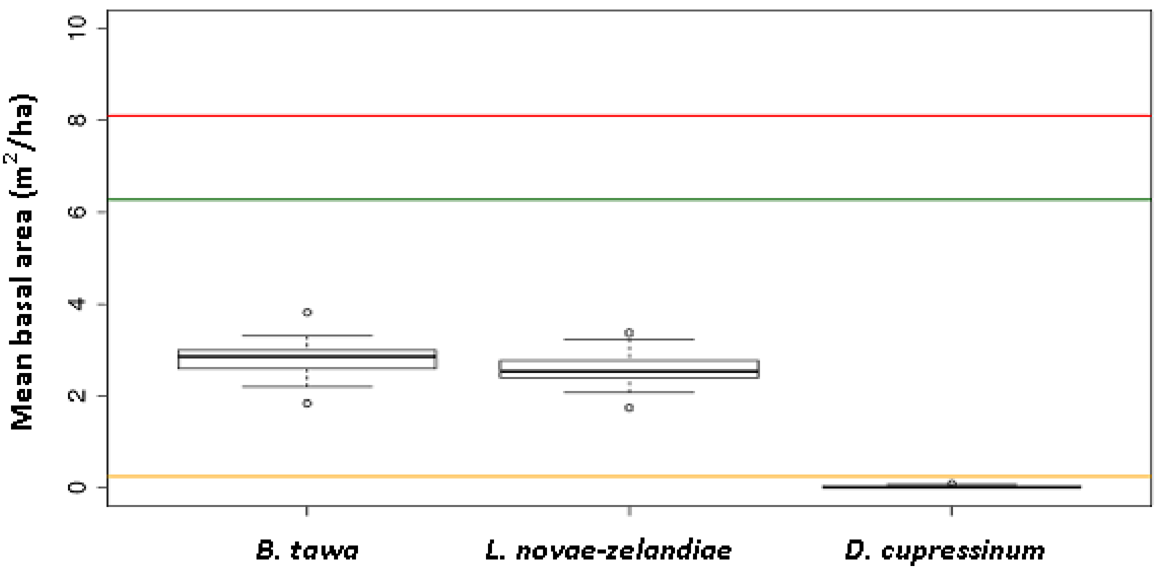


Figure 5.15 Boxplot of species mean basal area after 2000 years (*n* = 30 model realizations). Coloured lines represent mean basal area of species for *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* using field data obtained from the unfragmented forest (Chapter 2). Colour as per Figure 5.10.

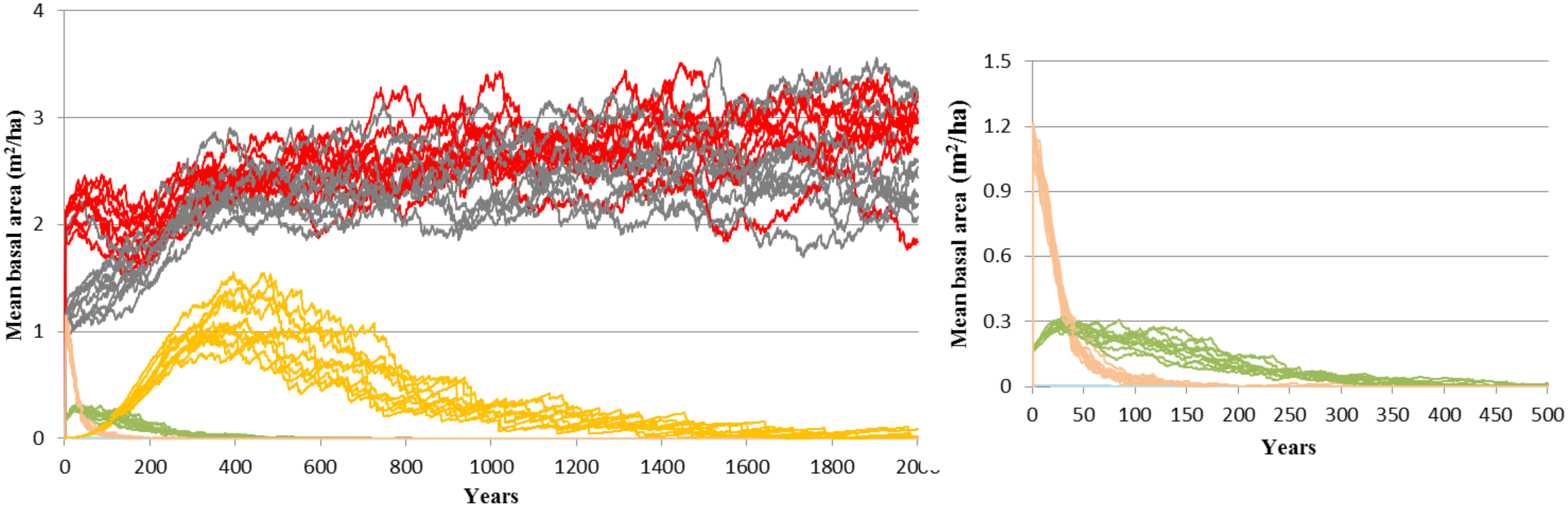


Figure 5.16 Mean basal area for each of the species across $n = 10$ randomly selected realizations, over 2000 years; colouring as per Figure 5.11. The graph on the right shows detail of the early successional species (*H. arborea*, *P.excelsum* and *M. ramiflorus*).

When compared to data collected from the unfragmented forest the model represents the proportion of individuals of the different tree species reasonably well. Although the model under-predicted the abundance of medium size-class individuals in comparison with the field data, other size classes were adequately predicted, set against another study with a higher number of samples (West 1986). In spite of the discrepancy with the observed data the size-class distribution generated by the model is, in general, plausible. The mean diameters are lower than the reference unfragmented forest but the models' results are still within a plausible range. Mean basal area of *B. tawa* and *L. novae-zelandiae* was underestimated in comparison with the observed data and the basal area values presented in other studies (West 1986). Overall, the model manages to represent the key structural and successional patterns observed in the reference unfragmented forest and has the potential for future improvements in the areas highlighted above.

5.4 Sensitivity analysis

Due to the stochastic nature of most of the components of the model (e.g. initialization, dispersal, etc.) the outputs of the model vary even when the input values are fixed. We conducted a sensitivity analysis to assess how sensitive the model is to its parameterization. Given the uncertainties in the parameter estimations, I wanted to determine how plausible the dynamics of the model were. For the sensitivity analysis 12 input parameters and seven state variables were used. The parameters assessed for their sensitivity were seedling survival, seedling transition, shade tolerance, suppression mortality, suppression tolerance, dispersal, reproductive age, sapling survival, seed production, herbivory, edge effect and long distance dispersal (LDD). The outputs (state variables) I considered were abundance, age, dbh, height, mean age, mean basal area and mean height of *all* species.

Based on the point at which the composition of the simulated forest stabilises (Figure 5.11) 1000 years was deemed an appropriate interval of time to use in the sensitivity analyses. We changed the baseline values by ±20 % for all species, one parameter at a time, and ran the model 30 times for 1000 years. We repeated this process for all 12 parameters. Thus the sensitivity analysis constitutes a local 'one-at-a-time' approach (see Hamby 1994) and so does not consider either parameter interactions or changes in spatial pattern.

To estimate each parameter's sensitivity, the mean for each state variable across the 30 replicate runs of the model for each parameter of interest was calculated. Each parameters' sensitivity was quantified using the formula proposed by Hamby (1994):

$$S_{y,x} = (\Delta y / y_b)/(\Delta x / x_b) \tag{5.9}$$

where: $S_{y,x}$ is the sensitivity of the state variable y with respect to change in parameter x, Δx and Δy are the absolute change in x and y between the baseline and the change in baseline values (± 20 %) and x_b and y_b are the values under baseline conditions. We deemed state variables (y) with $S_{y,x} > 1$ sensitive to changes in parameter (x) (Hamby 1994).

For each species the sensitivity values ($S_{y,x}$) of the parameters were ranked according to the response of the state variables (Appendix 2). The rankings of each species were then averaged to generate an overall ranked sensitivity (mean of the mean rank). We calculated the sensitivity values only for those species that survived until the end of the each run (*B. tawa*, *L. novae-zelandiae* and *D. cupressinum*). The most sensitive parameters for *B. tawa* were edge response, suppression tolerance, the intensity of herbivory, the rate of seedling-to-sapling transition and seedling survivorship. For *L. novae-zelandiae* the most sensitive parameters were the intensity of herbivory, edge response and the suppression tolerance. Finally, in the case of *D. cupressinum* the most sensitive parameters were the intensity of herbivory, edge response, suppression tolerance and the rate of seedling-to-sapling transition (Figure 5.17 and 5.18, Table 5.3). The complete results of the sensitivity ranking exercise are summarized in Appendix 2.

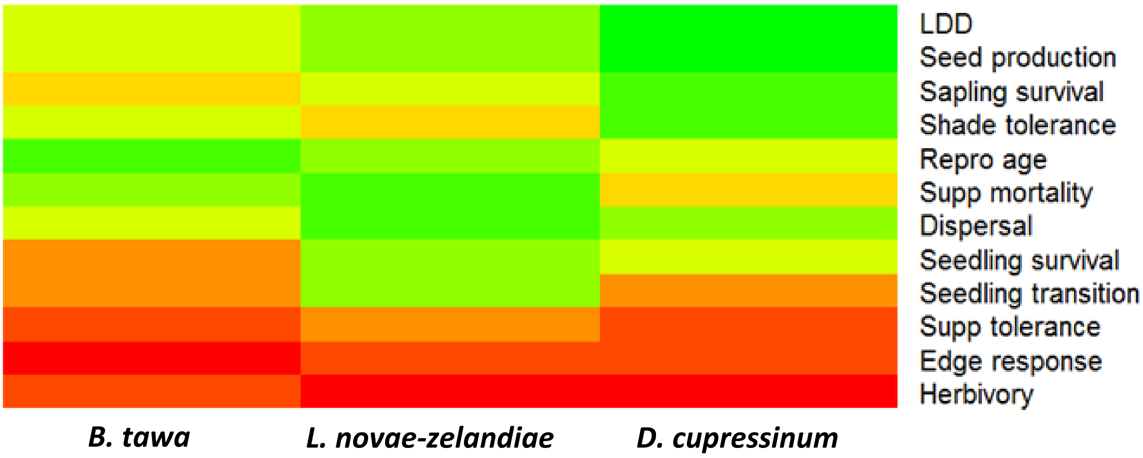


Figure 5.17 Heatmap showing the parameters' mean sensitivity rankings to a change of ± 20 % on all species parameters. The colour gradient from red to green represents high to low parameter sensitivity. Note that the ranks are reasonably consistent across all three species.

Table 5.3 Overall ranks of the parameters' sensitivity to a change of ± 20 % in *all* species parameters simultaneously. Description of the parameters is provided in Appendix 2. Species are (a) *B. tawa*, (b) *L. novae-zelandiae* and (c) *D. cupressinum*.

	Species			**Rank of the mean rank**
Parameter	**(a)**	**(b)**	**(c)**	
Herbivory	2	1	1	1
Edge response	1	2	2	2=
Suppression tolerance	2	3	2	2=
Seedling transition	3	6	3	3
Sapling survival	4	5	7	4=
Dispersal	5	7	6	5=
Reproductive age	7	6	5	5=
Seedling survival	3	6	5	4=
Shade tolerance	5	4	7	4=
Seed production	5	6	8	5=
LDD	5	6	8	5=
Suppression mortality rate	6	7	4	5=

We performed a second sensitivity analysis in which the baseline values of *B. tawa* were changed (by ± 20 %), while the parameterisation of all other species were held constant. The reason for this second analysis was to determine which parameters in the model control *B. tawa* dominance (it being the species of most interest). We used exactly the same approach as described above for the all species sensitivity analysis. The results showed that the most sensitive parameters for *B. tawa* were seedling survival, the rate of seedling-to-sapling transition, edge response, the intensity of herbivory and seed production (Table 5.4, Figure 5.18, Appendix 2). These sensitivity rankings were different from those obtained in the previous analysis considering all the species together, except for edge response which was ranked second in both analyses.

Table 5.4 Overall ranks of parameters' sensitivity to a change of ± 20 % on *B. tawa* state variables.

Parameter	**Overall ranking**
Seedling survival	1
Seedling transition	2=
Edge response	2=
Herbivory	3=
Seed production	3=
Suppression tolerance	4=
Sapling survival	4=
Shade tolerance	5=
Reproductive age	5=
Suppression mortality rate	6=
Dispersal	6=
LDD	6=

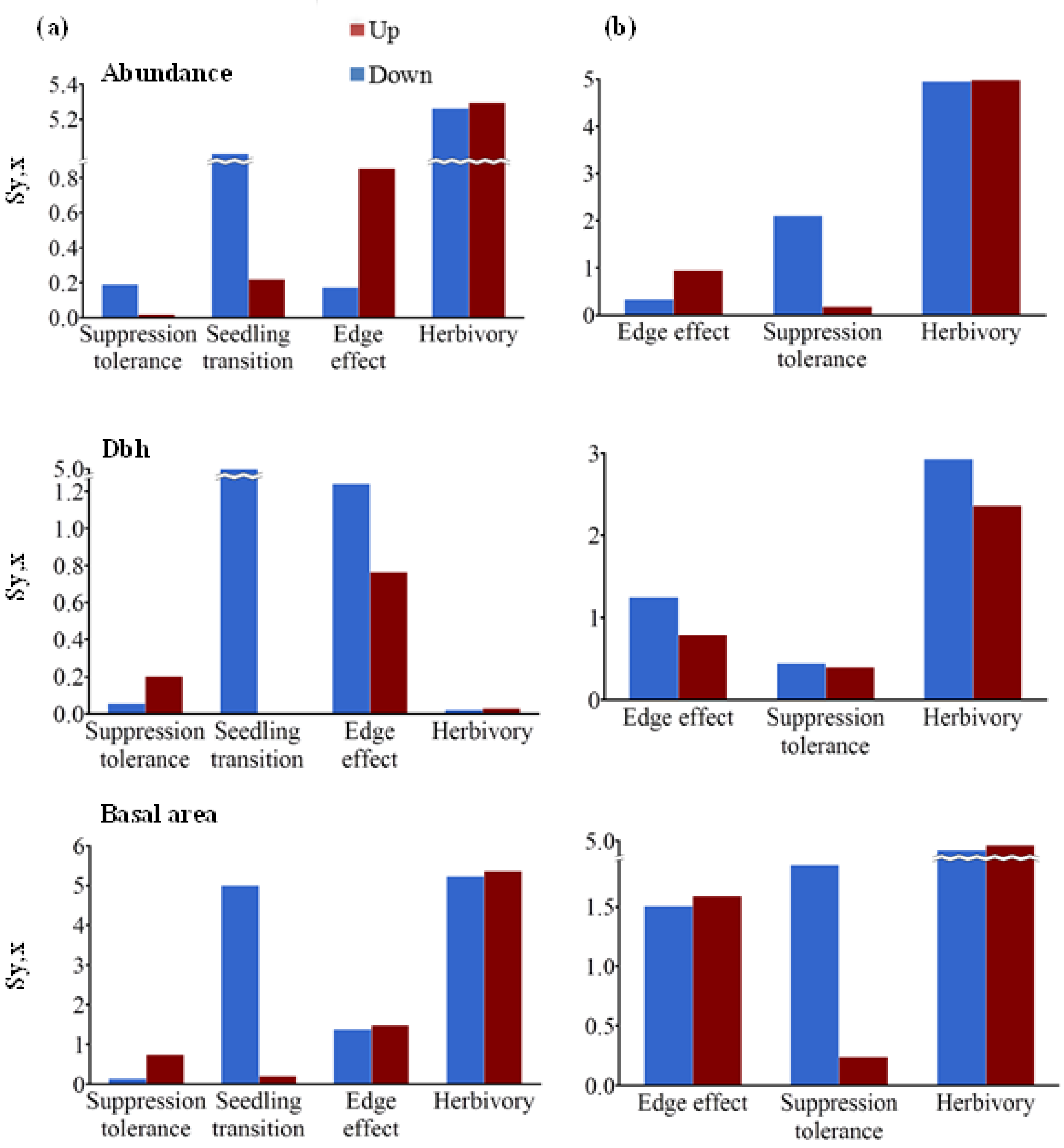


Figure 5.18 Sensitivity values ($S_{y,x}$) used in the sensitivity analysis on ± 20 % baseline values by parameter for the highest ranked parameters. Sensitivity responses for changes in parameters of all species for (a) *B. tawa*, (b) *L. novae-zelandiae* and (c) *D. cupressinum*. Sensitivity responses for changes only in *B. tawa* parameters are represented in graphic (d). Down represents the parameters default values (baseline fixed parameters values) minus 20 % and up represents the default values (baseline fixed parameters values) plus 20 %.

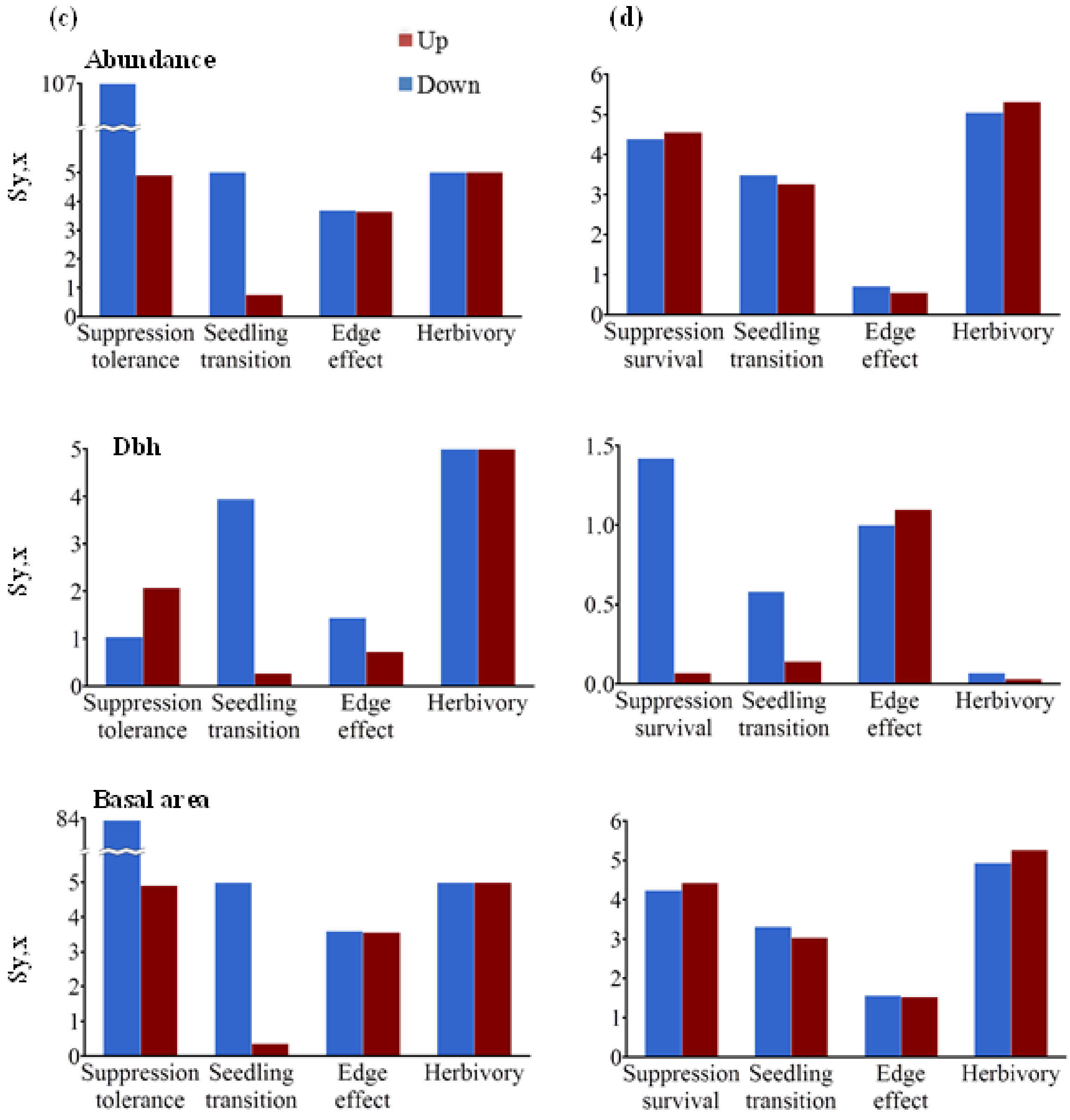


Figure 5.18 (continued) Sensitivity values ($S_{y,x}$) used in the sensitivity analysis on ± 20 % baseline values by parameter for the highest ranked parameters. Sensitivityresponses for changes in parameters of all species for (a) *B. tawa*, (b) *L. novae-zelandiae* and (c) *D. cupressinum*. Sensitivity responses for changes only in *B. tawa* parameters are represented in graphic (d). Down represents the parameters default values (baseline fixed parameters values) minus 20 % and up represents the default values (baseline fixed parameters values) plus 20 %.

The most sensitive parameters for *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* were those relating to anthropogenic influence (fragmentation and introduction of mammalian herbivores). In the analysis focussing on *B. tawa* it seems that the parameters that control its dominance are primarily those related to the early stages of its life cycle (seedling establishment) and changes in growth and survivorship cause by anthropogenic activities.

While there has been increased use of sophisticated reverse inference parameterization for forest simulation models, such approaches are computer intensive and require a large amount of data (Hartig et al. 2012, Hartig et al. 2014). Most of the sensitive parameters in the model were estimated using empirical data available in the literature (edge response, herbivory, etc). Making plausible parameter estimation for seedling survival, seedling transition and sapling survival was extremely difficult as there is relatively little published information available. The single most difficult parameter to estimate was sapling survival as there was little or no reliable information available for this for any of the species included in the model. Despite this, sapling survival in general had a sensitivity value of less than one meaning that the model's predictions were robust to it in most cases. Thus, any misestimating of that parameter should not unduly affect the robustness of the model's outcomes.

5.5 Conclusions

In this chapter I have provided a detailed description of a spatially explicit individually-based model (SEIBM) built to represent the long-term dynamics and viability of podocarp-tawa forest and, in particular, the fate of tawa (*B. tawa*). The main purpose of the first part of the chapter (Section 5.2) was to provide sufficient information about how the model represents fundamental ecological processes and how decisions about that representation were made. A baseline analysis was performed to determine how well the model captured the dynamics of a podocarp-tawa forest by comparing its performance with data obtained from an unfragmented forest. Finally, a sensitivity analysis was performed to determine how sensitive the model was to changes in the given parameter and variables (Section 5.4).

In New Zealand there have been only a few attempts to develop individual-based forest models. FORENZ, SORTIE/NZ and LINKNZ (DeVelice 1988, Kunstler et al. 2009, Hall and Hollinger 2000) represent the only three such efforts to date. These models were mostly developed for forests where members of the *Nothofagus* are the dominant species (FORENZ and SORTIE/NZ). LINKNZ provides the most comprehensive effort to test the applicability of a model to a wide range of species, providing insight into New Zealand conifer–hardwood and beech species forest successiosn. By contrast, the model developed here is one of the first attempts to model a podocarp-tawa forest and is designed to be used as a tool for long-term conservation strategies and restoration management activities. As such, my objectives were aimed at making the model simple enough to be modified to represent the dynamics of other forest types.

To set the parameters of the model I used a broad range of the available information regarding the New Zealand flora, and podocarp-tawa forests in particular. Most of the parameters were able to be estimated reasonably accurately. Despite an absence of empirical information for many of the species I represent, I endeavoured to incorporate all available information and corroborate that the parameters were reasonable and reflected real world dynamics. In general, the model’s estimations fell within plausible ranges. In some areas the model did not have a perfect fit with the field data but other studies showed that values were plausible (Chavasse and Travers 1966, West 1986, Smale et al. 2008). The differences I observed between what the model predicted and the available empirical data could be due to differences in the site characteristics (e.g. as type of soil, past history), which were not represented in the model. New Zealand native trees tend to be difficult to model as they can tolerate very long suppression periods (Smale et al. 1986, Hall and Hollinger 2000). Therefore the growth and mortality component of the model will need to be refined. Furthermore, the lottery mechanism described in this chapter needs to be improved because complete regeneration failure is not well represented. In scenarios where there is heavy herbivory and strong effect of fragment edge some simulations can drift towards a monodominant forest community because eventually a sapling will appear in a cell and make the transition to adulthood and, as described above, there is a strong lock-in between a species local density and its regeneration success. One way to represent regeneration failure might be to impose a probabilistic sapling density threshold which must be exceeded before the transition to adult stage occurs.

There is also a need to closely consider the spatial grain at which the model operates. ; a smaller patch size (5 x 5 m) may make the simulated fragments closer to the actual conditions of forest and fragments and so reduce some of the difficulties encountered in predicting density-based measures of forest structure. Diminishing the patch size could be very demanding in terms of computing resources so the use of supercomputing or Beowulf clusters may become necessary. In addition, the use of long term data (e. g. permanent plots as in the NIVS data base) to evaluate the outputs of the model and will be an excellent way to help to refine the model. Future modelling should initially be focussed on forest fragments that have long term data available. The addition of a module that account for soil or climate conditions would help to simulate the fragments under different conditions and also allow future researchers to determine the potential effect of climate change on forest and fragments.

The sensitivity analysis showed that the most sensitive parameters are, in general, those for which I had the most information available; that is, I was able to feed the model more accurate information regarding these parameters. The most sensitive parameters were in general the ones that represented anthropogenic activities (e.g. introduce herbivores, fragmentation) and the demography of the juvenile life-cycle stages (e.g. seedling survivorship). It is worrying that the same activities described by these parameters are also described as the current threats to these ecosystems (Dodd and Power 2007, Smale et al. 2008). Although the model can be improved (as any model can), I believe it is a useful tool and one capable of accomplishing the objectives for which it was designed. That is, it can serve as a valuable resource to both managers and decision makers regarding the long-term persistence of podocarp-tawa forest patches.

6. A SCENARIO-BASED EVALUATION OF THE LONG-TERM DYNAMICS OF PODOCARP - TAWA FOREST FRAGMENTS

6.1 Introduction

In Chapter 5 I described (i) the implementation of a spatially explicit individually-based model (SEIBM) designed to represent the long-term dynamics and viability of podocarp-tawa forest fragments under different management regimes (unfragmented forest, fenced and unfenced fragments) and (ii) a sensitivity analysis of that model. The sensitivity analysis showed that the most sensitive parameters were, in general, the ones that represented anthropogenic activities (e.g. introduced herbivores, fragmentation) and the demography of the juvenile life-cycle stages (e.g. seedling survivorship). In Chapters 2 and 3 I presented a series of analyses that, when combined, suggest that, in isolation, fencing as a management activity may be insufficient to ensure the survivorship of forest patches in some situations. In this chapter I use the model presented in Chapter 5 to answer two questions: (1) can forest fragments persist in the long-term (500 years) under current conditions with no further interventions and (2) to assess whether and how different restoration management activities (e.g. fencing, intensive restoration activities such as planting) affect the long-term fate of podocarp-tawa forest fragments.

As described in Chapter 1, restoration management activities can be loosely dichotomised as being either passive or interventionist (Holl and Aide 2011). The passive approach consists of performing one-off activities, such as fencing remnant vegetation, and then leaving the ecosystem to recover by itself. By contrast, a more interventionist approach involves performing ongoing actions to intervene in the ecosystem (e.g. planting seedlings, amending soils, translocation of birds, ongoing predator control) to kick-start or speed up its recovery.

Passive restoration is the typical practice for forest communities in New Zealand. One standard restoration management practice is to fence off forest fragments to keep out large herbivores (e.g. cattle and sheep) often followed by small mammalian pest control (Dodd et al. 2011, Burns et al. 2012). However, Burns et al. (2011) found that, in the Waikato, even with fencing and pest control indigenous species richness in fragments did not return to the levels seen in intact forest, nor did they allow canopy species to establish to levels sufficient for their replacement. Likewise, Myers and Court (2013) found that in fenced fragments on Tiritiri Matangi Island (Hauraki Gulf) even with active restoration the density of *B. taraire* did not increase but actually declined.

To determine the extent to which passive and/or interventionist approaches may facilitate the long-term persistence of forest fragments and the survival of key canopy species, I used a spatial simulation model to evaluate some of the key factors that might enhance restoration success. These factors included fencing itself, the seed rain from outside the fragment, edge effects and restoration activities (i.e. planting of seedlings). Because, in general, the effect of restoration activities in forest ecosystems can only be detected over the long-term (e.g. decades or even centuries), directly evaluating their impact is extremely challenging (Coreau et al. 2009). Furthermore, systematically testing the effect of these different activities in different combinations is effectively logistically impossible in the field. To circumvent the timeframe and impracticality problem I used a scenario-based simulation approach. The simulation of scenarios starts with a modelled ecosystem and adds a combination of processes such as long distance dispersal, seedling planting, herbivory, etc., to evaluate how these processes affect the long-term persistence of the forest ecosystem. The outcomes of the simulations are both qualitative (e.g. spatial distribution, graphical analyses) and quantitative (e.g. species abundances), both of which are important in understanding the underlying issues affecting ecosystem dynamics.

6.2 Methods

6.2.1 Long-term persistence of podocarp-tawa forest communities

I used the model described in Chapter 5 to explore the long-term dynamics of podocarp-tawa fragments across a range of management contexts, representing both fragmentation and fencing: unfragmented forest, fenced forest fragments and unfenced forest fragments (as described in Chapter 2). To simulate the dynamics of an unfenced fragment, the herbivory and edge effect would be 'on', in the case of fenced fragments only the edge effect would be 'on', and for forest fragments both switches would likely be 'off'. I used a timeframe of 500 years and performed 30 realisations per management activity. To avoid confounding management context with fragment area the simulation area was fixed at 25 ha for all scenarios. I used data obtained from the field to initialize the different scenarios (unfragmented forest, fenced fragment and unfenced fragment) (see Chapter 5). The abundance of the regeneration bank (seedlings and saplings) and canopy trees (i.e. the identity of the individual occupying each grid cell) across each species were used as measures of the condition of the forest.

6.2.2 Enhancing the long-term persistence of late successional species

Having considered both fragmented and unfragmented forests I evaluated the dynamics of dominant canopy species (represented by *Beilschmiedia tawa*, *Laurelia novae-zelandiae* and *Dacrydium cupressinum* in this model) in a 9 ha fenced forest fragment (30 × 30 grid of 10 × 10 m cells) under a range of different conditions for 100 years, again with 30 realizations per scenario. Although my forest fragments were on average < 5 ha (See Chapter 2), I chose to simulate a 9 ha fragment because a smaller fragment size would be impractical due to the model cell size. The percentage of area exposed to the edge effect (here a strip four [40 m] cells wide) in the 9 ha fenced forest fragment is 46 % of the total area which is almost the half of the fragment; in a larger fragment (25 ha) the impacted area by the edge effect would be 29 % of the total area. I used a shorter timeframe in these model evaluations, 100 instead of 500 years, as most restoration activities consider a timeframe of decades rather than centuries. Unfenced fragments were not considered in these evaluations because preliminary simulations showed that such fragments were unable to support the species of interest (Section 6.3.1).

To initialize the different scenarios I used data obtained from the field as described in Chapter 5. The scenarios that I simulated were the presence of long-distance seed dispersal (LDD) and restoration activities (planting of saplings into the fragments). The total long-distance seed dispersal (LDD) is calculated using a binomial distribution based on each species' abundance in the simulated landscape and the proportion of seeds actively dispersed between fragments by each species (p_{LDD}). p_{LDD} was set to 0.01 for all species (see Chapter 5). This representation of long-distance seed dispersal (LDD) assumes that the landscape as a whole is compositionally similar to the fragment. The purpose of evaluating the level of LDD was to determine whether the influx of seeds from nearby forests or fragments has any influence on the survivorship of the studied species (i.e. via buffering effects). Enhancing the provision of LDD is one desirable outcome of large restoration sites (such as Te Miro and Maungatautari) because they can act as a source of seeds for the surrounding areas, known as the "spill-over effect" (Brudwig et al. 2009).

Restoration planting was simulated by adding one sapling of *B. tawa, L. novae-zelandiae* and *D. cupressinum* to the sapling bank every five years (see Chapter 5); this equates to a planting density of 100 individuals per species per hectare. I set the interval at five years for two reasons: logistics and the availability of plant material. From a logistical point of view, fragments are usually located on privately-owned land and may have difficult access. Performing large-scale planting campaigns can disrupt farming activities in the surrounding areas and moving a huge quantity of plants to the fragments requires specialized vehicles (e.g. 4 × 4 trucks). Also, in my experience plant material can be very difficult to obtain (e.g. *B. tawa*) as only some specialized nurseries produce them; a five-year timeframe secures seedling availability.

LDD and planting were set to ‘on’ and ‘off’ producing four management combinations (e.g. LDD on × restoration off). I also varied the herbivory effect over three levels, from the complete absence of herbivory to a scenario where herbivory was persistent and intense. The herbivory scenarios were based on the fact that although fencing controls large mammalian herbivores (e.g. cattle, sheep) it provides little, if any, protection against small exotic mammalian herbivores (e.g. possums, rabbits, rats and mice). For the ‘normal’ herbivory scenario I used the same parameters as in Chapter 5 (Section 5.3). I decreased the herbivory parameter by 50 % to represent a lower impact herbivory scenario (e.g. cattle and sheep excluded and some ongoing control of small mammals). For all simulations, unless otherwise noted, I used the same parameter values that were used in the baseline and sensitivity analyses described in Chapter 5. The different scenarios and their parameterisation are shown in Figure 6.1 in the form of a pseudo-factorial design tree.

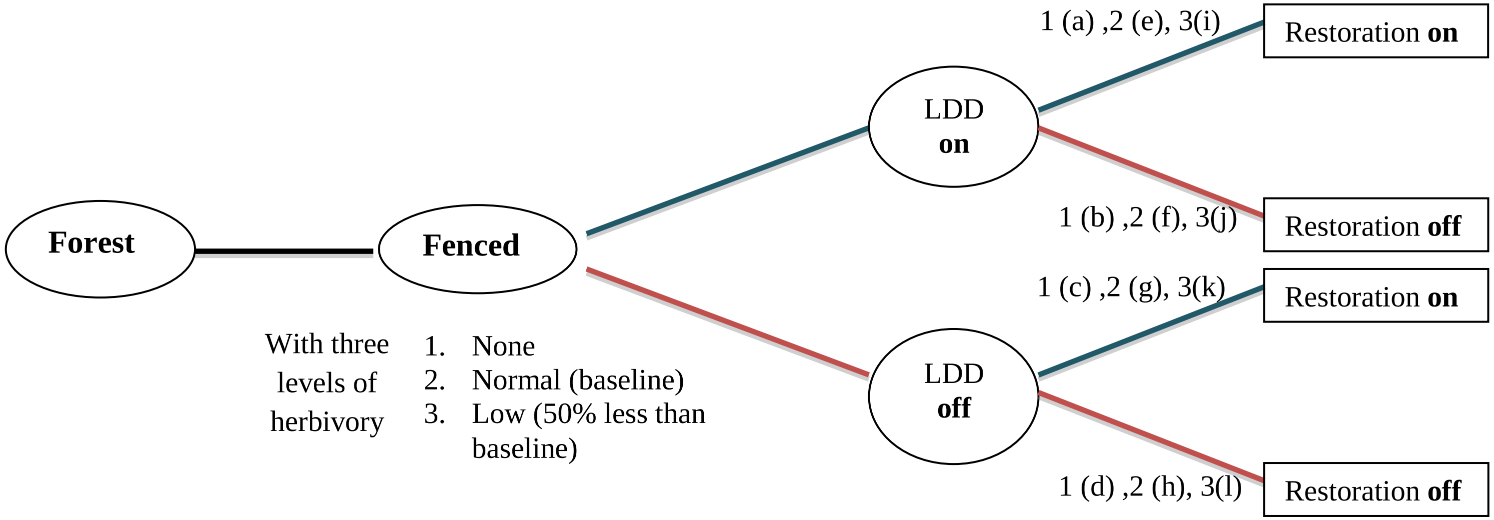


Figure 6.1 Schematic representation of the scenarios evaluated in this Chapter. Red lines indicate parameters that have been turned 'off'; blue lines indicate parameters that have been turned 'on'; $n = 30$ realisations for each of the 12 scenarios evaluated. Numbers indicate the herbivory treatment and letters correspond to the scenarios depicted in Figure 6.12.

I graphically analysed the abundance of the tree species, the composition of the regeneration bank (seedlings and saplings) and the basal area of the dominant late-successional species (*B. tawa*, *L. novae-zelandiae* and *D. cupressinum*) included in the model as measures of the effect of restoration on the forest communities. Although the model under predicts basal area, in a relative sense it is adequate for the purposes of this study. I grouped the different scenarios according to their effect on the abundance of adults of *B. tawa*, *L. novae-zelandiae*, *D. cupressinum* and for all six species using hierarchical agglomerative classification using the Euclidean distance and Ward's linkage method to identify similar clusters (Ward 1963). These classification analyses are portrayed as dendrograms.

6.3 Results

6.3.1 Long-term survival of forest fragments

At the end of the 500-year runs *B. tawa* and *L. novae-zelandiae* were the dominant species in the unfragmented forest with an abundance of 46.0 ± 3.0 and 44.0 ± 3.0 individuals per ha, respectively (mean ± 1 SD; $n = 30$); *D. cupressinum* and *H. arborea* had an abundance of 7.0 ± 1.0 and 0.3 ± 0.2 individuals per ha, respectively ($n = 30$). *D. cupressinum* started to decline after 200 years and *H. arborea* after approximately 50 years. The other two species present at the start of each model run (*P. excelsum* and *M. ramiflorus*) were absent after 500 years, and, in fact, began to decline after just 10 and 20 years, respectively (Figure 6.2a).

The regeneration bank in the unfragmented forest showed a similar temporal pattern to that seen in the canopy trees. The dominant species in the regeneration bank (seedlings plus saplings) were *B. tawa* and *L. novae-zelandiae* 1022.0 ± 73.0 and 975.0 ± 67 individuals per ha, respectively (on average). *D. cupressinum* and *H. arborea* had abundances of 162 ± 29.0

and 9.0 ± 6.0 individuals per ha, respectively. The *D. cupressinum* and *H. arborea* regeneration bank started to decline at the same time as the canopy trees (Figure 6.2b and 6.5). However the decline is less abrupt and is slower than that of the corresponding adult tree abundance (Figure 6.2).

Basal areas (m^2/ha) of *B. tawa* and *L. novae-zelandiae* are very similar, suggesting that individuals of these species are of similar size. The high basal area and low abundance of *D. cupressinum* suggests the persistence of scattered, but large, individuals. *H. arborea* has a low abundance and low basal area, which indicates the presence of few, small individuals, probably highly supressed by the dominant canopy trees (Figure 6.5).

The spatial pattern of the unfragmented forest after 500 years showed that *B. tawa* tends to form medium size tree clusters (Figure 6.2c). *D. cupressinum* also forms clusters but with a smaller number of large individuals, which reflects the biology of these long-lived pioneers (see Ogden and Stewart 1995). *L. novae-zelandiae* trees are more continuously distributed across the forest, reflecting its shade-tolerance. A few individuals of *H. arborea* are scattered through the forest – having occasionally captured tree fall gaps – with no strongly discernible spatial pattern (Figure 6.2c).

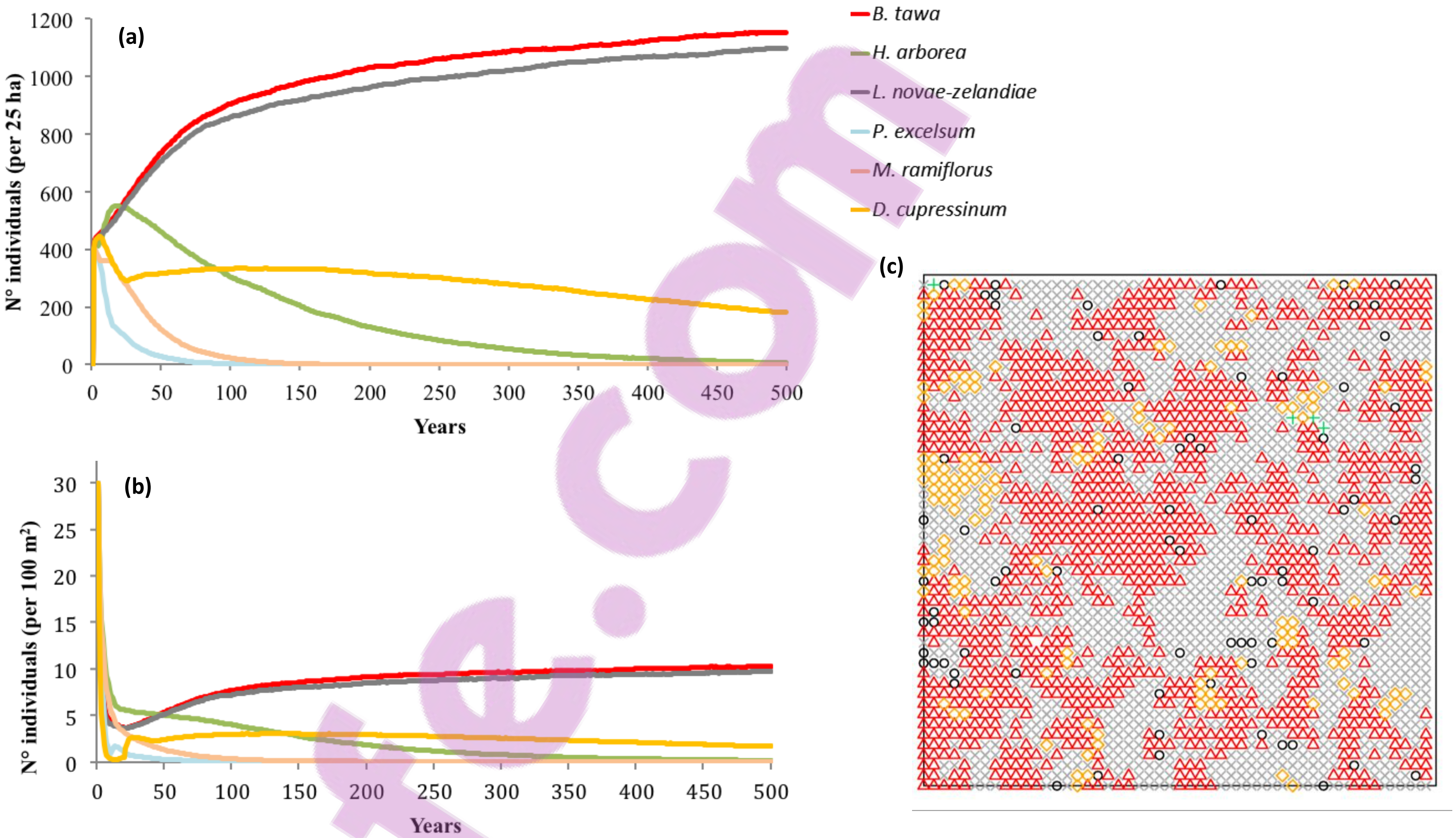


Figure 6.2 Average number of individuals resulting from a long-term simulation (500 years) of an unfragmented forest (25 ha) across *n* = 30 realizations, (a) adult tree abundances by species, (b) combined seedling and sapling abundances by species and (c) spatial distribution of trees in the unfragmented forest after 500 years, black circles denotes no tree presence.

In the fenced forest fragments, the dominant species were *B. tawa* and *L. novae-zelandiae* with mean density of 42.0 ± 3.0 and 41.0 ± 3.0 individuals per ha, respectively (almost identical to the unfragmented forest scenarios). *H. arborea* had a mean density of 9.0 ± 2.0 individuals per ha at the end of the experiment (500 years). The abundances of *H. arborea* were consistently higher (around 20%) than in the unfragmented forest, probably due to the species being favoured by edge effects. *D. cupressinum* and *M. ramiflorus* had the same mean density of 2.0 ± 1.0 individuals per ha. *P. excelsum* disappears approximately 70 years after the start of the simulation (Figures 6.3a and 6.5). *H. arborea* suffered a marked decline in density around 70 years but maintains its presence, albeit at low density, until the end of the 500 year model run. *D. cupressinum* never surpasses *H. arborea* density, and in fact almost disappears by the end of the simulations (Figures 6.3a and 6.5).

The regeneration bank (seedlings plus saplings) in the fenced fragments shows a trajectory similar to that seen in the canopy trees although the absolute abundances are, on average, 20 % lower. There are a high numbers of *B. tawa* and *L. novae-zelandiae* individuals in comparison with the others species, 876.0 ± 65.0 and 858.0 ± 65.0 individuals per ha, respectively (Figure 6.3b and 6.5). *H. arborea* is the third most abundant species with individuals (seedlings and saplings, combined) 185.0 ± 41.0 individuals per ha, which is consistent with the density of adult individuals. *D. cupressinum* and *M. ramiflorus* had the lowest presence in the regeneration bank with a density of 44.0 ± 12.0 and 33.0 ± 17.0 individuals per ha (seedlings and saplings, combined) at the end of the 500 year experiment (Figures 6.3b and 6.5).

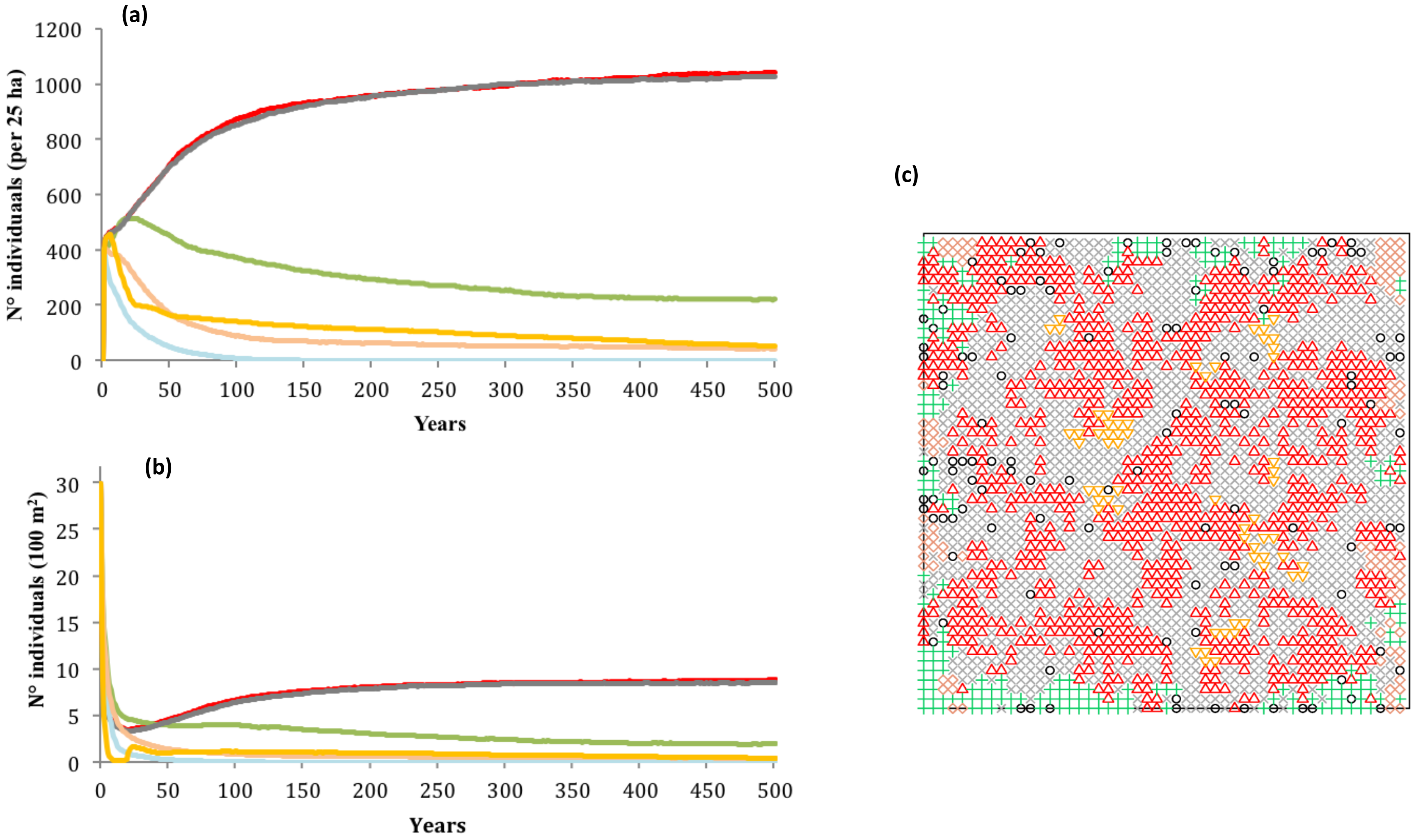


Figure 6.3 Average number of individuals resulting from a long-term simulation (500 years) of a fenced forest fragment (25 ha) with *n* = 30 realizations. (a) adult tree abundances by species, (b) combined seedling and sapling abundances by species and (c) spatial distribution of trees in the fenced forest fragment. Colouring and symbology as per Figure 6.2.

Basal areas of the two dominant canopy species, *B. tawa* and *L. novae-zelandiae* are similar to each other, but they are lower than in the unfragmented forest (Figure 6.5). Similarly, the abundance of these species is also lower than in the unfragmented forest; the abundance of smaller individuals is likely because trees near the edges are supressed due to the edge effect on growth. *D. cupressinum* has fewer individuals (lower than in the unfragmented forest) but maintains a high basal area, again indicating the presence of old large trees (Figure 6.5). *H. arborea* has a higher basal area and abundance than in the unfragmented forest scenarios. *M. ramiflorus* has a low basal area combined with low abundance because it is restricted to the margins of the fragment (Figure 6.5).

In terms of the spatial distribution of species in the fenced forest fragment, *B. tawa* and *L. novae-zelandiae* generally establish away from the edges. Some individuals of both species do survive in the edge and on average *B. tawa* and *L. novae-zelandiae* account for 27 % and 33 % of the individuals inhabiting the edge, although they are highly suppressed. *D. cupressinum* tends to avoid the edges and forms clusters of trees towards the centre of the fragment. *H. arborea* and *M. ramiflorus* do not dominate the edges of the forest fragment. *H. arborea* performed notably (and consistently) better 27 % of individuals) than *M. ramiflorus* (13 % individuals) (Figure 6.3c and 6.5).

In stark contrast to the dynamics seen in the simulated unfragmented forest and the fenced fragments, after 500 years the unfenced forest fragment is dominated by just one species, *B. tawa* (98.0 ± 0.4 individuals per ha; Figures 6.4a, 6.4c and 6.5), in all of the realizations (n = 30). *D. cupressinum* and *L. novae-zelandiae* persisted until the end of the runs but only at very low abundances, 0.05 ± 0.05 and 2.0 ± 0.04 individuals per ha, respectively (Figure 6.4a and 6.4c). The regeneration bank showed a similar pattern, *B. tawa* abundance was 2609.0 ±

59.0 individuals per ha which is an increase of 61 % relative to the unfragmented forest (Figures 6.4b and 6.5). *L. novae-zelandiae* and *D. cupressinum* had low seedling and sapling density of 31.0 ± 7.0 and 0.5 ± 0.63 individuals per ha respectively (Figures 6.4b and 6.5). At the end of the 500-year simulation, *B. tawa* basal area was very high in comparison with the other species present in the fragment. Based on their basal area and abundance both *L. novae-zelandiae* and *D. cupressinum* persist in the form of large individuals, but at very low density (Figure 6.5).

The simulated abundances and basal area values suggest that the composition of the unfenced forest fragment collapsed at some point before the end of the simulation period of 100 years. At least in part this dynamic happened because the model cannot adequately represent a complete failure of regeneration; the lottery mechanism described in Chapter 5 means that so long as there is one individual present in the regeneration bank that species will eventually capture an empty site (ways this representation could be improved are discussed in Section 5.X). Because the model does not represent complete regeneration failure, I deemed that collapse had happened when the forest became mono-dominant, that is when a single species dominates (occupies more than 50% of) the canopy. This mono-dominance occurs because of the representation of gap capture in the lottery model process coupled with the positive feedback between local abundance and regeneration described in Chapter 5. It is important to note that a species becoming mono-dominant never occurred before under baseline conditions described in Chapter 5 or in our most degraded fragments in the field. The results of this simulation suggest that without fencing and with high levels of herbivory a forest fragment is extremely unlikely to persist in a compositionally diverse state over the long term (Figure 6.5).

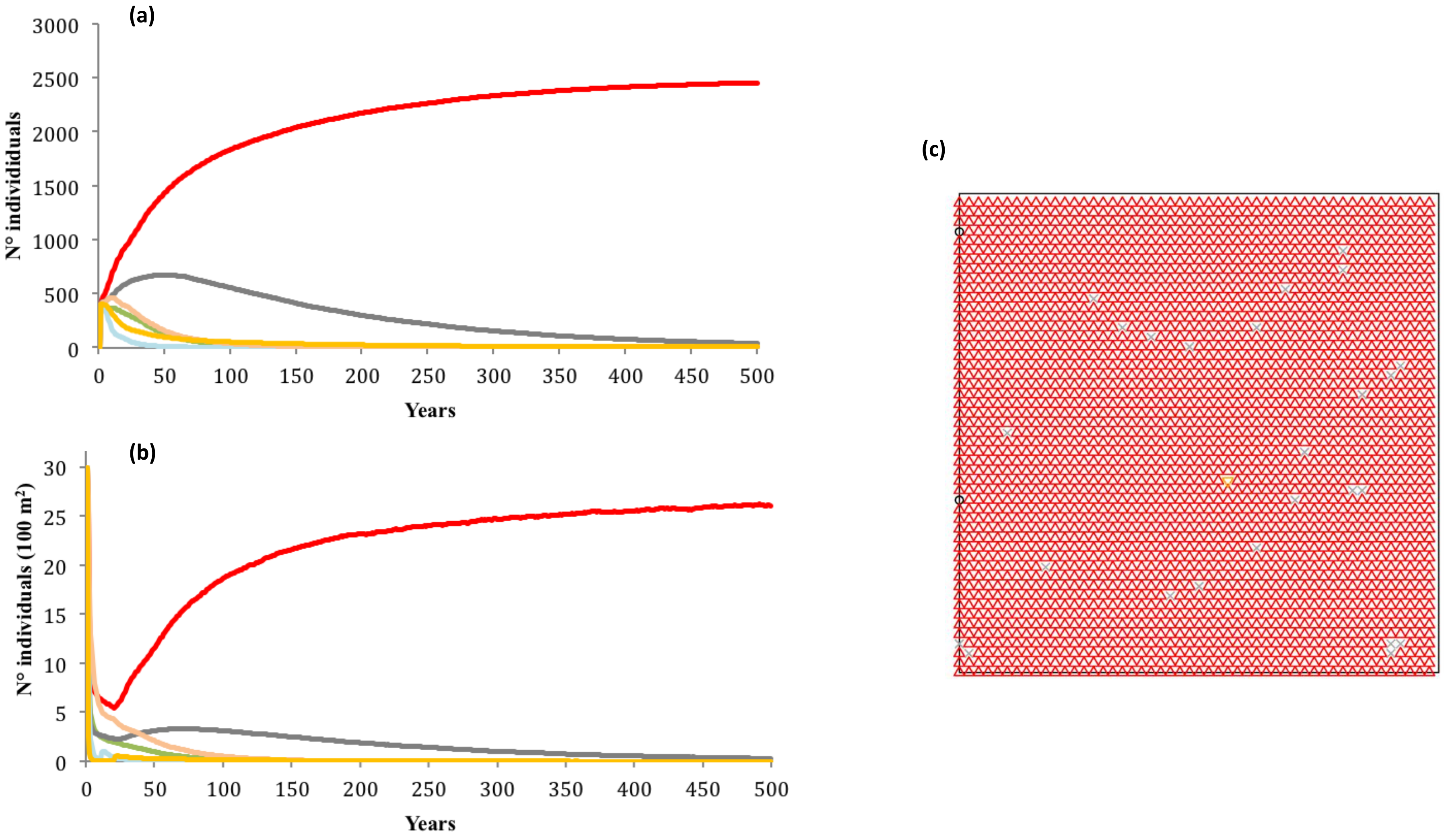


Figure 6.4 Average number of individuals resulting of a long term simulation (500 years) of unfenced forest fragment with *n* = 30 realizations. (a) adult tree abundances, (b) combined seedling and sapling abundances and (c) spatial distribution of trees in the unfenced forest. The unfenced forest fragment will collapse in 43.8 ± 10.5 years (mean ± 1 SD). Colouring and symbology as per Figure 6.2.

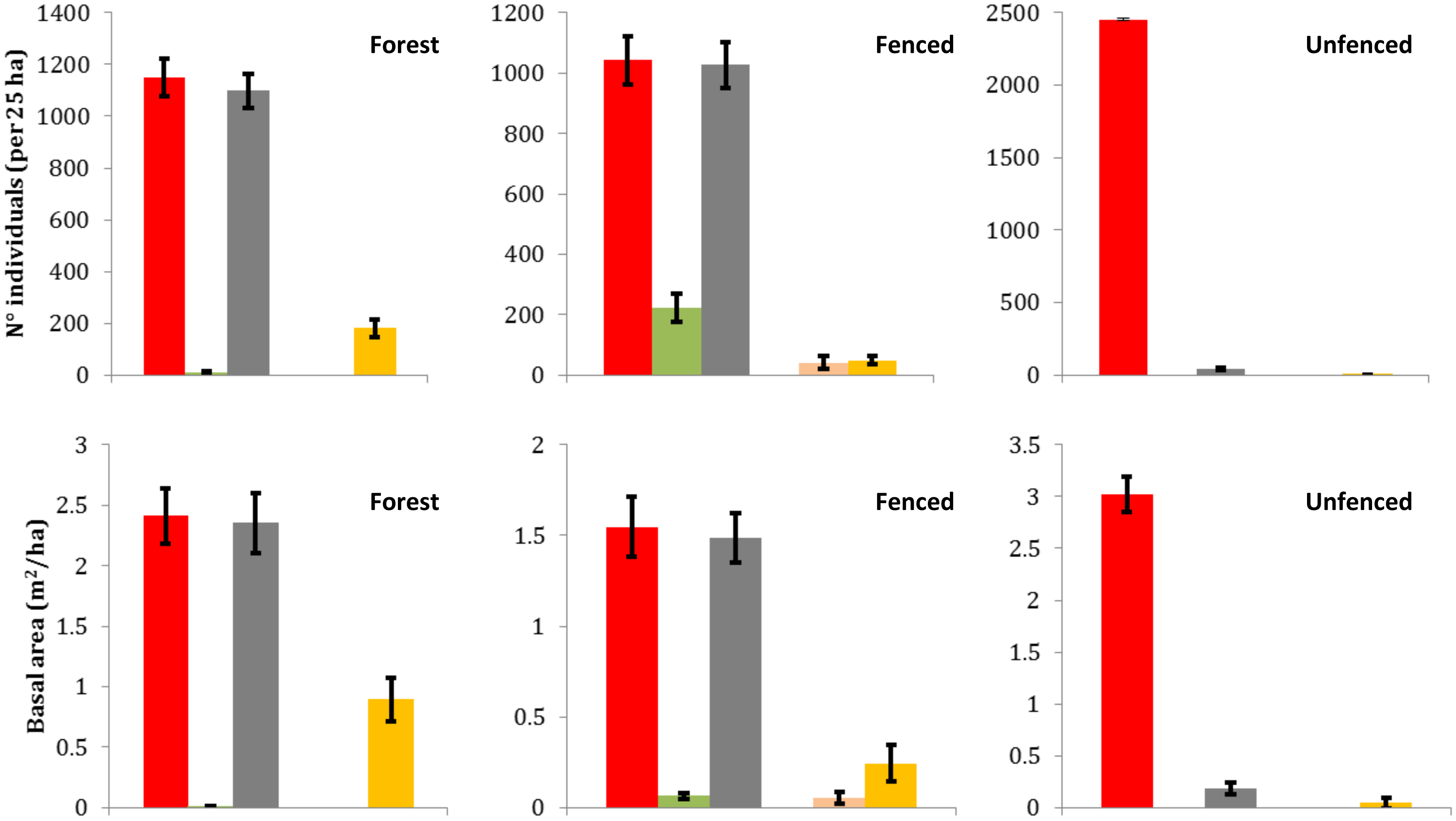


Figure 6.5 Mean number of individuals and mean basal area resulting of a long term simulation (500 years) for unfragmented forest (forest), fenced fragment (fenced) and unfenced fragment (unfenced) management with *n* = 30 realizations, colouring as per Figure 6.2. Errors bars represent standard deviation (1 ± SD).

6.3.2 Long-term survival of late successional tree species

Fenced fragments without herbivory

Simulation experiments showed that long distance dispersal (LDD) had only a minimal effect on the abundance of *B. tawa* (32.0 ± 4.0 and 31.0 ± 4.0 individuals per ha with LDD off/on), *L. novae-zelandiae* (31.0 ± 3.0 and 33.0 ± 4.0 individuals per ha with LDD off/on) or *D. cupressinum* (4.0 ± 1.0 and 4.0 ± 1.0 individuals per ha with LDD off/on) (Figure 6.6). However, a slight effect on the abundance of seedlings and saplings of *L. novae-zelandiae* was detected. An average increase of 8 (158 ± 11 and 166 ± 16 individuals per ha with LDD off/on), and 12 (147 ± 18 and 206 ± 23 individuals per ha with LDD off/on) individuals per ha for the 70 and 100-year period respectively was seen when LDD was active; such marginal increases are unlikely to be ecologically significant (Figure 6.7b and 6.7c). Despite the fact that LDD did not strongly influence the abundance of the species, it is worth noting that LDD has other benefits that this model does not consider (e.g. genetic mixing) that could protect or enhance an ecosystem (Fayard et al. 2009).

Restoration activities (planting) helped to maintain a community composition similar to that seen in simulations of an unfragmented forest, irrespective of whether LDD was intact. *B. tawa, L. novae-zelandiae* and *D. cupressinum* were the dominant species in these scenarios. Abundances of *B. tawa* and *L. novae-zelandiae* were almost identical to the unfragmented forest simulations (on average within ± 2.0 individuals [or less than 0.25 individuals/ha] after 100 years). *D. cupressinum* had a higher abundance in the fenced fragment under restoration (22.0 ± 2.0 individuals per ha) than in the unfragmented forest (13.0 ± 2.0 individuals per ha). *H. arborea* abundance decreased from 12.0 ± 1.4 individuals/ha in the unfragmented forest to 2.0 ± 0.6 individuals in the fenced fragment under restoration (with LDD active) (Figure 6.6).

The decrease in abundance of *H. arborea* can be explained because it was not planted and as consequence was under-represented in the lottery competition for canopy space.

In terms of the regeneration bank, the number of seedlings and saplings in the fenced fragment under restoration planting was lower than in the unfragmented forest (e.g. *B. tawa* for 254.0 ± 12.0 versus 760.0 ± 43.0 individuals per ha; Figures 6.7a and 6.7b). This reduced density is an outcome of the edge effect in the fragmented forest.

The spatial distribution of species did not appear to change in the presence of LDD. *D. cupressinum* form small clusters of trees and *B. tawa* had a patchy distribution. *L. novae-zelandiae* tends to form a more continuous distribution although some clustering of trees is apparent. *H. arborea* established throughout the fragment; *M. ramiflorus* mainly colonized the borders of the fragment. *P. excelsum* was present in small numbers near the edges and scattered across the fragment (Figure 6.8).

With restoration planting the spatial distribution of the species changed dramatically. *B. tawa, L. novae-zelandiae* and *D. cupressinum* were widespread throughout the fragment, even establishing near the edges. Of the early successional species, *H. arborea* was scattered in small numbers and *M. ramiflorus* and *P. excelsum* were absent, which indicates that these species would be supressed by the larger shade-tolerant species (Figure 6.8).

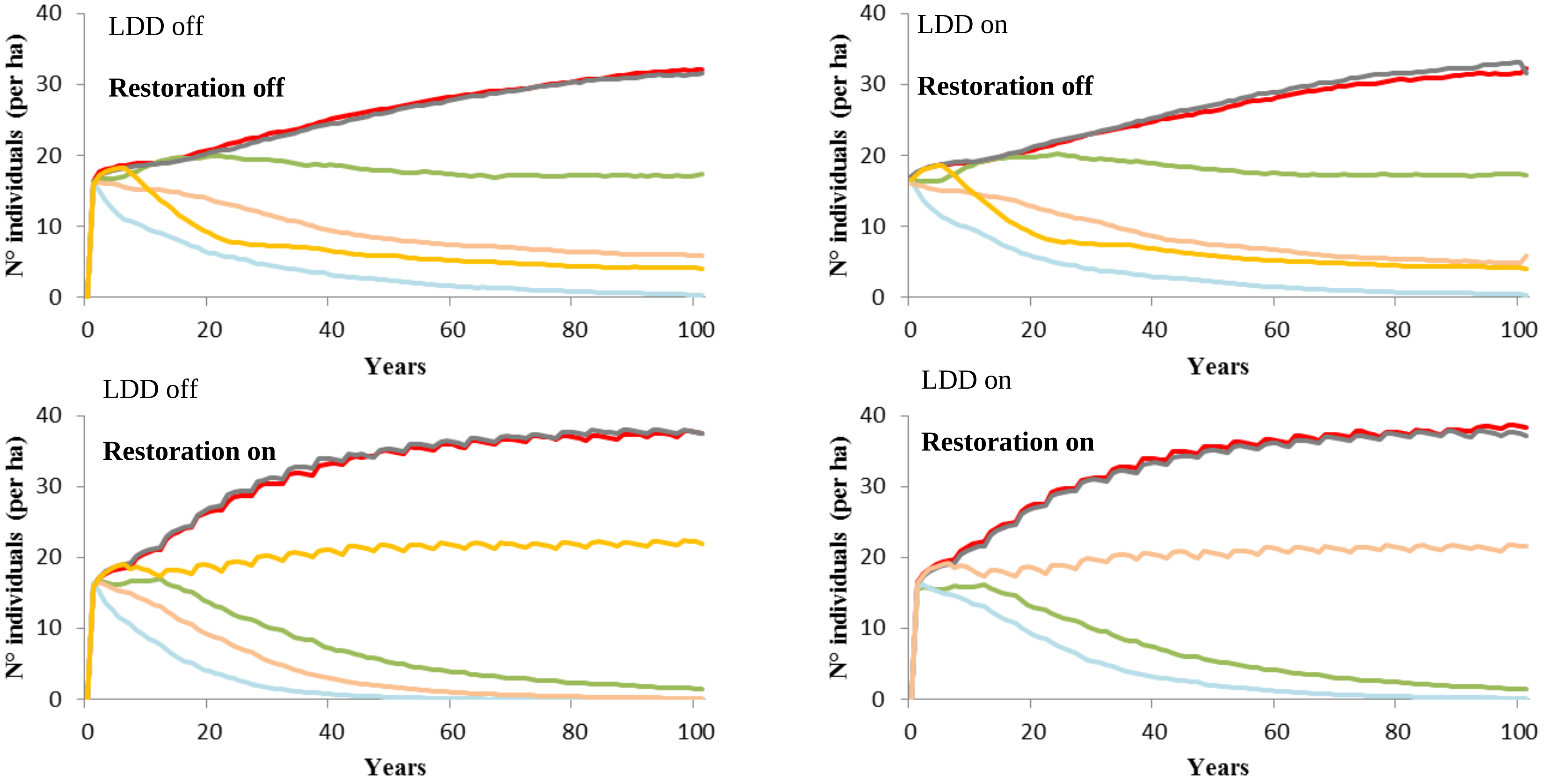


Figure 6.6 Mean abundances of trees in fenced forest fragment (9 ha) with no herbivory under different management strategies, figures were built using *n* = 30 realizations. Colouring and symbols as per Figure 6.2. Restoration refers to planting of individuals of *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* every 5 years (which is reflected in the repeated pulses in their abundance).

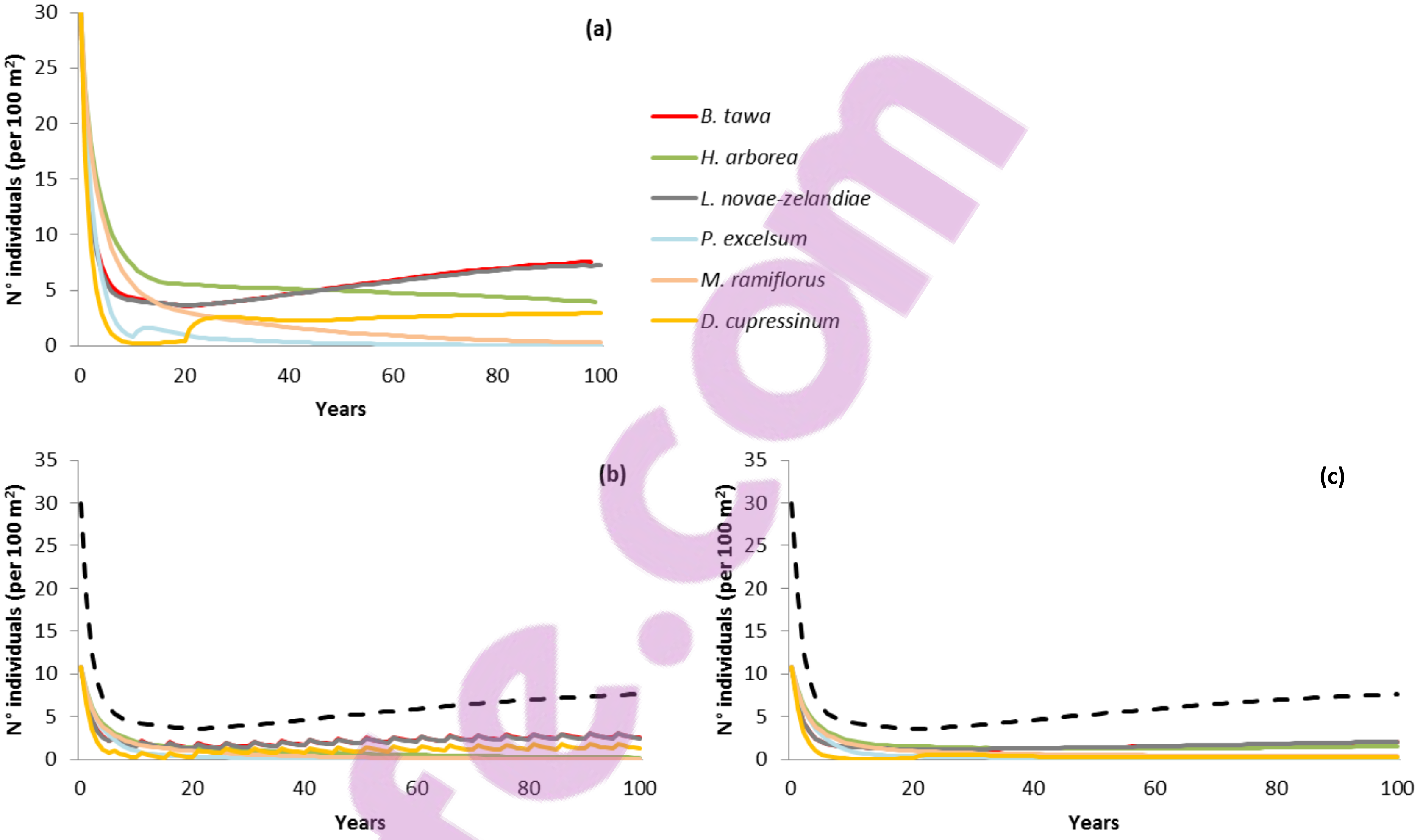
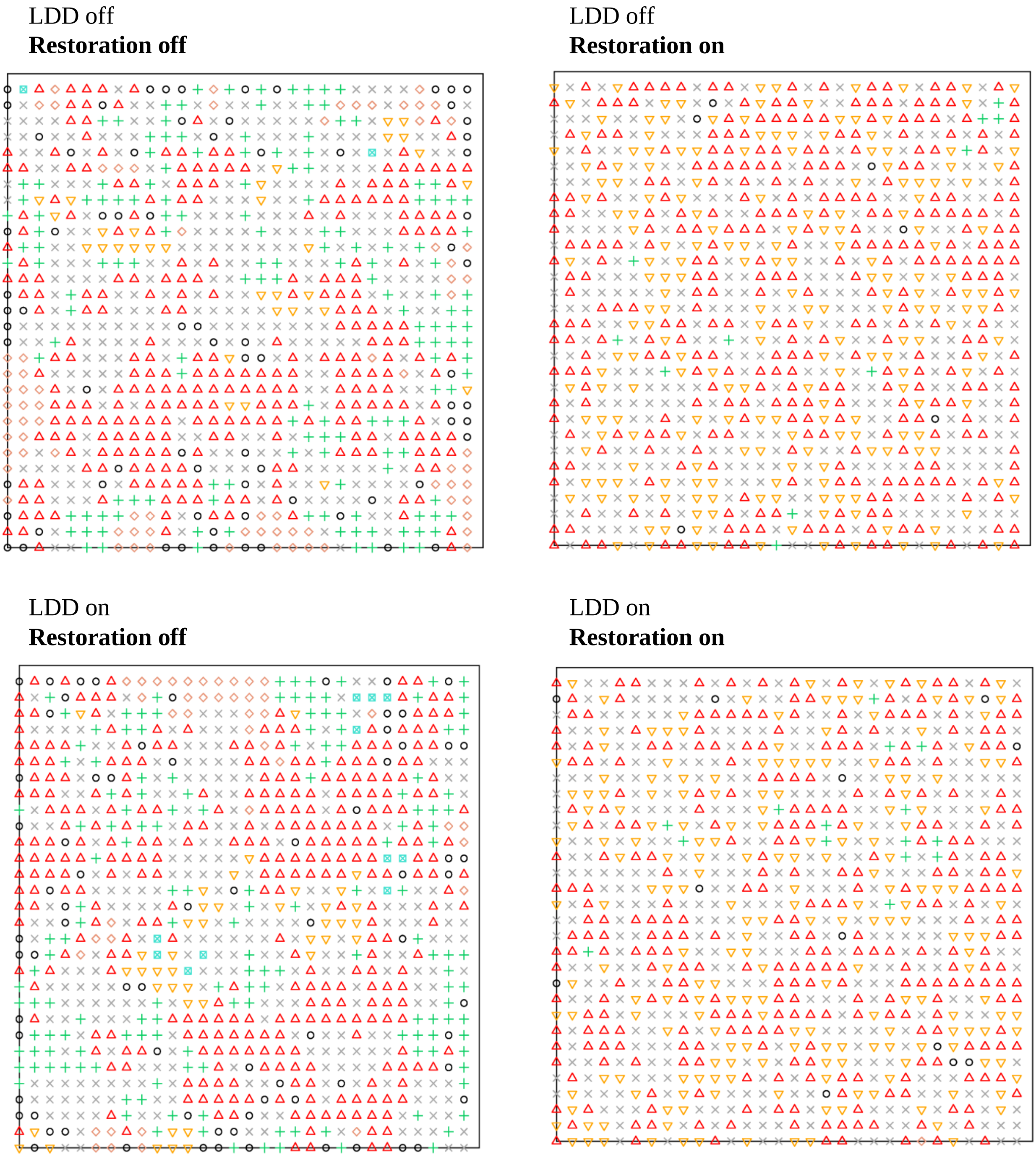


Figure 6.7 Average regeneration bank abundances (seedlings and saplings) with *n* = 30 realizations in (a) unfragmented forest, (b) fenced fragment with restoration activities (LDD active) and (c) fenced fragment without restoration (LDD active). The sawtooth pattern in (b) clearly shows the effect of pulsed recruitment via seedling planting. Black dashed lines represent the average of individuals of *B. tawa* in unfragmented forest.



LDD off
Restoration off

LDD off
Restoration on

LDD on
Restoration off

LDD on
Restoration on

Figure 6.8 The simulated spatial distribution of trees in the fenced forest fragment (9 ha) with no herbivory under four different management strategies, figures were built using one random realization from *n* = 30 realizations. Colouring and symbols as per Figure 6.2. Restoration refers to planting of individuals of *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* every 5 years.

Fenced fragment with herbivory

The simulation experiments indicated that neither LDD nor restoration planting could reverse the deleterious effects of intense herbivory pressure on community composition. *B. tawa* increased until it almost completely dominated the fragment, indicating the collapse of the fenced forest fragment (Figures 6.9, 6.10a, 6.10b). However, the individual trees were quite small with a mean dbh of 7.0 ± 0.4 cm and a basal area of just 1.0 ± 0.17 m^2/ha. In all of the scenarios where herbivory was included the collapse of the fragments started after 50 years, irrespective of whether LDD or restoration planting was in place. The effect of restoration planting was insufficient to increase the abundance of *L. novae-zelandiae* and *D. cupressinum.* In comparison with the scenario with no restoration, planting resulted in a periodic increase in seedlings and saplings (Figures 6.8c and 6.8d), but herbivory pressure meant that few of these successfully made the transition to trees (Figure 6.9). As Figure 6.11 shows *B. tawa* was widespread throughout the fragments, and was present in high numbers becoming the dominant species (Figure 6.9).

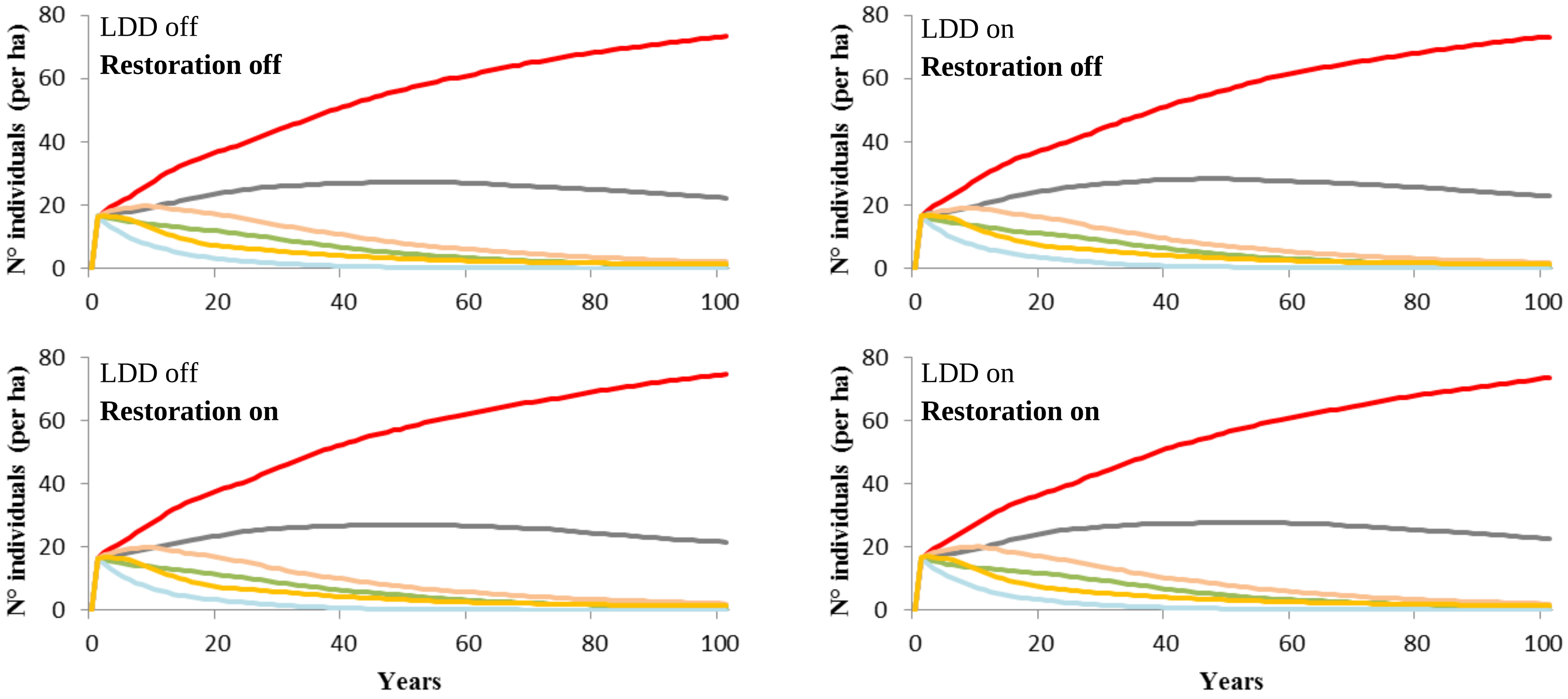


Figure 6.9 Mean abundances of trees in fenced forest fragment (9 ha) with herbivory under different management strategies, figures were built using *n* = 30 realizations. Colouring and symbols as per Figure 6.2. Restoration refers to planting of individuals of *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* every 5 years.

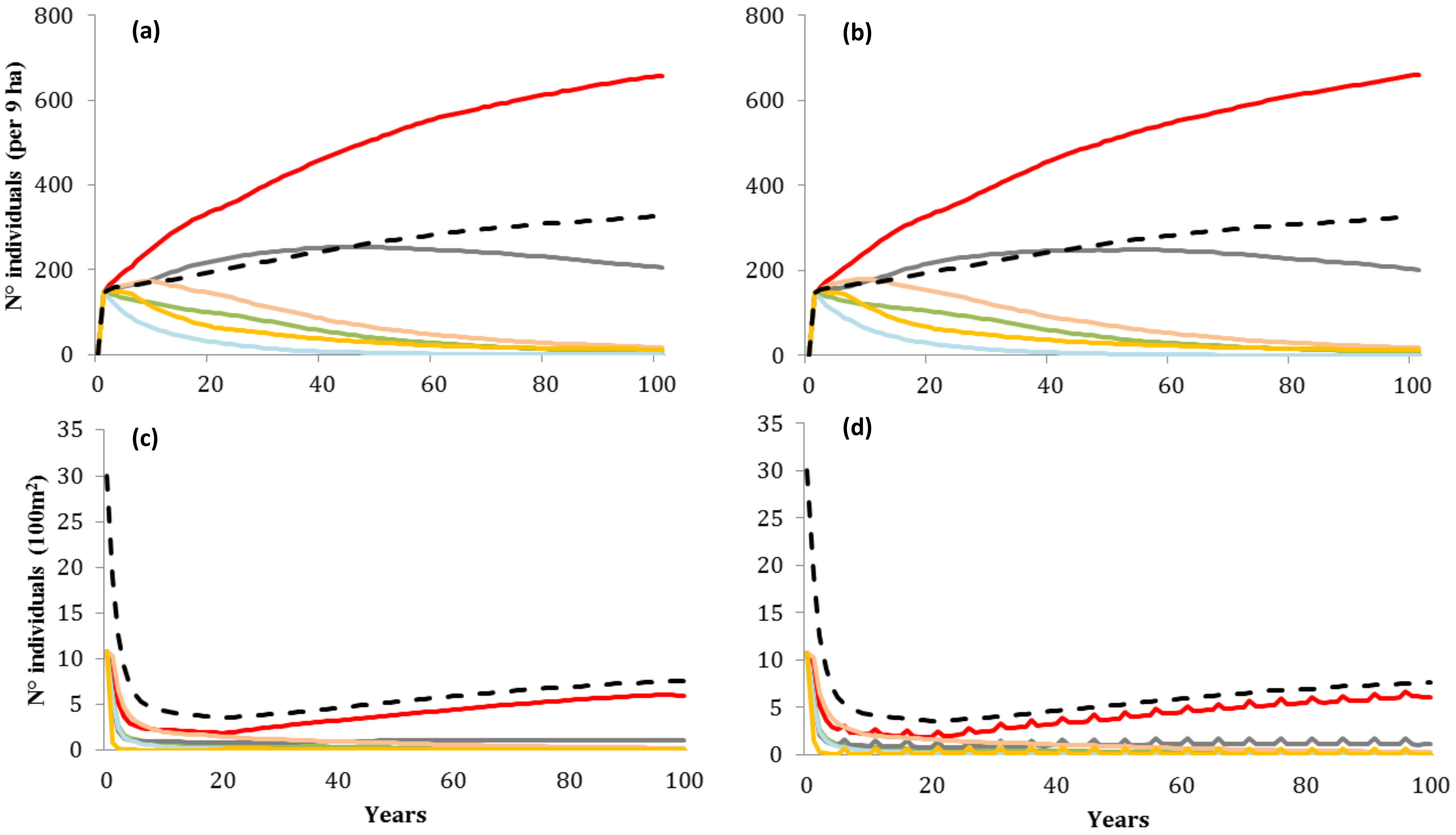


Figure 6.10 Fenced fragment (9 ha) under herbivory. Mean tree abundances with n = 30 in (a) fenced forest fragment without restoration (LDD active) and (b) fenced forest fragment with restoration (LDD active). Mean regeneration bank abundances with n = 30 (seedlings and saplings) in (c) fenced forest fragment without restoration (LDD active) and (d) fenced fragment with restoration (LDD active). Colouring as per Figure 6.2. Black dashed lines represent the average of *B. tawa* individuals for the unfragmented forest.

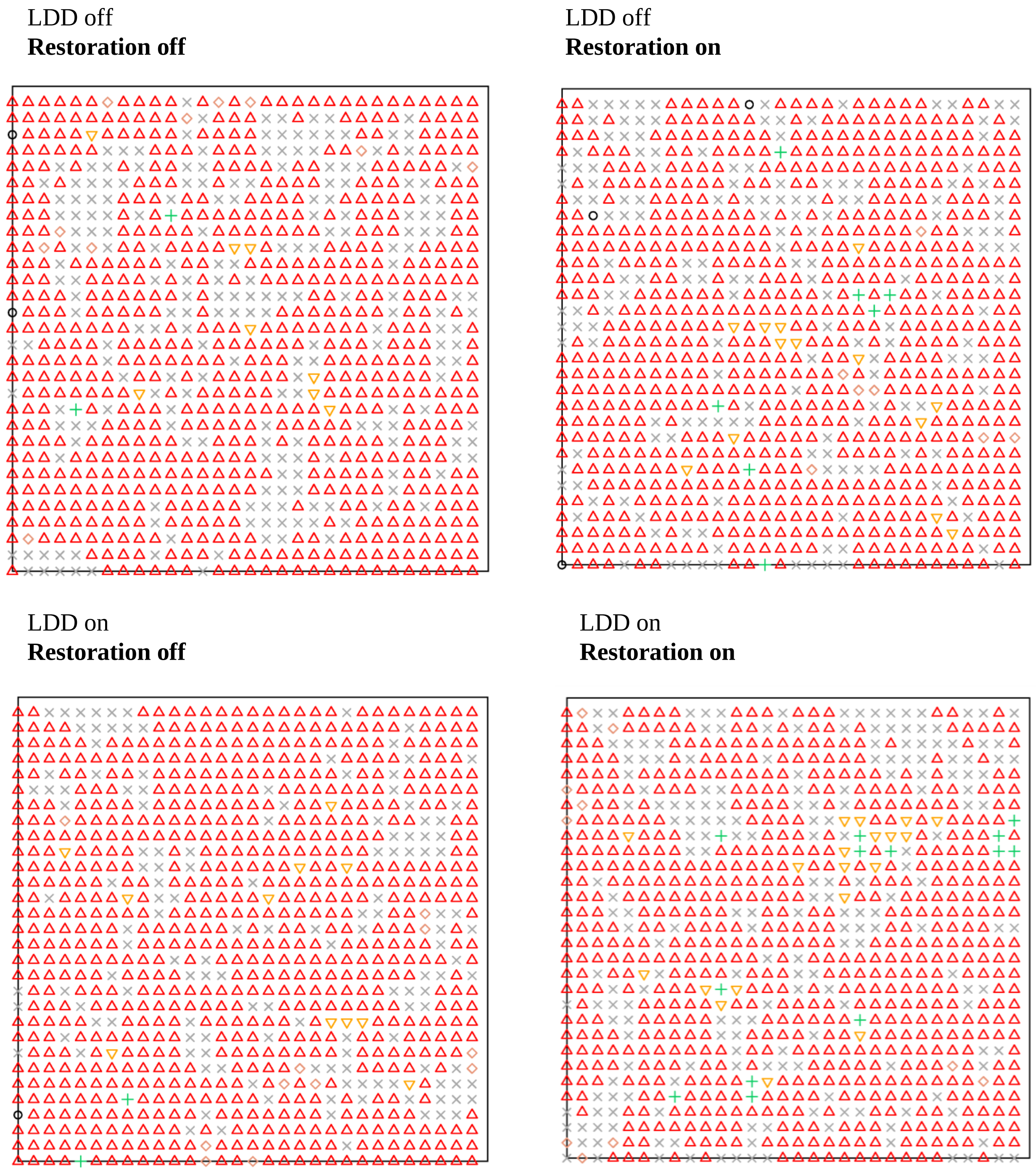


Figure 6.11 The simulated spatial distribution of trees in the fenced forest fragment (9 ha) with herbivory under different management strategies, figures were built using one random realization from n = 30 realizations. Colouring as per Figure 6.2. Restoration refers to planting of individuals of *B. tawa, L. novae-zelandiae* and *D. cupressinum* every 5 years.

Fenced fragment with low herbivory pressure

Simulations showed that in cases where herbivory pressure was reduced (50 % lower than the baseline), LDD can buffer the negative effects that herbivory has on the regeneration process. When both LDD and restoration were inactive the total number of adult individuals was low, 287 ± 32 (32 ± 4 per ha) and 184 ± 17 (20 ± 2 per ha) individuals after 100 years for *B. tawa* and *L. novae-zelandiae* (Figure 6.12 and 6.13a), but these species abundances increased to 601 ± 22 (67 ± 3 per ha) and 257 ± 24 (29 ± 3 per ha) individuals, respectively, after 100 years when LDD was occurring (Figure 6.12 and 6.13a). When restoration planting is occurring no effect of LDD could be discerned and similar abundances to the scenario with LDD were observed (Figure 6.12 and 6.13a).

In terms of the regeneration bank, there is a periodic increase of seedlings and saplings (mirroring the planting cycle), when restoration planting is active. However, these increases in abundance are short-lived and are followed by a drop in the number of seedlings and saplings due to herbivory (a negative effect) and because some individuals are transitioning to trees (a positive effect) (Figures 6.13c and 6.13d).

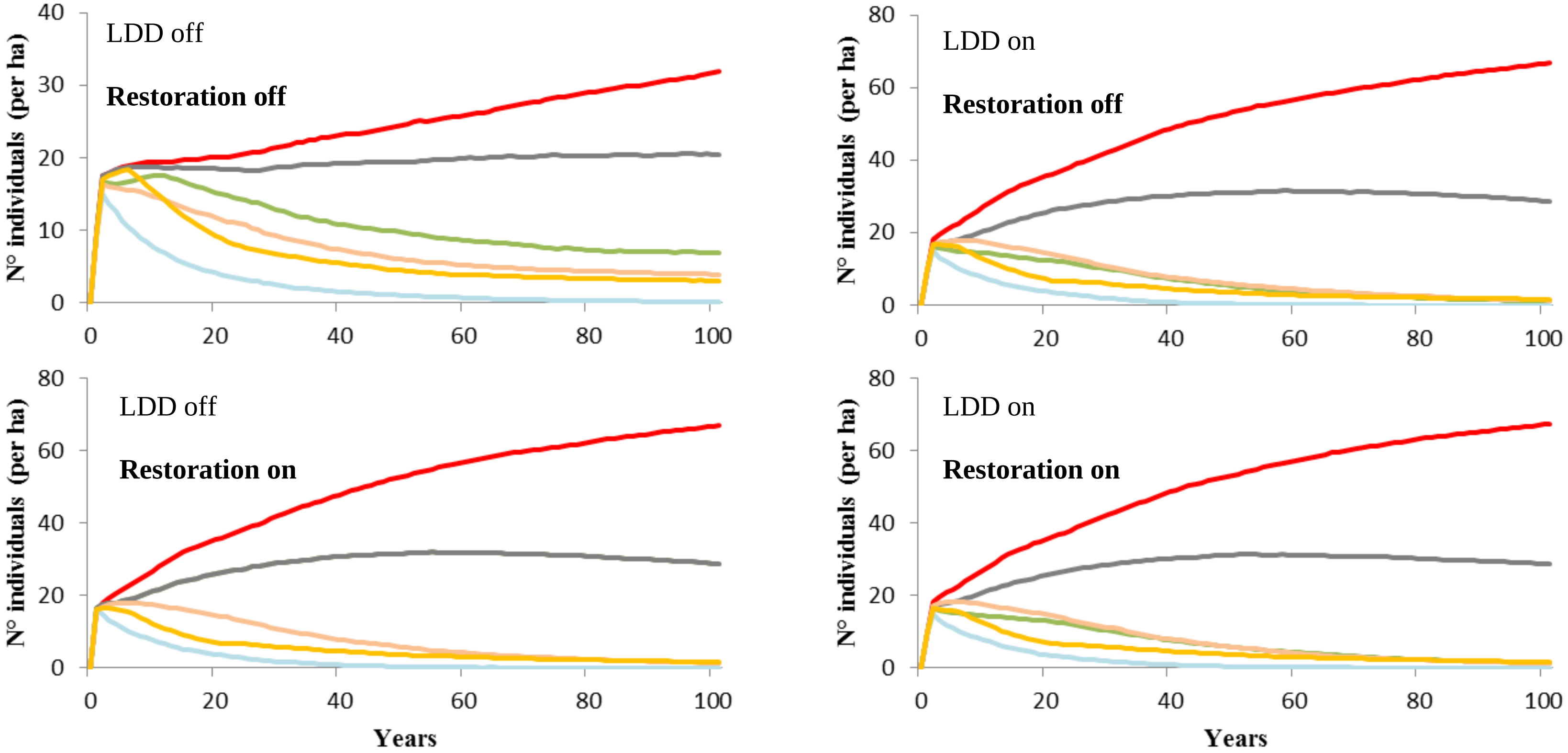


Figure 6.12 Mean abundances of trees in fenced forest fragment (9 ha) with low herbivory pressure (50 % lower than normal herbivory) under different management strategies, figures were built using *n* = 30 realizations. Colouring and symbols as per Figure 6.2. Restoration refers to planting of individuals of *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* every 5 years.

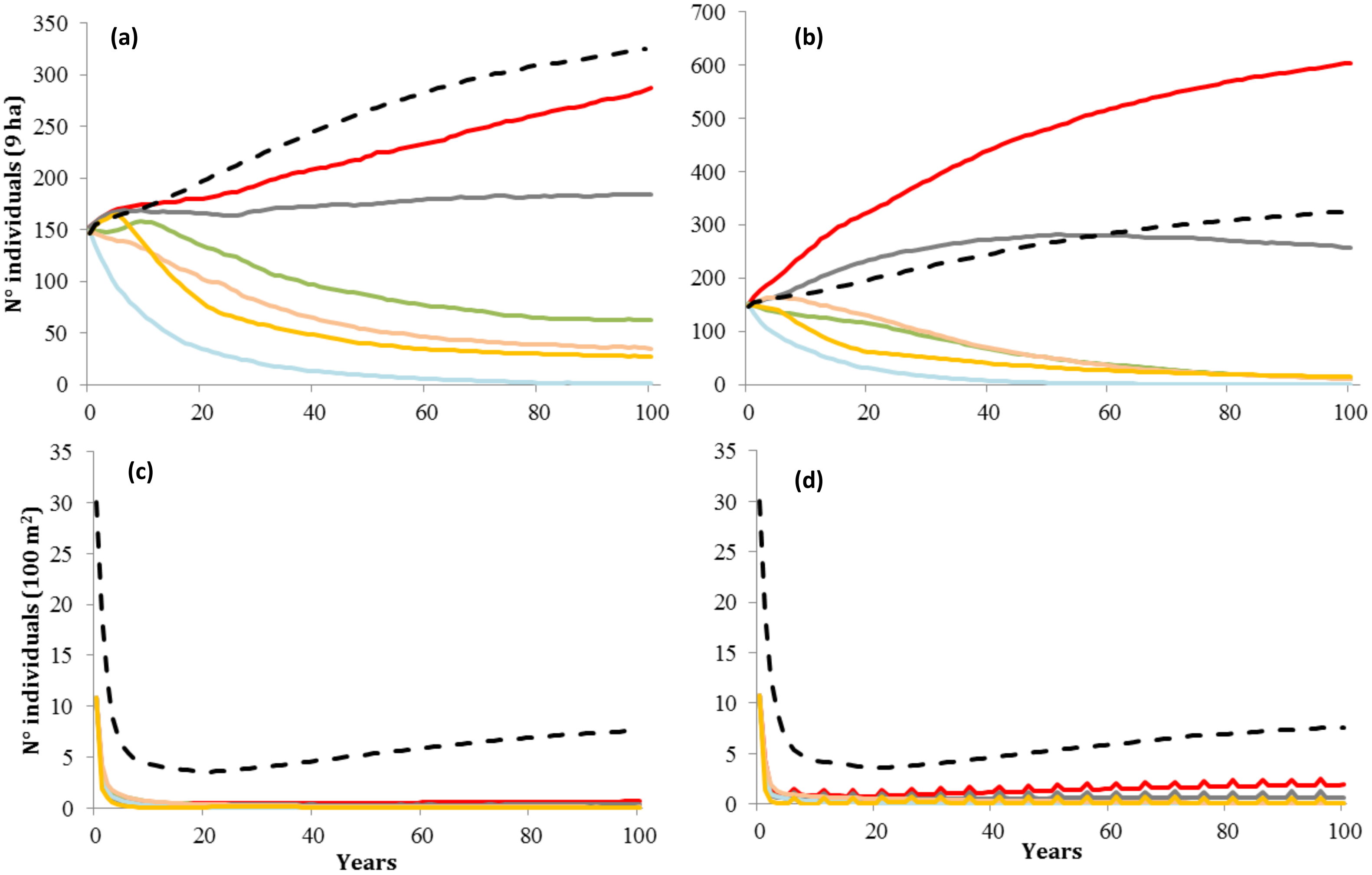
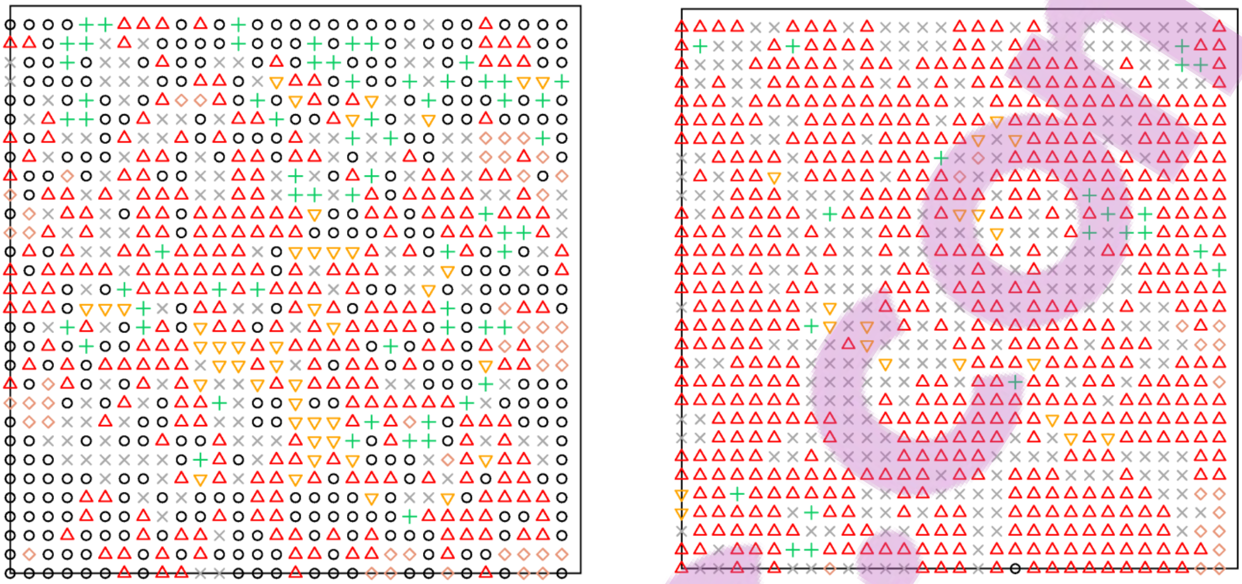


Figure 6.13 Fenced fragment, low herbivory scenarios; mean tree abundances with $n = 30$ in (a) fenced forest fragment without restoration (LDD off) and (b) fenced forest fragment with restoration (LDD active). Mean regeneration bank abundances with $n = 30$ (seedlings and saplings) in (c) fenced forest fragment without restoration (LDD off) and (d) fenced fragment with restoration (LDD active). Colouring and symbols as per Figure 6.2. Black dashed lines represent the average of *B. tawa* individuals for the unfragmented forest.

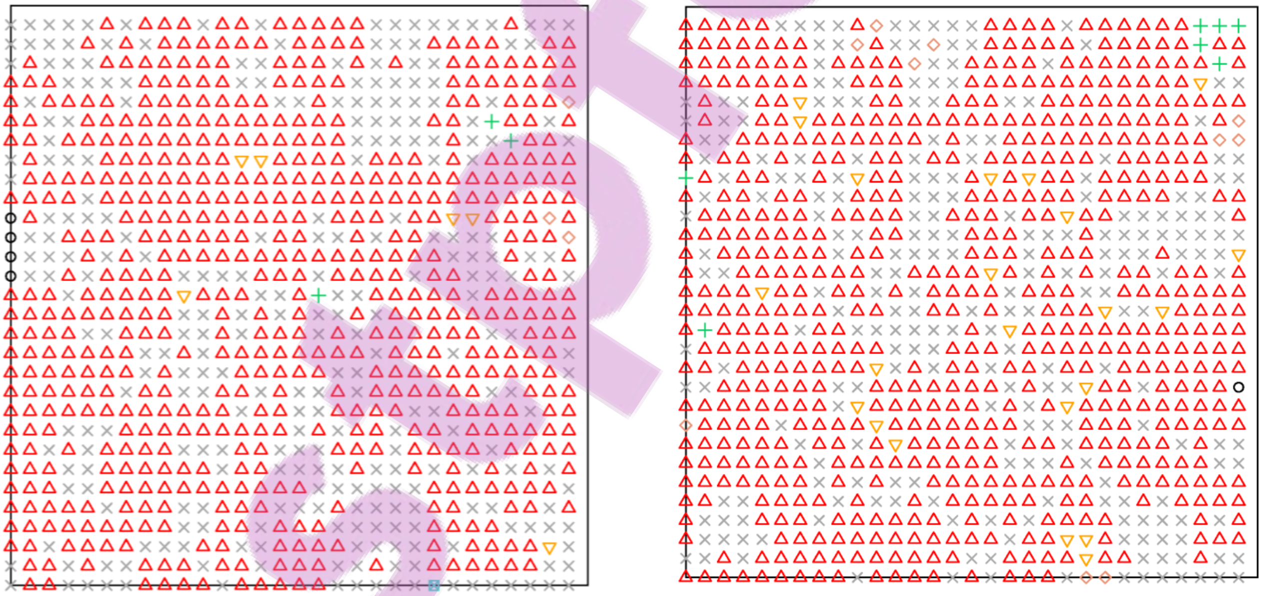
Despite ongoing LDD and restoration planting seeming to be able to counter the effects of herbivory at low intensity, the proportional abundances of the dominant species under such conditions are quite different when compared to those where herbivory is absent. Nevertheless, reducing herbivory pressure certainly delays the collapse of the fragments (perhaps buying time for other restoration interventions), and fragments can maintain the proportional balance between *B. tawa* and *L. novae-zelandiae* for at least 70 years before *B. tawa* starts to dominate.

In terms of spatial distribution, when neither LDD nor restoration planting are active there are some gaps in the forest (Figure 6.14; see LDD off restoration off). This means that the regeneration bank was depleted and there were insufficient juveniles to colonize gaps forming as older trees senesced and died. When LDD and restoration are active *B. tawa* and *L. novae-zelandiae* managed to establish themselves in the fragment including at the edges. *D. cupressinum* and *H. arborea* were also present, but in low numbers, and they were scattered throughout the fragment (Figure 6.14).



LDD off
Restoration off

LDD off
Restoration on



LDD on
Restoration off

LDD on
Restoration on

Figure 6.14 The simulated spatial distribution of trees in the fenced forest fragment (9 ha) with low herbivory pressure (50 % lower than normal herbivory) under different management strategies, figures were built using one from *n* = 30 realizations. Colouring as per Figure 6.2. Restoration refers to planting of individuals of *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* every 5 years.

Summary of results

The scenarios that resulted in positive outcomes in terms of community composition of species were those with no herbivory (Figures 6.12 and 6.13). In the case of fenced fragments with no herbivory and restoration (planting) active the fragments tend to have a similar species composition to the simulated unfragmented forest. The scenarios with reduced herbivory pressure were also successful in some cases, especially when restoration (planting) was active. However, for some species (*D. cupressinum*) less herbivore pressure had no effect on their abundances.

When herbivore pressure was more intense even with restoration active all of the scenarios resulted in *B. tawa* mono-dominant stands; I considered this to represent the collapse of the fragments (Figures 6.12 and 6.13). In the case of the scenario with reduced herbivore pressure, no LDD and no restoration the forest did not become mono-dominant. However, I consider that those scenarios resulted in a collapse of the fragment because there was a lack of regeneration and only a few individuals surviving (Figures 6.12 and 6.13).

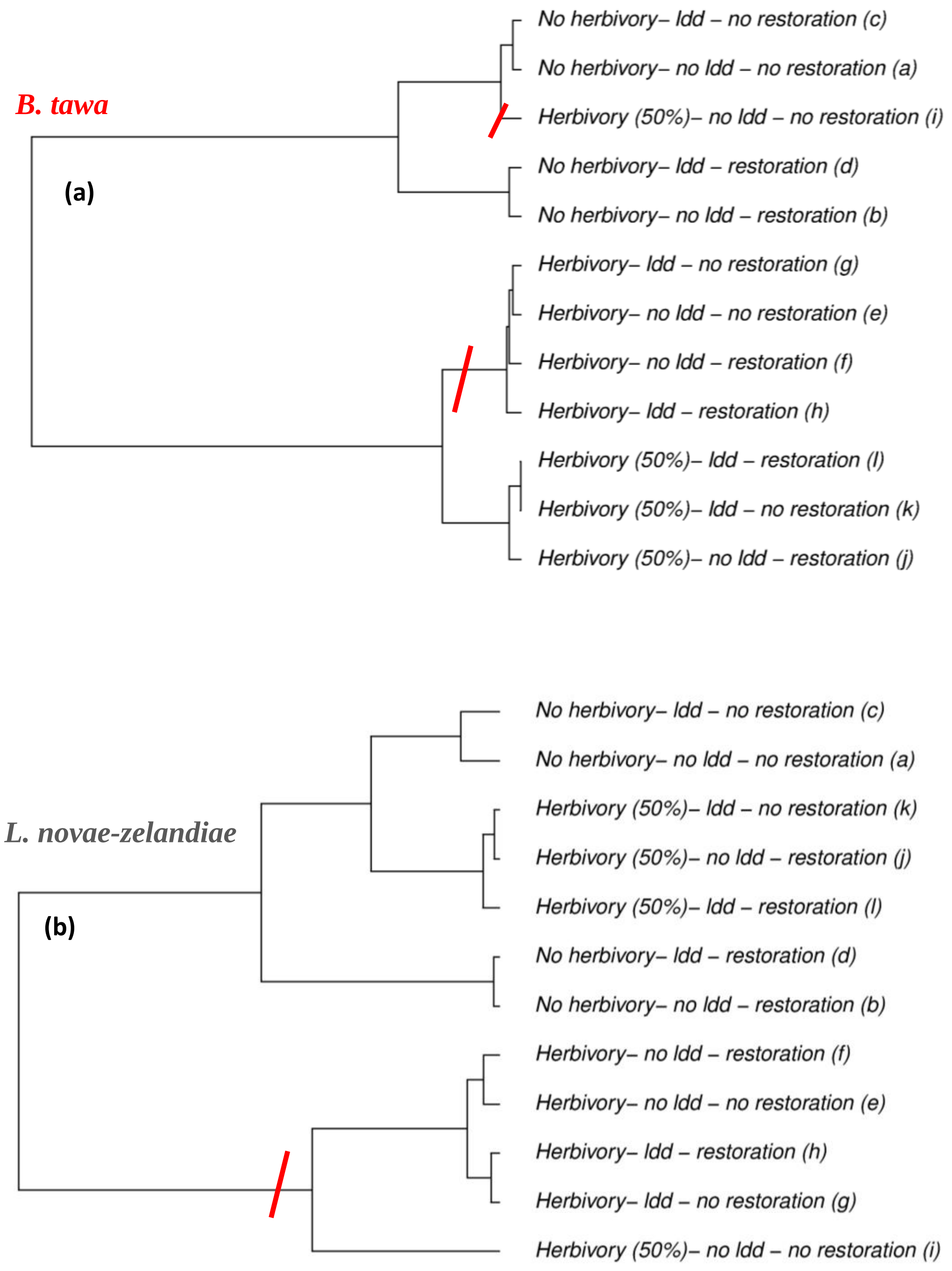


Figure 6.12 The relationship between the different scenarios. Scenarios are grouped according to their effect on abundance of trees of each species. (a) *B. tawa*, (b) *L. novae-zelandiae* and (c) *D. cupressinum*. The red line indicates scenario branches that are not viable due to the collapse or disappearance of the species of interest. Scenario letter codes as per Figure 6.1.

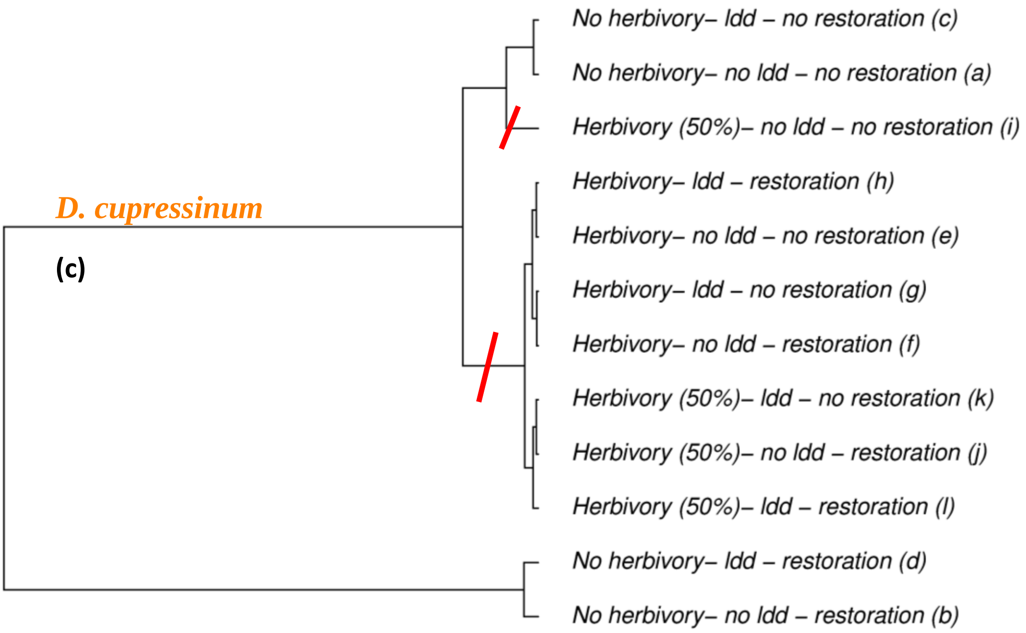


Figure 6.12 (contd.) The relationship among the different scenarios. Scenarios are grouped according to their effect on abundance of trees of each species. (a) *B. tawa*, (b) *L. novae-zelandiae* and (c) *D. cupressinum*. The red line indicates scenario branches that are not viable due to the collapse or disappearance of the species of interest. Scenario letter codes as per Figure 6.1.

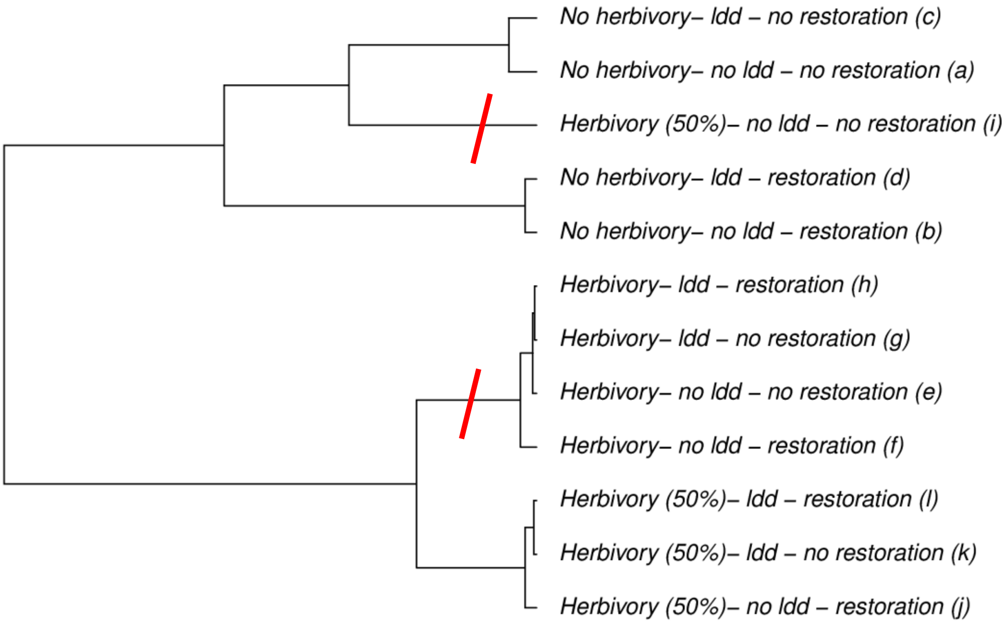


Figure 6.13 The relationship among the different scenarios. Scenarios are grouped according to their effect on abundance of trees of all six simulated species. The red line indicates scenario branches that are not viable due to the collapse. Scenario letter codes as per Figure 6.1.

6.4 Conclusions

In this chapter I used the forest simulation model described in Chapter 5 to evaluate four different scenarios (Figure 6.1). I was interested in assessing the impact of different management and restoration strategies, such as fencing and planting, and long-distance seed dispersal on the long-term persistence of podocarp-tawa forest fragments.

The outcomes of the simulation experiments suggest that fencing is necessary to ensure the long-term persistence of the dominant tree species (*B. tawa, L. novae-zelandiae* and *D. cupressinum*) in small fragments because it greatly reduces herbivore pressure from large mammals (e.g. cattle and sheep). However, the results also show that even at reduced levels herbivory continues to have a huge negative impact on the dynamics of the podocarp-tawa forest fragments I consider. The most positive results with regards to the long-term survivorship and persistence of the tree species of interest were obtained when long-distance seed dispersal (LDD) services were intact, fencing was coupled with an absence of herbivory and restoration activities such as planting were in place (Figures 6.11 and 6.12). In this case, the proportion of the tree abundances was similar to the simulated unfragmented forest. It is important to note that when herbivory pressure was reduced but there was no restoration planting, LDD increases the abundances of the canopy dominant trees. This dynamic indicates a potential “spill-over effect”, as described by Brudwig et al. (2009), which could be an important landscape-level outcome of large-scale restoration projects.

However, incorporating all of these restoration activities simultaneously is very expensive. In practical terms reducing herbivory of both small and large mammals is a crucial first step after fencing. A second step would be to reduce the edge effect and here planting can play an important role, especially by planting fast-growing native species around the edges. However this approach must be consider with caution as it must be site-specific. Achieving these two first steps will likely be sufficient to secure the persistence of the fragment over a 100 year window. Depending on the availability of resources, more intensive management activities, such as the periodic reintroduction of seeds and seedlings that will to help to improve the species composition and structure of the forest fragment, may also be beneficial. Ultimately restoration activities could go even further with the development of projects to improve the connection between fragments (e.g. improving biological corridors) and increase the influx of seeds from other fragments or forest reserves (e.g. reintroduction of native birds).

In all scenarios that incorporated herbivory (using baseline levels; Section 5.3) the fragments shifted to a mono-dominant forest, which I deemed to represent the collapse of the fragments. It is quite possible that allelopathic effects could be heightened under such conditions. Anaya (1999) found that alleopathy is strongly coupled with other stresses in the environment, which can often enhance allelochemical production and increase the potential for allelopathic interference (see Chapter 4). Although not represented in the model such allelopathic effects would further reduce the success of regeneration. The collapse of the fragments occurred even if the fenced fragments were protected against large herbivores such cattle, as small mammals (e.g. lagomorphs and rodents) will continue to exert a huge impact on the long-term community dynamics of small forest fragments. Such dynamics seem a likely outcome in most of the fenced fragments considered here. Innes et al. (2010) and King et al. (2011) suggest that rats reinvade forest fragments rapidly after eradication unless the eradication plan put in place includes all adjacent areas or predator-proof fencing is installed, which is unlikely to be the case on privately owned land. When herbivory pressure was reduced to 50 % of baseline levels the proportional abundance of the tree species of interest still differed from the unfragmented forest. However, a reduction in the intensity of herbivory meant that the community composition persisted for longer (at least over the timeframe of 100 years). Nevertheless, even with active restoration in the form of planting the abundance of individuals was different to the simulated unfragmented forest, probably due to selective browsing by herbivores.

Based on my results, a combination of fencing, which excludes both large and small herbivores, intact long distance seed dispersal services and interventionist restoration activities is required to maintain forest fragments over extended time periods (Figure 6.12). Our results also suggest that if the microclimatic edge effect is not buffered, fenced forest fragments will not be capable of sustaining themselves without constant support.

Management of surrounding areas and the design of better restoration strategies can help to decrease the effects of fragmentation. Meurk and Hall (2006) outlined how connectivity among native fragments could be enhanced by using streams with riparian vegetation, native hedgerows and exotic plantations surrounded by native species as connecting corridors. While appealing, such solutions involve a lot of coordination between different landowners and other stakeholders if they are to be implemented, and could take a long time to develop. Another solution is the use of fast-growing tree species such as *Pinus radiata* to help to diminish the climatic effects of the edge effect as proposed by Denyer et al. (2006) and Becerra and Montenegro (2013). This solution is easier to implement, as *P. radiata* tends to grow very quickly so may potentially have a positive effect in a short period of time. Furthermore it is economically useful and can provide some income to the landowners and so serve as an incentive to protect fragment edges. However if exotic tree species are to be used the species must be carefully selected to avoid propagating invasive pest species.

What I have presented here is a simulation but, at the least, it provides a valuable qualitative indication of the expected trends under specific circumstances. Quantitative analyses were used to contrast the different plausible scenarios but were not intended to be used as numeric predictions. The scenario-based approach (Coreau et al. 2009, Thompson et al. 2012) was useful to explore and understand the dynamics and the relationships between a set of plausible conditions (e.g. fencing, restoration). Furthermore, the model-based scenario evaluations offer a useful way to test different hypotheses that would be almost impossible in real ecosystems, as they would need a level of manipulation far beyond our current capabilities, continuous monitoring for decades and a huge amount of economic and human resource investment. Even if field-based experiments were implemented most of the information needed to make decisions now would not be available for decades, but most of the fragments that I deal with cannot wait that long. Future studies in this area would do well to consider new restoration techniques (e.g. develop of mechanical or biological barriers) and carry out new field studies to evaluate which restoration activities would best ameliorate the edge effect pervasive in forest fragments.

7. GENERAL CONCLUSIONS

The forests of the Waikato region of the North Island of New Zealand's form part of an extremely fragmented landscape, comprising approximately 5000 individual fragments each less than 25 ha (Burns et al. 2011). Forest fragments are concentrated on private land and, despite their potentially high conservation value, are not usually protected. Fencing of forest fragments is the most common conservation management activity implemented to protect them. However, the effectiveness of this strategy in ensuring the long-term viability of forest fragments, and especially those where *Beilschmiedia tawa* is an important component remains uncertain.

7.1 Empirical Context

In **Chapter 2,** I explored the consequences of different types of management (fragmentation and fencing) on the current-day composition and structure of podocarp-tawa forest fragments in the Waikato and the associated abiotic conditions (soil, light and climate). The effects of fragmentation were still apparent even after 20 years of fencing mirroring the findings of Burns et al. (2011). In general, the fragmented sites had different species composition and forest structure when compared with the unfragmented forests, although these differences were not significant (see Chapter 2, Section 2.3.1). Overall, fencing did not have an effect in mitigating the species composition and structure of the forest fragments, although 20 years may be too a short time-frame for shifts in such slow processes to occur or be detectable. These results indicate that the effects of management vary even within the same management type. In terms of species densities some fenced fragments were similar to the unfragmented forest but others were similar to the unfenced fragments, that is to say the effects of fencing were site-specific. Our results are similar to what Rodrigues et al. (2011) found in an Atlantic

Forest biome in Brazil where some sites were able to recover by themselves but others needed active restoration activities (e. g. seed and seedlings reintroduction). The decision of what sites need active restoration activities were dependant on past land use, forest cover and level of fragmentation.

The hope is that fencing will improve the regeneration of tree species, such as *B. tawa*, in those fragments where it is put in place. However, I found the same lack of juvenile individuals of *B. tawa* (saplings) in fenced and unfenced fragments. Therefore the effects of fragmentation seem to persist after fencing. This legacy effect has been seen in other studies (Benitez-Malvido 1998, Bruna 2002) where a lower number of juveniles were observed in fragmented sites in comparison to unfragmented forest, even though fragments had a wire fence. Furthermore, most of the adult individuals at those sites (both fenced and unfenced) were in the large size classes (old trees) showing that there is a regeneration gap (as previously described by Burns et al. 2011).

Fragmented sites also had different abiotic conditions than the unfragmented forest. Soil analyses revealed lower water and nutrient content in the fragmented sites versus the unfragmented forest, this was an expected result as previous studies in the Brazilian Amazon (Carmago and Kapos 1995, Bruna 2002) and in Midwestern USA (Gehlhausen et al. 2000) found a similar pattern (lower water and nutrient content) in fragmented vesus unfragmented sites. In general, fencing appears to have improved some of the abiotic conditions in the fragments, although I cannot imply cause and effect as the original status of the fragment cannot be determined. There was a trend towards the sites that have been fenced being closer to the unfragmented forest sites, especially in their nitrogen, carbon and water content. These results differ from Dodd et al. (2011) who showed that soil fertility (C;N) was different between a grazed forest fragment and an ungrazed forest. However, the same author argued that soil fertility properties (e.g. phosphorous, carbon and nitrogen) can vary greatly between forest fragments because of the different stock management and the use of different doses of fertilizers. In addition I found that the fencing had a buffering effect on microclimate but this effect disappeared during extreme climate conditions such as the drought experienced in early 2013.

Data from age increments cores showed that the youngest individual was on average 50 years old meaning that the lack of regeneration (saplings) began in the last 50 years. It is important to note that age is from the smallest tree that I could core (7 cm dch) so is an upper estimate of the timing of failure, but the lack of saplings in the fragmented sites make us strongly suspect that there are some factors acting that are not improved by fencing (see Chapter 2, Figure 2.7).

Nevertheless, fragmentation continues to have a negative effect on the composition and structure of the forests I considered. Fencing seems to have had a limited effect in improving the composition and structure of fragments, at least over the last 20-years. I believe that the edge effect has an important role in the state of the fragments and fencing cannot reverse or neutralize its negative consequences. Furthermore, the particular history of each fragment may help to explain their particular current composition and structure, and also the differences evident even within the same management groups. Site history of a particular fragment has been found to explain the current composition and structure of fragements in studies by Rodrigues et al. (2011) in an Atlantic Forest biome in Brazil and in New Zealand (Burns et al. 2011) but is very difficult to control for in landscape-level experiments.

In **Chapter 3**, I sought to determine the role of fragmentation and fencing on the survivorship of *B. tawa* seedlings and identify the factors explaining the recruitment problems the species faces. The main factors that affected *B. tawa* potted seedlings survivorship were desiccation and herbivory. I found an overall negative effect of fragmentation on the survivorship of *B. tawa* potted seedlings. However, fencing did not have any effect on improving survivorship by diminishing desiccation. Our results are consistent with other studies where desiccation has been suggested as one of the main factor of tree mortality in fragmented forests (e. g. Laurence et al. 2006 in Amazonia). Mortality by desiccation started after a severe drought in early 2013 and the levels of desiccation were higher in the fenced fragments than in the unfragmented forest. This higher rate of mortality by desiccation in the fenced fragments supports our results from Chapter 2 that showed that the climatic buffering effect of fencing vanished during the drought. On the other hand, fencing did reduce herbivory by large mammals, e.g. cattle (*Bos taurus*) and sheep (*Ovis aries*), but not by small mammals (e.g. rabbits (*Oryctolagus cuniculus*), and ship rats (*Rattus rattus*). These results were expected because the type of stock-fence used is designed specifically to impede the access of large mammals (Hayward and Kerly 2009). In general, *B. tawa* potted seedlings grew faster in the unfragmented forest than in the fragmented sites (Figure 3.3). Growth of *B. tawa* potted seedlings was not improved by fencing. Again these results are in line with studies from elsewhere, such as Laurance et al. (2006), which suggest that fragmentation hinders plant growth especially of late successional species such as *B. tawa.*

When I compared fenced versus unfenced fragments, fencing did not increase the number of naturally established canopy tree seedlings. The abundance of seedlings was low in the fenced fragments, especially for dominant canopy species including *B. tawa*, *L. novae-zelandiae* and *D. cupressinum.* It is interesting to note that one fenced site had a particularly high density of seedlings of *B. tawa* and *L. novae-zelandiae*. These high densities may indicate that factors other than the fencing itself are at play (e.g. abiotic conditions similar to the unfragmented forest). I suggest in Chapter 2 that site history has an important role in the response of plant communities to fencing, as has been seen in forests in the Brazilian Amazon (Rodrigues et al. 2011), Mexico (Muñiz-Castro et al. 2006), New Zealand (Burns et al. 2011) and USA (Grman et al. 2013).

Tree replacement data showed that some of the successional relationships between the different functional types (tree ferns, subcanopy trees, canopy trees and *B. tawa*) present in the unfragmented forest and fragmented sites are absent from the fenced fragments. However, the relationships present in the fenced fragments have a higher number of individuals in comparison with the unfenced fragments. The differences in the relationships between the different functional types across the different type of management suggest different future successional trajectories. For example, in the fragmented forest canopy dominant trees and *B. tawa* will persist over time. On the other hand, in the fenced fragments *B. tawa* and other canopy dominant tree species will become less prevalent, being replaced by sub-canopy tree species. These results coincide with those obtained by Laurance et al. (2006) who showed that old-growth species tend to decline in forest fragments in favour of pioneer and habitat generalist species.

In conclusion, fragmentation did have a negative effect on survivorship or on *B. tawa* seedlings' growth rate and a negative effect on the survivorship of *B. tawa* natural seedlings, as studies of the dynamics of dominant canopy trees in other ecosystems have suggested. Fencing did not improve the survival odds or growth of *B. tawa*; rather the most important effect of fencing was in diminishing herbivory by large mammals.

The results of Chapters 2 and 3 suggest that the direct drivers behind the lack of regeneration of *B. tawa* in some sites could have more to do with the abiotic conditions, than biotic conditions such as herbivory. Some authors have suggested that when plants are stressed, allelopathic effects could be more significant and may negatively affect otherwise healthy individuals. In **Chapter 4** I sought to determine whether *B. tawa* leaf leachate could have a potential allelopathic effect. It seemed possible that allelopathy plays a role in the germination and growth of *B. tawa*, particularly in disturbed sites where other stresses are also acting.

While *B. tawa* leaf leachate had a negative effect on germination of *L. sativa* seeds, it had no discernible effect on its own seeds. However, *B. tawa* leaf leachate did have a significant negative effect on radicle elongation of *B. tawa* seeds at high concentrations, but a positive effect at lower concentrations. Soil from different sites under different management types did not have a significant effect on germination. Results from the soil experiment showed that the allelopathic compounds are not present in soils, or at least not at a sufficient concentration to cause any biologically relevant effect.

Our results showed that *B. tawa* leaf leachate had a positive effect on the germination of *B. tawa* seeds at lower leachate concentrations. In addition, *B. tawa* leaf leachate had a negative effect on radicle elongation, which is a critical part of the plant for nutrient absorption. Also, our experiments showed that germination is accelerated when the seed does not have a mesocarp. In conclusion, our evidence suggests that the best scenario for a seed to establish is to have the mesocarp removed by kererū (*Hemiphaga novaeseelandiae*) and is dispersed to a safe site where the abiotic conditions do not permit the leachate to percolate to the soil in higher concentrations.

7.2 Environmental modelling

In **Chapter 5** I gave a detailed description of the development of a spatially explicit individually-based model (SEIBM) developed to represent the long-term dynamics and viability of podocarp-tawa forest and with which I could analyse the likely fate of *B. tawa*. A baseline analysis was performed to determine how well the model simulated the dynamics of an actual podocarp-tawa forest by comparing its performance with data obtained from an unfragmented forest (the field data discussed in Chapter 2). Finally, a sensitivity analysis was performed to determine how sensitive the model was to changes in the given parameters and variables.

In New Zealand there have been surprisingly few attempts to model native forest, but some notable examples are FORENZ (DeVelice 1988), LINKNZ (Hall and Hollinger 2000), SORTIE/NZ (Kunstler et al 2009) and Landclim (Thrippleton et al. 2014). These earlier efforts have all involved using modelling frameworks developed elsewhere and applying them to NZ forest communities. The model I implemented is based in part of early gap models such as as JABOW (ref to Botkin), and is one of the first attempts to model a podocarp-tawa forest. The model is designed it to be used as a tool for long-term conservation strategies and restoration management activities and is simple enough (relative to, for example, SORTIE) to be highly customizable in and adaptable to other types of forest.

In general, our model's estimations were within plausible ranges. In some of its predictions the model did not perfectly fit the field data, but the values it produced were within the range of plausible outcomes suggested by other studies. The most sensitive parameters were in general those that represented anthropogenic activities (e.g. introduced herbivores, fragmentation) and juvenile life-cycle demography (e.g. seedling survivorship), which is consistent with our understanding of the actual threats to fragmented ecosystems around the world (Saunders et al. 1991, Laurence at al. 2002, Hobbs and Yates 2003) and particularly for podocarp-tawa ecosystems (Dodd and Power 2007, Smale et al. 2008). The model was capable of predicting the key structural and successional patterns observed in the reference unfragmented forest and in data provided in the literature (e. g. Chavasse and Travers 1966, West 1986, Smale et al. 2008). Nevertheless, the model failed to adequately predict some key facets of forest stand structure. In particular, basal area was consistently underestimated, but as I discuss in Chapter 5, New Zealand native trees tend to be difficult to represent adequately as they can tolerate very long suppression periods, so this was not an unexpected outcome (and is one described also by Hall and Hollinger 2000). Although underestimation or overestimations are expected, as I am dealing with a simplification of real systems, this does not invalidate those outcomes of the model which fell within plausible ranges (e. g. Seagle and Liang 2001, Wehrli et al. 2007, Dislitch et al. 2009).In future versions of the model and when and as more data become available some improvements can be instigated to deal with some of these problems. In conclusion, the model is a powerful tool that can help decision making for conservation and restoration, as models have proved in other fragmented ecosystems (e.g. Scotland (Tanentzap et al. 2013), USA (Holm et al. 2013), and also to improve the likelihood that podocarp-tawa fragments will persist into the long –term.

In **Chapter 6** I used the ecological model described in Chapter 5 to simulate different scenarios to assess the impact of different management and restoration strategies, such as fencing and planting, and the level of long-distance seed dispersal on the long-term persistence of podocarp-tawa forest fragments.

The model simulations showed that fencing is a necessary first step to ensure the long-term survival of dominant canopy tree species in forest fragments, including *B. tawa*. In general, fencing prevents large mammals from accessing the fragments, but small mammals (e.g. ship rats) will continue to have a huge negative impact on the dynamics of podocarp-tawa forest fragments.

Simulations showed that the most successful scenarios were those where herbivory was not present and when there was an influx of seeds from nearby unfragmented forests or forest fragments. In addition, restoration activities by planting proved to be an efficient way to obtain a similar composition to that in the unfragmented forest. Applying all of these management activities simultaneously is sometimes not viable economically; I suggest that fencing and a plan of eradication of small exotic mammalian herbivores is a good first step, but is unlikely to be sufficient in the long term. In addition, simulation experiments suggest that edge effects have a huge impact on the dynamics of podocarp-tawa fragments. Measures to decrease the negative impacts of the edge effects are required; in Chapter 6 I consider some potential management activities that could be of use in this context.

7.3 Conclusion

As a general conclusion to this work, I found evidence that podocarp-tawa fragments need more than fencing to persist in the long term; this is especially the case for *B. tawa*, which has been suffering ongoing regeneration failure for some time (potentially for 50 years in the fragments considered here). Regeneration failure is not only an issue affecting *B. tawa* as it has been reported in other species in different forest ecosystems (Palmer et al. 2004, Hall 2008). For example, Evans and Keen (2013) provided evidence of a lack of regeneration of pignut hickory (*Carya glabra*) in the fragmented forests of Santa Catalina's Island, Georgia, USA, in the past 65 years. In New Zealand Myers and Court (2013) have reported the lack of regeneration of *Beilschmiedia taraire*, a congener of *B. tawa*, in forest remnants in Tiriti Matangi Island despite active restoration efforts (e.g. planting of seedlings). They showed that regeneration within existing forest remnants is slow and that seedlings of taraire were very sparsely distributed, with density decreasing from 1983 to 2005 despite management efforts. In this case replanting through the extensive revegetation programme on the island did not result in a recovery of the understory of the remnant.

Conventional stock-fencing is an important tool for mitigating the herbivory problems associated with large vertebrates, but in terms of improving regeneration, forest composition, forest structure, and protection against climatic fluctuation it is not enough. *B. tawa* seedlings were present at all the sites I studied but in most of them at low densities. The low density of juvenile individuals (saplings) in fragmented sites suggests that seedlings are not transitioning to trees despite the protection provided by fencing.

Various lines of evidence presented here suggest that the factors behind the ongoing regeneration failure in fragments were enhanced desiccation and herbivory by small mammals. The data also suggest that some abiotic factors (e.g. water content, high phosphorus levels) can be acting synergistically with biotic factors to drive fragment dynamics. The impact of these negative factors has probably become more noticeable in the last 50 years (the youngest individual cored had an age of approximately 50 years). In addition, I believe that a combination of historic activities (e.g. logging, level of past herbivory), the severity of edge effects (e.g. lack of protection from a nearby forest) and current activities (e.g. percolation of fertilizers, decrease in ground water levels) explain this regeneration failure.

I believe that passive restoration in the case of podocar-tawa forest fragments is not enough to ensure their long term persistence, especially in the case of *B. tawa*. Based on our results, management strategies would do well to focus on an active restoration approach where issues such as edge effects are actively mitigated and strategies to exclude both large and small mammalian herbivores are considered. Although I know that active restoration can be expensive at the onset, it seems that in the long run it would be more efficient if I consider that eradication plans need constant maintenance (e.g. reinvasion of small mammals after eradication; see Innes et al. 2010, King et al. 2011).

The appropriate strategy will of course be dependent both site and species dependant. My results showed that one restoration recipe did not fit all situations and fencing alone is, in some cases, not enough to promote the recovery of forest fragments, as several authors have previously suggested (e.g. Spooner et al. 2002, Harris et al. 2006, Hayward and Kerley 2009, Rodriguez et al. 2011, Morales et al. 2015). The particular condition of each fragment and its past history need to be taken into consideration when restoration plans are designed. However, in large scale projects developing conservation or restoration plans tailored for each one of the forest fragments of interest could be daunting.

Ecological modelling has proven to be a helpful tool to test different management activities without the cost involved of applying them in “real life”. Model-based scenario evaluations can also provide some guidelines regarding how to decide when a particular management activity will be sufficient to ensure the viability and recovery of different forest fragments (e.

g. Seagle and Liang 2001, Tanentzap et al. 2013). The spatially explicit individual based model developed for this thesis shows promise in this regard. Although some refinement to both process representation and parameterisation is needed to improve its performance, preliminary scenario simulations have shown it to be a useful tool for management purposes and for the assessment of the long term viability of forest fragments. The use of ecological modelling in conservation and restoration ecology will help to design specific management activities depending on their particular situation. I recommend that future studies exploring similar issues focus on a larger scale to determine if the results described here are a general trend among the landscape of the Waikato region.

8. REFERENCES

Allan HH (1982) Flora of New Zealand, Volume 1. Government printer, Wellington. 1085pp.

Allen RB, Fitzgerald AE and Efford MG (1997) Long-term changes and seasonal patterns in possum (*Trichosurus vulpecula*) leaf diet, Orongorongo Valley, Wellington, New Zealand. New Zealand Journal of Ecology 21(2):181–186.

Anaya AL (1999) Allelopathy as a Tool in the Management of Biotic Resources in Agroecosystems. Critical Reviews in Plant Sciences, 18:6, 697-739.

Anderson MJ, Ellingsen KE and McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecology Letters (9): 683-693.

Aronson MFJ, Handel SN (2011) Deer and Invasive Plant Species Suppress Forest Herbaceous Communities and Canopy Tree Regeneration. Natural Areas Journal 31 (4):400-407.

Bach CE and Kelly D (2004) Effects of forest edges, fruit display size, and fruit colour on bird seed dispersal in a New Zealand mistletoe, Alepis flavida. New Zealand journal of Ecology 28 (1)

Banfield J, Black D, Collins D, Hyland B, Lee J and Pranowo S (1994) Constituents of Some Species of Beilschmiedia and Endiandra (Lauraceae): New Endiandric Acid and Benzopyran Derivatives Isolated From *B. oligandra*. Australian Journal of Chemistry 47(4):587-607.

Bates D, Maechler M, Bolker B and Walker S (2014) Lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. http://CRAN.R-project.org/package=lme4.

Becerra PI and Montenegro G (2013) The widely invasive tree *Pinus radiata* facilitates regeneration of native woody species in a semi-arid ecosystem. Applied Vegetation Science 16 (2):173-183.

Benitez-Malvido J (1998) Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conservation Biology 12 (2):380-389.

Beveridge AE (1964) Animal modification of native vegetation: Dispersal and destruction of seed in central North Island podocarp forests. Proceedings of the New Zealand Ecological Society 11:48–56.

Bisutti I, Hilke I and Raessler M (2004) Determination of total organic carbon – an overview of current methods. TrAC Trends in Analytical Chemistry 23(10–11):716-726.

Botkin DB (1993) Forest Dynamics: An Ecological Model. Oxford University Press.

Botkin DB, Janak JF and Wallis JR (1972) Some Ecological Consequences of a Computer Model of Forest Growth. Journal of Ecology 60(3):849-872.

Bray R and Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. Soil Science 59 (1):39-46.

Brudvig LA, Damschen EI, Tewksbury JJ, Haddad NM and Levey DJ (2009) Landscape connectivity promotes plant biodiversity spillover into non-target habitats. Proceedings of the National Academy of Sciences 106 (23):9328-9332.

Bryant D, Ducey M, Innes J, Lee T, Eckert R and Zarin D (2005) Forest community analysis and the point-centered quarter method. Plant Ecology 175 (2):193-203.

Burns B, Innes J and Day T (2012) The Use and Potential of Pest-Proof Fencing for Ecosystem Restoration and Fauna Conservation in New Zealand. In: Somers MJ, Hayward M (eds) Fencing for Conservation. Springer New York, pp 65-90.

Benitez-Malvido J (1998) Impact of Forest Fragmentation on Seedling Abundance in a Tropical Rain Forest. Conservation Biology 12 (2):380-389.

Birch JC, Newton AC, Aquino CA, Cantarello E, Echeverría C, Kitzberger T, Schiappacasse I, Garavito NT (2010) Cost-effectiveness of dryland forest restoration evaluated by spatial analysis of ecosystem services. Proceedings of the National Academy of Sciences 107 (50):21925-21930.

Botkin DB, Janak JF, Wallis JR (1972) Some Ecological Consequences of a Computer Model of Forest Growth. Journal of Ecology 60 (3):849-872.

Bowers M, Dooley J, Jr. (1993) Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia 94 (2):247-254.

Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141 (7):1745-1757.

Bruna E (2002) Effects of forest fragmentation on Heliconia acuminata seedling recruitment in central Amazonia. Oecologia 132 (2):235-243.

Bugmann H (2001) A Review of Forest Gap Models. Climatic Change 51 (3-4):259-305.

Burns BR, Floyd CG, Smale MC and Arnold GC (2011) Effects of forest fragment management on vegetation condition and maintenance of canopy composition in a New Zealand pastoral landscape. Austral Ecology 36(2):153-166.

Burns B, Innes J, Day T (2012) The Use and Potential of Pest-Proof Fencing for Ecosystem Restoration and Fauna Conservation in New Zealand. In: Somers MJ, Hayward M (eds) Fencing for Conservation. Springer New York, pp 65-90.

Burrowes JA (1999) A functional attributes approach to secondary succession pathways in New Zealand. M.Sc. thesis. University of Canterbury Christchurch.

Burrows CJ (1999) Germination behaviour of seeds of the New Zealand woody species *Beilschmiedia tawa*, *Dysoxylum spectabile*, *Griselinia lucida*, and *Weinmannia racemosa*. New Zealand Journal of Botany 37(1):95-105.

Butts CT (2014). Sna: Tools for Social Network Analysis. R package version 2.3-2. http://CRAN.R-project.org/package=sna

Camargo JLC, Kapos V (1995) Complex Edge Effects on Soil Moisture and Microclimate in Central Amazonian Forest. Journal of Tropical Ecology 11 (2):205-221.

Cambie RC, Cain BF and La Roche S (1961) A New Zealand phytochemical survey. Part 2. The Dycotyledones. New Zealand Journal of Science 12.

Campbell DJ and Atkinson IAE (2002) Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. Biological Conservation 107:19-35.

Carnicer J, Coll M, Pons X, Ninyerola M, Vayreda J, Peñuelas J (2014) Large-scale recruitment limitation in Mediterranean pines: the role of Quercus ilex and forest successional advance as key regional drivers. Global Ecology and Biogeography 23 (3):371-384.

Carswell FE, Doherty JE, Allen RB, Brignall-Theyer ME, Richardson SJ and Wiser SK (2012) Quantification of the effects of aboveground and belowground competition on growth of seedlings in a conifer–angiosperm forest. Forest Ecology and Management 269 (0):188-196.

Caspersen JP, Saprunoff M (2005) Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. Canadian Journal of Forest Research 35 (4):978-989.

Charles J, Sancey B, Morin-Crini N, Badot P-M, Degiorgi F, Trunfio G and Crini G (2011) Evaluation of the phytotoxicity of polycontaminated industrial effluents using the lettuce plant (Lactuca sativa) as a bioindicator. Ecotoxicology and Environmental Safety 74 (7):2057-2064.

Chavasse C and Traverts W (1966) Growth Habits of Rimu in Westland's Terrace Forests and their Implications for Forest Management. New Zealand Journal of Forestry 11 (1):4-19

Chaverri C and Ciccio JF (2010) Essential Oils From *Beilschmiedia pendula* (Sw.) Hemsl. (Lauraceae) From Costa Rica. Journal of Essential Oil Research 22(3):259-262.

Chiapusio G, Sánchez AM, Reigosa MJ, González L and Pellissier F (1997) Do Germination Indices Adequately Reflect Allelochemical Effects on the Germination Process? Journal of Chemical Ecology 23(11):2445-2453.

Chon SU and Nelson CJ (2010) Allelopathy in Compositae plants. A review. Agronomy for Sustainable Development 30(2):349-358.

Chouna JR, Nkeng-Efouet PA, Lenta BN, Devkota KP, Neumann B, Stammler H-G, Kimbu SF and Sewald N (2009) Antibacterial endiandric acid derivatives from Beilschmiedia anacardioides. Phytochemistry 70(5):684-688.

Coreau A, Pinay G, Thompson JD, Cheptou P-O and Mermet L (2009) The rise of research on futures in ecology: rebalancing scenarios and predictions. Ecology Letters 12 (12):1277-1286.

Cramer JM, Mesquita RCG, Bruce Williamson G (2007) Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biological Conservation 137 (3):415-423.

Crawley MJ (2007) Mixed-effects models. In: The R Book. John Wiley & Sons, Ltd, pp 627-660.

Crossman ND and Bryan BA (2009) dentifying cost-effective hotspots for restoring natural capital and enhancing landscape multifunctionality. Ecological Economics 68:654-668.

Cummings J, Parker I and Gilbert G (2012) Allelopathy: a tool for weed management in forest restoration. Plant Ecology 213 (12):1975-1989.

De Mendiburu F (2012) agricolae: Statistical Procedures for Agricultural Research. Agricultural Research. R package version 1.1-2

DeAngelis DL, Mooij WM (2005) Individual-Based Modeling of Ecological and Evolutionary Processes. Annual Review of Ecology, Evolution, and Systematics 36:147-168.

Debinski DM and Holt RD (2000) A survey and overview of habitat fragmentation experiments.Conservation Biology 14(2):342-355.

Denyer K, Burns B and Ogden J (2006) Buffering of native forest edge microclimate by adjoining tree plantations. Austral Ecology 31 (4):478-489.

Department of ConservationConservation (DOC) (2014) Te Miro and Te Tapui Scenic Reserves hunting. http://www.doc.govt.nz/parks-and-recreation/hunting/where-to-hunt/waikato/te-miro-and-te-tapui-scenic-reserves-hunting/.

DeVelice RL (1988) Test of a forest dynamics simulator in New Zealand. New Zealand Journal of Botany 26: 387–392.

Dislich C, Günter S, Homeier J, Schröder B and Huth A (2009) Simulating forest dynamics of a tropical montane forest in South Ecuador. Erdkunde 63(4):347-364.

Dodd M, Barker G, Burns B, Didham R, Innes J, King C, Smale M and 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.

Dodd MB and Power IL (2007) Recovery of Tawa-dominated forest fragments in the Rotorua Basin, New Zealand, after cessation of livestock grazing. Ecological Management & Restoration 8(3):208-217.

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB and Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology & Evolution 28 (10):605-613.

Echeverria C, Coomes D, Salas J, Rey-Benayas JM, Lara A, Newton A (2006) Rapid deforestation and fragmentation of Chilean Temperate Forests. Biological Conservation 130 (4):481-494.

Echeverría C, Newton AC, Lara A, Benayas JMR, Coomes DA (2007) Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. Global Ecology and Biogeography 16 (4):426-439.

Einhellig FA (1987) Interactions among allelochemicals and other stress factors of the plant environment. In: Waller GR (ed.) In Symposium on Allelochemicals: Role in Agriculture and Forestry. vol NO. 330. Am. Chem. Soc, Washington, D.C, pp. 343-357.

Evans JP and Keen EM (2013) Regeneration Failure in a Remnant Stand of Pignut Hickory (Carya glabra) on a Protected Barrier Island in Georgia, USA. Natural Areas Journal 33 (2):171-176.

Ewers RM and Didham RK (2007) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81 (1):117-142.

Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS and Didham RK (2006) Past and future trajectories of forest loss in New Zealand. Biological Conservation 133 (3):312-325.

Fayard J, Klein EK and Lefevre F (2009) Long distance dispersal and the fate of a gene from the colonization front. Journal of Evolutionary Biology 22 (11):2171-2182.

Fernandez C, Voiriot S, Mévy J-P, Vila B, Ormeño E, Dupouyet S, Bousquet-Mélou A (2008) Regeneration failure of Pinus halepensis Mill.: The role of autotoxicity and some abiotic environmental parameters. Forest Ecology and Management 255 (7):2928-2936.

Ferreira LV, Laurance WF (1997) Effects of Forest Fragmentation on Mortality and Damage of Selected Trees in Central Amazonia. Conservation Biology 11 (3):797-801.

Friedman J and Waller GR (1985) Allelopathy and autotoxicity. Trends in Biochemical Sciences 10(2):47-50.

Friedman J and Waller GR (1985) Allelopathy and autotoxicity. Trends in Biochemical Sciences 10 (2):47-50.

Fritz D, Bernardi AP, Haas JS, Ascoli BM, Bordignon SL and Von Poser G (2007) Germination and growth inhibitory effects of Hypericum myrianthum and H. polyanthemum extracts on Lactuca sativa L. Revista Brasileira de Farmacognosia 17:44-48.

Froude VA (1980) The allelopathic potential of some abundant New Zealand forest and scrub plants (trans: division E). Department of Scientific and Industrial Research, Lower hutt, New Zealand.

Gascon C, Williamson GB and da Fonseca GAB (2000) Receding Forest Edges and Vanishing Reserves. Science 288 (5470):1356-1358.

Gauch, HG (1982) Multivariate analysis and community structure. Cambridge University Press, Cambridge.

Gawronska H and Golisz A (2006) Allelopathy and biotic stresses. In: Reigosa MJ, Pedrol N, González L (eds.) Allelopathy a physiological process with ecological implications Springer Netherlands, pp 211-227.

Gehlhausen S, Schwartz M, Augspurger C (2000) Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology 147 (1):21-35.

Goodenough AE and Goodenough AS (2012) Development of a rapid and precise method of digital image analysis to quantify canopy density and structural complexity. ISRN Ecology 2012 (Article ID 619842):11.

Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Pe'er G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rüger N, Strand E, Souissi S, Stillman RA, Vabø R, Visser U and DeAngelis DL (2006) A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198 (1–2):115-126.

Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J and Railsback SF (2010) The ODD protocol: A review and first update. Ecological Modelling 221 (23):2760-2768.

Grimm V, Railsback SF (2005) Individual-based modeling and ecology. Princeton : Princeton University Press c2005., Princeton.

Grimm V, Wyszomirski T, Aikman D, Uchmański J (1999) Individual-based modelling and ecological theory: synthesis of a workshop. Ecological Modelling 115 (2–3):275-282.

Grman E, Bassett T and Brudvig LA (2013) Confronting contingency in restoration: management and site history determine outcomes of assembling prairies, but site characteristics and landscape context have little effect. Journal of Applied Ecology 50(5):1234-1243.

Gudex MC (1959) Native of flora of Maunga-kawa (Waikato). Transactions of the royal society of New Zealand 87 (1-2)

Hall JS (2008) Seed and seedling survival of African mahogany (Entandrophragma spp.) in the Central African Republic: Implications for forest management. Forest Ecology and Management 255 (2):292-299.

Hall GMJ and Hollinger DY (2000) Simulating New Zealand Forest Dynamics with a Generalized Temperate Forest Gap Model. Ecological Applications 10 (1):115-130

Hamby DM (1994) A review of techniques for parameter sensitivity analysis of environmental models. Environ Monit Assess 32 (2):135-154.

Hamilton Halo Project Report (2012) Report to cetnral zone sub committee – July 2012. File number 950851M. pp. 63-78.

Hartig F, Dislich C, Wiegand T and Huth A (2014) Technical Note: Approximate Bayesian parameterization of a process-based tropical forest model. Biogeosciences 11 (4):1261-1272.

Hartig F, Dyke J, Hickler T, Higgins SI, O'Hara RB, Scheiter S and Huth A (2012) Connecting dynamic vegetation models to data - an inverse perspective. Journal of Biogeography 39 (12):2240-2252.

Haugland E and Brandsaeter L (1996) Experiments on bioassay sensitivity in the study of allelopathy. Journal of Chemical Ecology 22(10):1845-1859.

Hayward MW, Kerley GIH (2009) Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? Biological Conservation 142 (1):1-13.

Herrera JM and Garcia D (2010) Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. Conservation Biology 24(4):1089-1098.

Hobbs RJ and Yates CJ (2003) TURNER REVIEW No. 7. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. Australian Journal of Botany 51(5):471-488.

Hobbs RJ and Harris JA (2001) Restoration Ecology: Repairing the Earth's Ecosystems in the New Millennium. Restoration Ecology 9 (2):239-246.

Hobbs, RJ, Hallett, LM, Ehrlich, PR and Mooney, HA (2011) Intervention ecology: applying ecological science in the twenty-first century. BioScience 61:442–450.

Holl K, Crone EE and Schultz CB (2003) Landscape restorarion: moving from generalities to methodologies. BioScience 53:491-502.

Holl KD and Aide TM (2011) When and where to actively restore ecosystems? Forest Ecology and Management 261(10):1558-1563.

Hothorn T, Hornik K, Van de Wiel M and ZeileisWiel A (2008) Implementing a class of permutation tests: The coin package. Journal of Statistical Software 28(8):1-23.

Husheer SW, Hansen QW and Urlich SC (2005) Effects of red deer on tree regeneration and growth in Aorangi Forest, Wairarapa. New Zealand Journal of Ecology 29 (2):271–277.

Huxel GR and Hastings A (1999) Habitat Loss, Fragmentation, and Restoration. Restoration Ecology 7 (3):309-315.

Iida S, Nakashizuka T (1995) Forest fragmentation and its effect on species diversity in sub-urban coppice forests in Japan. Forest Ecology and Management 73 (1–3):197-210.

Inderjit, Weiner J (2001) Plant allelochemical interference or soil chemical ecology? Perspectives in Plant Ecology, Evolution and Systematics 4 (1):3-12.

Innes J, King CM, Bridgman L, Fitzgerald N, Arnold G and Cox N (2010) Effect of grazing on ship rat density in forest fragments of lowland Waikato, New Zealand. New Zealand Journal of Ecology 34(1):227-232.

Ismail SA, Ghazoul J, Ravikanth G, Kushalappa CG and Uma Shaanker R (2014) Forest trees in human modified landscapes: ecological and genetic drivers of recruitment failure in *Dysoxylum malabaricum* (Meliaceae). PLoS ONE 9(2): e89437.

Jackson JE (1991) A user's guide to Principal Components. Wiley, New York

James I (1998) Growth and survival of rimu seedlings in South Westland forests. New Zealand Journal of Forestry 42(4):28-30.

Joseph LN, Field SA, Wilcox C and Possingham HP (2006) Presence–Absence versus Abundance Data for Monitoring Threatened Species

June SR (1976) Investigations on allelopathy in a red beech forest Mauri ora 4:87-91

Kalra YP and Maynard DG (1991) Methods manual for forest soil and plant analysis. Forestry Canada, Northwest Region, Edmonton, Alberta.

Kaval P (2004) The Maungatautari Ecological Island Trust: An Economic Analysis. A Report Prepared for Environment Waikato. Department of Economics University of Waikato Management School. 17pp.

Kelly D, Ladley JJ, Robertson AW, Anderson SH, Wotton DM and Wiser SK (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit dispersal in New Zealand. New Zealand Journal of Ecology 34:66–85.

Kimball S and Mattis P (2013) GIMP(GNU Image Manipulation Program). Version 2.8.10.

King C, Innes J, Gleeson D, Fitzgerald N, Winstanley T, O'Brien B, Bridgman L and Cox N (2011) Reinvasion by ship rats (*Rattus rattus*) of forest fragments after eradication. Biological invasions 13 (10):2391-2408.

Knowles B and Beveridge AE (1982) Biological flora of New Zealand 9. *Beilschmiedia tawa* (A. Cunn.) Benth. et Hook. F. ex Kirk (Lauraceae) Tawa. New Zealand Journal of Botany 20:37-54.

Kostermans AH (1964) Bibliographia *Lauracearum*. Archipel – Bogor, Indonesia. 1450pp.

Kueffer C, Kaiser-Bunbury CN (2013) Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. Frontiers in Ecology and the Environment 12 (2):131-137.

Kunstler G, Coomes DA and Canham CD (2009). Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. Journal of Ecology 97:685–695.

Kuznetsova A, Brockhoff PB and Christensen RHB (2014) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-6. http://CRAN.R-project.org/package=lmerTest

Landcare Research (2005) Ecological Traits of New Zealand Flora. Landcare Research. http://ecotraits.landcareresearch.co.nz/. Accessed July 2013.

Laurance WF (2000) Do edge effects occur over large spatial scales? Trends in Ecology & Evolution 15 (4):134-135.

Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Conservation: Rainforest fragmentation kills big trees. Nature 404 (6780):836-836.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conservation Biology 16 (3):605-618.

Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ribeiro JELS, Giraldo JP, Lovejoy TE, Condit R, Chave J, Harms KE and D'Angelo S (2006) Rapid decay of tree-community composition in Amazonian forest fragments. Proceedings of the National Academy of Sciences 103 (50):19010-19014.

Lê S, Josse J and Husson F (2008) FactoMineR: An R Package for Multivariate Analysis. Journal of Statistical Software. 25(1). pp. 1-18.

Liu J, Ashton PS (1995) Individual-based simulation models for forest succession and management. Forest Ecology and Management 73 (1–3):157-175.

Mander C, Hay R and Powlesland R (1998) Monitoring and management of kereru (*Hemiphaga novaeseelandiae*) vol 15. Department of Conservation, Wellington, New Zealand.

McGlone MS, Hall GMJ, Wilmshurst JM (2011) Seasonality in the early Holocene: Extending fossil-based estimates with a forest ecosystem process model. The Holocene 21 (4):517-526.

Melo FPL, Pinto SRR, Brancalion PHS, Castro PS, Rodrigues RR, Aronson J and Tabarelli M (2013) Priority setting for scaling-up tropical forest restoration projects: Early lessons from the Atlantic Forest Restoration Pact. Environmental Science & Policy 33 (0):395-404.

Meurk CD and Swaffield SR (2000) A landscape ecological framework for indigenous regeneration in rural New Zealand-Aotearoa. Landscape and Urban Planning 50 (1-3):129-144.

Meurk CD and Hall GMJ 2006. Options for enhancing forest biodiversity across New Zealand’s managed landscapes based on ecosystem modelling and spatial design. New Zealand Journal of Ecology 30: 131–146.

Mitchell K (2007) Quantitative analysis by the point-centered quarter method. arXiv:1010.3303

Moss MR (2000) Interdisciplinarity, landscape ecology and the `Transformation of Agricultural Landscapes'. Landscape Ecology 15 (3):303-311.

Morales NS, Becerra PI, Arellano E, Gilabert H (2015) Effect of large and small herbivores on seed and seedling survival of Beilschmiedia miersii in central Chile. Bosque. In press.

Muller CH (1969) Allelopathy as a factor in ecological process. Plant Ecology 18(1):348-357.

Mulligan M, Wainwright J (2013) Modelling and Model Building. In: Environmental Modelling. John Wiley & Sons, Ltd, pp 7-26.

Muñiz-Castro MA, Williams-Linera G, Benayas J, eacute, Mar, iacute, Rey a (2006) Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. Journal of Tropical Ecology 22 (04):431-440.

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution 10 (2):58-62.

Murcia C (1997) Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. Forest Ecology and Management 99 (1–2):163-170.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB and Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Myers SC and Court AJ (2013) Regeneration of taraire (*Beilschmiedia tarairi*) and kohekohe (*Dysoxylum spectabile*) in a forest remnant on Tiritiri Matangi Island, northern New Zealand. New Zealand Journal of Ecology 37 (3):353-358.

NIWA (National Institute of Water and Atmospheric Research) (2014a) Annual Climate Summary 2013. NIWA National Climate Centre. 29pp.

NIWA (National Institute of Water and Atmospheric Research) (2014b) The national climate database. http://cliflo.niwa.co.nz/. Accessed May 2014.

Norbury G, Hutcheon A, Reardon J, Daigneault A (2014) Pest fencing or pest trapping: A bio-economic analysis of cost-effectiveness. Austral Ecology 39 (7):795-807.

Norton DA (2009) Ecological restoration in New Zealand – current trends and future challenges. Ecological Management & Restoration 10 (2):76-77.

Norton DA, Palmer JG, Ogden J (1987) Dendroecological studies in New Zealand 1. An evaluation of tree age estimates based on increment cores. New Zealand Journal of Botany 25 (3):373-383.

Ogden J (1983) Community matrix model predictions of future forest composition at Russell State Forest New Zealand Journal of Ecology 6:71-77.

Ogden J and Stewart GH (1995) Community dynamics of the New Zealand conifers. 4. 81-1 19, In: Enright, N., and R.H. Hill (eds), Ecology of the Southern Conifers. Melbourne University Press.

Ogden J and West CJ (1981) Annual rings in Beilschmiedia tawa (Lauraceae). New Zealand Journal of Botany (19):397-400

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH and Wagner H (2013) Vegan: community ecology package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Ooi M.K.J., Auld T.D. and Whelan R.J. (2004) Comparison of the cut and tetrazolium tests for assessing seed viability: a study using Australian native Leucopogon species. Ecological Management & Restoration 5, 141-143

Palmer SCF, Mitchell RJ, Truscott AM and Welch D (2004) Regeneration failure in Atlantic oakwoods: the roles of ungulate grazing and invertebrates. Forest Ecology and Management 192 (2–3):251-265.

Perry GLW and Millington JDA (2008) Spatial modelling of succession-disturbance dynamics in forest ecosystems: Concepts and examples. Perspectives in Plant Ecology, Evolution and Systematics 9 (3-4):191-210.

Perry GLW and Enright NJ (2007) Contrasting outcomes of spatially implicit and spatially explicit models of vegetation dynamics in a forest-shrubland mosaic. Ecological Modelling 207 (2–4):327-338.

Perry GLW, Ogden J, Enright NJ and Davy LV (2010) Vegetation patterns and trajectories in disturbed landscapes, Great Barrier Island, northern New Zealand. New Zealand Journal of Ecology 34: 311-323.

Pollard JH (1971) On distance estimators of density in randomly distributed forests. Biometrics 27: 991-1002.

Primack R, Rozzi R, Feinsinger P, Dirzo R and Massardo F (2001) Fundamentos de Conservacion Biologica: Perspectivas Latinoamericanas. Fondo de Cultura Economica, Mexico.

Quinn GP and Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge, UK ; New York : Cambridge University Press 2002, Cambridge, UK ; New York.

R Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ranal MA and Santana DGD (2006) How and why to measure the germination process? Brazilian Journal of Botany 29:1-11.

Rawat MSM, Pant G, Prasad D, Joshi RK, and Pande CB (1998) Plant growth inhibitors (Proanthocyanidins) from *Prunus armeniaca*. Biochemical Systematics and Ecology 26(1):13-23.

Reigosa R, Pedrol MJ and Nuria GL (2006) Allelopathy : a physiological process with ecological implications. Springer, Dordrecht, Netherlands

Reuter H, Breckling B, Jopp F (2011) Individual-Based Models. In: Jopp F, Reuter H, Breckling B (eds) Modelling Complex Ecological Dynamics. Springer Berlin Heidelberg, pp 163-178.

Rice EL (1995) Biological control of weeds and plant diseases: advances in applied allelopathy. Norman: University of Oklahoma Press, © 1995.

Robertson AW, Trass A, Ladley JJ and Kelly D (2006) Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. Functional Ecology 20 (1):58-66.

Rodrigues RR, Gandolfi S, Nave AG, Aronson J, Barreto TE, Vidal CY, Brancalion PHS (2011) Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. Forest Ecology and Management 261 (10):1605-1613.

Roper GH (1967) Morphological, ontogenetic and embryological studies in the flowers of *Beilschmiedia tawa* (A. Cunn.) Benth. Et Hook. F. ex Kirk (Lauraceae). Unpublished M.Sc. Thesis. Victoria University of Wellington, New Zealand, 111pp.

Russell GB and Fraser JG (1969) Identification of Isoboldine as the major Alkaloid from berries of Beilschmiedia tawa. New Zealand Journal of Science 12:694-695.

Sampaio AB, Holl KD, Scariot A (2007) Does Restoration Enhance Regeneration of Seasonal Deciduous Forests in Pastures in Central Brazil? Restoration Ecology 15 (3):462-471.

Saunders DA, Hobbs RJ and Margules CR (1991) Biological Consequences of Ecosystem Fragmentation: A Review. Conservation Biology 5(1):18-32.

Schmiegelow FKA, Machtans CS, Hannon SJ (1997) Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78 (6):1914-1932.

Scott J (2003) History of Maungatautari. http://www.maungatrust.org/files/6648/History_of_Maungatautari.pdf

Seagle SW, Liang S-Y (2001) Application of a forest gap model for prediction of browsing effects on riparian forest succession. Ecological Modelling 144 (2–3):213-229.

Shackelford N, Hobbs RJ, Burgar JM, Erickson TE, Fontaine JB, Laliberté E, Ramalho CE, Perring MP, Standish RJ (2013) Primed for Change: Developing Ecological Restoration for the 21st Century. Restoration Ecology 21 (3):297-304.

Shugart HH (1984) A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag. pp 278

Shugart HH and Smith TM (1996) A review of forest patch models and their application to global change research. Climatic Change 34 (2):131-153.

Smale MC, Bathgate JL and Guest R (1986) Current prospects for tawa. New Zealand Journal of Forestry 31:13-18.

Smale MC, Dodd MB, Burns BR and Power IL (2008) Long-term impacts of grazing on indigenous forest remnants on North Island hill country, New Zealand. New Zealand Journal of Ecology 32(1):57–66.

Smale MC, Ross CW and Arnold GC (2005) Vegetation recovery in rural kahikatea (Dacrycarpus dacrydioides) forest fragments in the Waikato region, New Zealand, following retirement from grazing. New Zealand Journal of Ecology 29:261-269.

Smuts-Kennedy C, Kevin AP (2013) Reconstructing avian biodiversity on Maungatautari. Notornis 60 (1): 93-106.

Sodhi N, Posa M, Lee T, Bickford D, Koh L and Brook B (2010) The state and conservation of Southeast Asian biodiversity. Biodiversity and Conservation 19 (2):317-328.

Speedy C, Day T, and Innes J (2007) Pest eradication technology – the critical partner to pest exclusion technology: the Maungatautari experience. Managing Vertebrate Invasive Species: Proceedings of an International Symposium (eds. G.W. Witmer, W.C. Pitt & K.A. Fagerstone), pp. 115 – 126. USDA/APHIS/WS, National Wildlife Research Centre, Fort Collins.

Spooner P, Lunt I, Robinson W (2002) Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. Ecological Management & Restoration 3 (2):117-126.

Stanturf JA, Palik BJ, Dumroese RK (2014) Contemporary forest restoration: A review emphasizing function. Forest Ecology and Management 331 (0):292-323.

Stevenson BA (2004) Changes in phosphorus availability and nutrient status of indigenous forest fragments in Pastoral New Zealand Hill country. Plant and Soil 262 (1-2):317-325.

Stillman RA, Railsback SF, Giske J, Berger U, Grimm V (2014) Making Predictions in a Changing World: The Benefits of Individual-Based Ecology. BioScience. In press.

Suding KN and Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. Trends in Ecology & Evolution, 24:271–279.

Tabanez AAJ, Viana VM (2000) Patch Structure within Brazilian Atlantic Forest Fragments and Implications for Conservation. Biotropica 32 (4b):925-933.

Tanentzap AJ, Zou J, Coomes DA (2013) Getting the biggest birch for the bang: restoring and expanding upland birchwoods in the Scottish Highlands by managing red deer. Ecology and Evolution 3 (7):1890-1901.

Tarara JM and Hoheisel G-A (2007) Low-cost shielding to minimize radiation errors of temperature sensors in the field. HortScience 42 (6):1372-1379.

Thrippleton T, Dolos K, Perry GLW, Groeneveld J, Reineking B (2014) Simulating long-term vegetation dynamics using a forest landscape model: the post-Taupo succession on Mt. Hauhungatahi, North Island, New Zealand. New Zealand Journal of Ecology 38 (1):26-38.

Thompson JR, Wiek A, Swanson FJ, Carpenter SR, Fresco N, Hollingsworth T, Spies TA and Foster DR (2012) Scenario Studies as a Synthetic and Integrative Research Activity for Long-Term Ecological Research. BioScience 62(4):367-376.

Thrippleton T, Dolos K, Perry GLW, Groeneveld J and Reineking, B (2014) Simulating long-term vegetation dynamics using a forest landscape model: the post-Taupo succession on Mt. Hauhungatahi, North Island, New Zealand. New Zealand Journal of Ecology 38(1):26-38.

Uriarte M, Bruna EM, Rubim P, Anciães M, Jonckheere I (2010) Effects of forest fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site limitation. Ecology 91 (5):1317-1328.

Waikato Regional Council (2009) Environmental Information. Forest Fragmentation. Key points. http://www.waikatoregion.govt.nz/Environment/Environmental-information/Environmental-indicators/Biodiversity/veg3-key-points/

Wallis FP and James IL (1972) Introduced animal effects and erosion phenomena in the Northern Urewera forests. New Zealand Journal of Forestry 17 (1):21–36.

Walters CJ (1986) Adaptive Management of Renewable Resources. McMillan Publishing Co., New York, USA.

Wang Y, Naumann U, Wright S and Warton D (2013) Mvabund: statistical methods for analysing multivariate abundance data. R package version 3.8.4. http://CRAN.R-project.org/package=mvabund.

Ward JH (1963) Hierarchical Grouping to Optimize an Objective Function. Journal of the American Statistical Association 58(301):236-244.

Wardle DA, Ahmed M and Nicholson KS (1991) Allelopathic influence of nodding thistle (Carduus nutans L.) seeds on germination and radicle growth of pasture plants. New Zealand Journal of Agricultural Research 34(2):185-191.

Warton DI (2011) Regularised sandwich estimators for analysis of high dimensional data using generalized estimating equations. Biometrics 67(1): 116-123.

Warton DI, Wright ST and Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution 3 (1):89-101.

Wehrli A, Weisberg PJ, Schönenberger W, Brang P, Bugmann H (2007) Improving the establishment submodel of a forest patch model to assess the long-term protective effect of mountain forests. Eur J Forest Res 126 (1):131-145.

West C (1995) Sustainability of *Beilschmiedia tawa* dominated Forest in New Zealand: Population Predictions Based on Transition Matrix Model Analysis. Australian Journal of Botany 43 (1):51-71.

West CJ (1986) Population ecology of *Beilschmiedia tawa* at Pureora Forest. Unpublished PhD thesis, University of Auckland, Auckland.

White JW, Rassweiler A, Samhouri JF, Stier AC and White C (2014) Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123 (4):385-388.

White N, Engeman R, Sugihara R and Krupa H (2008) A comparison of plotless density estimators using Monte Carlo simulation on totally enumerated field data sets. BMC Ecology 8(1):6.

Wilensky U (1999) NetLogo, Center for Connected Learning and Computer-Based Modeling, Northwestern University., Evanston, Il.

Wiser SK, Hurst JM,Wright EF and Allen R (2011) New Zealand's forest and shrubland communities: a quantitative classification based on a nationally representative plot network. Applied Vegetation Science 14:506–523.

Wyse SV, Burns B (2013) Effects of Agathis australis (New Zealand kauri) leaf litter on germination and seedling growth differs among plant species. New Zealand Journal of Ecology 37 (2):178-183.

Young A, and Mitchell N (1994) Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biological Conservation 67(1):63-72.

Zahawi RA, Reid JL and Holl KD (2014) Hidden Costs of Passive Restoration. Restoration Ecology 22 (3):284-287.

Zambrano J, Coates R and Howe HF (2014) Effects of forest fragmentation on the recruitment success of the tropical tree Poulsenia armata at Los Tuxtlas, Veracruz, Mexico. Journal of Tropical Ecology 30 (03):209-218.

APPENDIX 1

Reduced and additive model tables

Table A. Results of the analysis using a reduced model on mean abundance of trees

	Res.Df	Df.diff	Dev	Pr(>Dev)
Level of management	6	2	41.32	0.37
Site	5	1	32.90	0.38
Level of management × Site	3	2	71.68	0.32

Table B. Results of the analysis using an additive model on mean abundance of trees

	Res.Df	Df.diff	Dev	Pr(>Dev)
Level of management	6	2	55	0.36
Carbon	5	1	96	0.38
Nitrogen	4	1	67	0.33
Water	3	1	12643	0.092

Table C. Results of the analysis using a reduced model on mean abundance of canopy trees

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	5	2	14.81	0.54
Site	4	1	2.17	0.98
Level of management × Site	2	2	66.32	0.11

Table D. Results of the analysis using an additive model on mean abundance of canopy trees

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	5	2	14.81	0.59
Carbon	4	1	16.78	0.4
Nitrogen	3	1	45.08	0.14
Water	2	1	15.173	0.47

Table E. Results of the analysis using a reduce model on mean abundance of subcanopy trees

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	6	2	14.1	0.26
Site	5	1	3.3	0.74
Level of management × Site	3	2	29.3	0.26

Table F. Results of the analysis using an additive model on mean abundance of subcanopy trees

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	6	2	14.11	0.29
Carbon	5	1	5.14	0.57
Nitrogen	4	1	5.33	0.69
Water	3	1	36.26	0.09

Table G. Results of the analysis using a reduce model on mean abundance of seedlings

	Res.Df	Df.diff	Dev	Pr(>Dev)
Level of management	6	2	54.94	0.28
Site	5	1	54.90	0.18
Level of management × Site	3	2	50.57	0.74

Table H. Results of the analysis using a reduce model on mean abundance of seedlings

	Res.Df	Df.diff	Dev	Pr(>Dev)
Level of management	6	2	55	0.32
Carbon	5	1	96	0.1
Nitrogen	4	1	67	0.6
Water	3	1	12643	0.2

Table I. Reduce model results of the analysis on mean abundance of canopy seedlings.

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	6	2	8.47	0.78
Site	5	1	2.71	0.83
Level of management * Site	3	2	6.59	0.96

Table J. Additive model results of the analysis on mean abundance of canopy seedlings.

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	6	2	8.47	0.78
Water	5	1	3.63	0.81
Nitrogen	4	1	21.11	0.61
Carbon	3	1	11.39	0.71

Table K. Reduce model results of the analysis on mean abundance of subcanopy seedlings.

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	6	2	7.12	0.83
Site	5	1	8.99	0.43
Level of management * Site	3	2	35	0.39

Table L. Additive model results of the analysis on mean abundance of subcanopy seedlings.

	Res.Df	**Df.diff**	**Dev**	**Pr(>Dev)**
Level of management	6	2	7.12	0.79
Water	5	1	3.41	0.82
Nitrogen	4	1	26.05	0.36
Carbon	3	1	89.34	0.078

APPENDIX 2

Table A2.1. Parameters of the model.

Parameter	**Description**	**Unit**	**Tawa**	**Pigeonwood**	**Pukatea**	**Kawakawa**	**Mahoe**	**Rimu**	**Reference**
Shade tolerance	Shade tolerance of species, relative position on light gradient (0.25-0.55)	n/a	0.25	0.4	0.25	0.4	0.55	0.35	All values were estimated using Ecological traits of New Zealand Flora (2005)
Reproductive age	Minimum age for seed set (10-20)	Years	20	10	20	10	10	20	All values were collected from Ecological traits of New Zealand Flora (2005)
Gap maker	Make a gap on dying (Boolean)	n/a	1	0	1	0	0	1	Ecological traits of New Zealand Flora (2005)
Suppression tolerance	Level of suppression (proportion of optimal growth five-year average) below which mortality risk increases (0.35-0.80)		0.35	0.50	0.35	0.80	0.50	0.40	Estimated using Knowles and Beveridge (1982), Burrowes (1999), Ecological traits of New Zealand Flora (2005), Smale(2008)
Suppression mortality rate	Annual mortality rate for suppressed trees (0.025-0.1)		0.025	0.10	0.025	0.10	0.10	0.05	Estimated using Knowles and Beveridge (1982), Burrowes (1999), Ecological traits of New Zealand Flora (2005), Smale(2008)

Table A2.1. Parameters of the model.

Parameter	**Description**	**Unit**	**Tawa**	**Pigeonwood**	**Pukatea**	**Kawakawa**	**Mahoe**	**Rimu**	**Reference**
Herbivory	Proportion of seeds lost to herbivory (0.1-0.8)		0.8	0.5	0.5	0.5	0.8	0.1	Estimated using Wallis and James (1972), Allen et al. (1997), Husheer (2005), Ecological traits of New Zealand Flora (2005)
Edge response	Growth modifier at edge (0.1-0.5)		0.1	0.5	0.1	0.3	1.0	0.1	Young and Mitchell (1994)
Sapling survival	Proportion of saplings that survive each year (0.7-0.85)		0.70	0.85	0.70	0.70	0.80	0.70	*B. tawa* calibrated based on West (1995) and informal calibration
Seedling survival	Proportion of seedlings that survive each year (0.5-0.6)		0.5	0.6	0.5	0.6	0.6	0.5	Estimated using Knowles and Beveridge (1982), West (1986), James(1998), Ecological traits of New Zealand Flora (2005)
seedling-transition	Proportion of seedlings that become saplings (0.03-0.1)		0.04	0.07	0.04	0.10	0.07	0.03	Estimated using Burrowes (1999), Knowles and Beveridge (1982), Ecological traits of New Zealand Flora (2005)

Table A2.2 Results of the sensitivity analysis on ± 20 % baseline values of all species for *B. tawa*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. Ranking represents how sensitive the parameter is, 10 being non-sensitive and 1 highly sensitive. Ranking values in bold are the most sensitive.

Tawa					**Abundance**		**Age**		**dbh**		**Height**		**Mean age**		**Mean Basal area**		**Mean height**	
					Ranking		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.25	0.2	0.3	1	4	10	11	4	4	3	11	**1**	4	**1**	6	3	4	3
Seedling transition	20	16	24	2	2	5	**1**	12	**1**	11	**1**	11	**1**	10	2	7	**1**	10
Shade tolerance	1	0.8	1.2	5	10	4	9	5	9	8	6	10	9	9	10	6	8	8
Suppression mortality	2	1.6	2.4	6	6	9	4	6	10	12	12	8	5	11	5	9	12	11
Suppression tolerance	0.35	0.28	0.42	4	3	6	10	**1**	3	2	5	3	3	2	3	4	3	2
Dispersal	0.025	0.02	0.03	6	12	11	7	8	8	6	3	9	7	8	12	12	9	5
Reproductive age	0.8	0.64	0.96	5	11	8	5	9	12	10	8	7	12	12	11	10	10	12
Sapling survival	0.1	0.08	0.12	4	8	3	3	7	11	4	7	12	11	4	9	5	11	4
Seed production	0.5	0.4	0.6	3	9	7	12	10	7	9	9	6	8	7	8	8	5	9
Herbivory	0.7	0.56	0.84	3	**1**	**1**	2	2	6	7	4	4	10	5	**1**	**1**	7	7
Edge effect	0.04	0.032	0.048	2	5	2	6	3	2	**1**	2	2	2	3	4	2	2	**1**
LDD	0.01	0.008	0.012	6	7	12	8	11	5	5	10	5	6	6	7	11	6	6

Table A2.3 Sensitivity values used in the sensitivity analysis on ± 20 % baseline values of all species for *B. tawa*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. We considered state variables (y) with $S_{y,x} > 1$ sensitive to changes in parameter (x).

Tawa					Abundance		Age		dbh		Height		Mean age		Mean Basal area		Mean height	
					$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.25	0.2	0.3	1	0.192	0.017	0.037	0.288	0.056	0.202	0.000	2.655	0.048	7.984	0.134	0.747	0.036	0.157
Seedling transition	20	16	24	2	5.000	0.219	5.000	0.000	5.000	0.002	5.000	0.000	5.000	0.006	5.000	0.216	5.000	0.003
Shade tolerance	1	0.8	1.2	5	0.037	0.230	0.113	0.175	0.009	0.019	0.003	0.000	0.011	0.015	0.053	0.254	0.006	0.010
Suppression mortality	2	1.6	2.4	6	0.150	0.075	0.208	0.107	0.005	0.000	0.000	0.002	0.025	0.004	0.140	0.081	0.001	0.003
Suppression tolerance	0.35	0.28	0.42	4	2.064	0.120	0.097	0.652	0.395	0.420	0.005	0.022	0.381	0.575	1.829	0.529	0.269	0.301
Dispersal	0.025	0.02	0.03	6	0.010	0.014	0.145	0.069	0.017	0.034	0.009	0.002	0.021	0.015	0.004	0.022	0.005	0.033
Reproductive age	0.8	0.64	0.96	5	0.024	0.082	0.201	0.044	0.003	0.006	0.001	0.002	0.007	0.002	0.021	0.071	0.003	0.000
Sapling survival	0.1	0.08	0.12	4	0.087	0.571	0.262	0.090	0.004	0.123	0.003	0.000	0.007	0.114	0.082	0.452	0.002	0.092
Seed production	0.5	0.4	0.6	3	0.080	0.100	0.029	0.014	0.019	0.015	0.001	0.003	0.011	0.017	0.095	0.084	0.023	0.008
Herbivory	0.7	0.56	0.84	3	5.263	5.293	0.442	0.499	0.021	0.027	0.006	0.005	0.010	0.030	5.231	5.361	0.015	0.019
Edge effect	0.04	0.032	0.048	2	0.174	0.853	0.192	0.436	1.241	0.765	0.014	0.029	0.807	0.398	1.374	1.483	0.962	0.569
LDD	0.01	0.008	0.012	6	0.150	0.006	0.119	0.013	0.028	0.035	0.001	0.004	0.021	0.027	0.122	0.047	0.022	0.022

Tab;e A2.4 Results of the sensitivity analysis on ± 20 % baseline values of all species for *L. novae-zelandiae*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. Ranking represents how sensitive the parameter is, 10 being non-sensitive and 1 highly sensitive. Ranking values in bold are the most sensitive.

Pukatea					**Abundance**		**Age**		**dbh**		**Height**		**Mean age**		**Mean Basal area**		**Mean heigth**	
					Ranking		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.25	0.2	0.3	6	10	8	11	9	4	10	11	8	4	7	8	11	6	9
Seedling transition	20	16	24	6	**1**	6	7	8	9	11	5	11	10	12	**1**	7	9	11
Shade tolerance	1	0.8	1.2	4	7	4	3	10	5	6	3	6	5	6	6	5	4	6
Suppression mortality	2	1.6	2.4	7	11	11	5	6	12	8	12	7	11	9	12	8	11	8
Suppression tolerance	0.35	0.28	0.42	3	3	5	12	2	3	3	7	3	3	2	3	4	3	3
Dispersal	0.025	0.02	0.03	7	12	12	10	5	7	7	10	5	8	8	11	10	7	7
Reproductive age	0.5	0.4	0.6	6	6	9	4	4	11	12	6	4	9	11	9	12	8	12
Sapling survival	0.1	0.08	0.12	5	9	3	8	7	8	4	9	9	7	4	10	3	10	4
Seed production	0.5	0.4	0.6	6	8	7	9	11	6	9	8	10	6	10	7	6	5	10
Herbivory	0.7	0.56	0.84	1	2	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	2	**1**	**1**	**1**
Edge effect	0.04	0.032	0.048	2	4	2	2	3	2	2	2	2	2	3	4	2	2	2
LDD	0.01	0.008	0.012	6	5	10	6	12	10	5	4	12	12	5	5	9	12	5

Table A2.5 Sensitivity values used in the sensitivity analysis on ± 20 % baseline values of all species for *L. novae-zelandiae*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. We considered state variables (*y*) with $S_{y,x} > 1$ sensitive to changes in parameter (*x*).

Pukatea					**Abundance**		**Age**		**dbh**		**Height**		**Mean age**		**Mean Basal area**		**Mean height**	
					$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.25	0.2	0.3	6	0.009	0.050	0.124	0.124	0.065	0.015	0.000	0.003	0.058	0.032	0.050	0.036	0.038	0.010
Seedling transition	20	16	24	6	5.553	0.169	0.206	0.153	0.011	0.011	0.005	0.001	0.009	0.000	5.525	0.165	0.012	0.005
Shade tolerance	1	0.8	1.2	4	0.048	0.237	0.320	0.113	0.064	0.049	0.007	0.004	0.049	0.040	0.114	0.197	0.053	0.030
Suppression mortality	2	1.6	2.4	7	0.004	0.016	0.284	0.356	0.004	0.025	0.000	0.004	0.003	0.023	0.016	0.045	0.011	0.010
Suppression tolerance	0.35	0.28	0.42	3	2.105	0.176	0.121	0.869	0.450	0.397	0.002	0.020	0.426	0.570	1.848	0.240	0.293	0.290
Dispersal	0.025	0.02	0.03	7	0.003	0.002	0.138	0.357	0.029	0.027	0.000	0.005	0.024	0.025	0.025	0.036	0.026	0.029
Reproductive age	0.5	0.4	0.6	6	0.049	0.033	0.315	0.420	0.006	0.000	0.003	0.009	0.010	0.005	0.038	0.026	0.012	0.001
Sapling survival	0.1	0.08	0.12	5	0.009	0.370	0.185	0.277	0.026	0.125	0.001	0.001	0.030	0.101	0.029	0.263	0.012	0.086
Seed production	0.5	0.4	0.6	6	0.041	0.160	0.170	0.110	0.047	0.024	0.001	0.001	0.036	0.007	0.094	0.178	0.042	0.010
Herbivory	0.7	0.56	0.84	1	4.949	4.980	2.175	3.165	2.928	2.363	0.609	1.795	2.442	1.926	4.920	4.966	2.013	1.419
Edge effect	0.04	0.032	0.048	2	0.340	0.940	0.472	0.483	1.250	0.797	0.018	0.031	0.808	0.417	1.507	1.592	0.967	0.596
LDD	0.01	0.008	0.012	6	0.144	0.017	0.243	0.038	0.009	0.063	0.005	0.000	0.001	0.057	0.141	0.039	0.000	0.038

Table A2.6 Results of the sensitivity analysis on ± 20 % baseline values of all species for *D. cupressinum*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. Ranking represents how sensitive the parameter is, 10 being non-sensitive and 1 highly sensitive. Ranking values in bold are the most sensitive.

Rimu					**Abundance**		**Age**		**dbh**		**Height**		**Mean age**		**Mean Basal area**		**Mean height**	
					Ranking		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.35	0.28	0.42	5	6	4	9	5	9	5	10	6	9	5	6	6	9	5
Seedling transition	20	16	24	3	2	7	**1**	11	**1**	7	**1**	9	**1**	7	2	7	**1**	6
Shade tolerance	1	0.8	1.2	7	8	12	7	6	6	10	9	11	6	10	10	9	6	12
Suppression mortality	2	1.6	2.4	4	4	5	5	8	5	11	5	5	5	11	5	4	5	10
Suppression tolerance	0.4	0.32	0.48	2	**1**	2	3	2	4	2	4	2	4	2	**1**	2	4	2
Dispersal	0.05	0.04	0.06	6	7	10	6	4	10	6	12	8	10	6	7	10	8	8
Reproductive age	0.1	0.08	0.12	5	10	8	10	10	7	4	6	7	7	4	8	11	7	4
Sapling survival	0.1	0.08	0.12	7	9	6	8	7	11	12	7	4	12	12	9	5	11	11
Seed production	0.5	0.4	0.6	8	11	9	12	9	12	8	11	12	11	8	12	12	12	7
Herbivory	0.7	0.56	0.84	1	3	**1**	2	**1**	2	**1**	2	**1**	2	**1**	3	**1**	2	**1**
Edge effect	0.03	0.024	0.036	2	5	3	4	3	3	3	3	3	3	3	4	3	3	3
LDD	0.01	0.008	0.012	8	12	11	11	12	8	9	8	10	8	9	11	8	10	9

Table A2.7 Sensitivity values used in the sensitivity analysis on ± 20 % baseline values of all species for *D. cupressinum*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. We considered state variables (*y*) with $S_{y,x} > 1$ sensitive to changes in parameter (*x*).

Rimu					**Abundance**		**Age**		**dbh**		**Height**		**Mean age**		**Mean Basal area**		**Mean height**	
					$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.35	0.28	0.42	5	0.867	1.854	0.250	0.454	0.204	0.419	0.046	0.143	0.148	0.338	0.803	1.200	0.119	0.269
Seedling transition	20	16	24	3	5.000	0.757	5.000	0.036	5.000	0.275	5.000	0.054	5.000	0.230	5.000	0.360	5.000	0.227
Shade tolerance	1	0.8	1.2	7	0.505	0.143	0.348	0.442	0.360	0.079	0.048	0.041	0.291	0.136	0.099	0.240	0.302	0.001
Suppression mortality	2	1.6	2.4	4	3.937	1.748	0.646	0.281	0.571	0.072	0.218	0.164	0.447	0.053	2.811	1.718	0.459	0.048
Suppression tolerance	0.4	0.32	0.48	2	107.050	4.910	2.378	4.168	1.037	2.074	0.515	3.988	0.616	2.316	83.931	4.894	0.774	2.260
Dispersal	0.05	0.04	0.06	6	0.509	0.335	0.391	0.608	0.082	0.321	0.008	0.110	0.098	0.300	0.324	0.219	0.135	0.184
Reproductive age	0.1	0.08	0.12	5	0.207	0.422	0.220	0.055	0.319	0.461	0.123	0.133	0.280	0.367	0.233	0.184	0.207	0.385
Sapling survival	0.1	0.08	0.12	7	0.305	1.417	0.309	0.354	0.062	0.027	0.068	0.190	0.012	0.027	0.190	1.338	0.055	0.008
Seed production	0.5	0.4	0.6	8	0.124	0.369	0.085	0.082	0.053	0.269	0.024	0.022	0.087	0.218	0.083	0.032	0.016	0.218
Herbivory	0.7	0.56	0.84	1	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000
Edge effect	0.03	0.024	0.036	2	3.689	3.640	0.934	1.186	1.438	0.730	0.740	0.878	1.218	0.741	3.593	3.555	0.936	0.514
LDD	0.01	0.008	0.012	8	0.064	0.256	0.163	0.010	0.224	0.218	0.067	0.049	0.180	0.204	0.083	0.327	0.101	0.160

Table A2.8 Results of the sensitivity analysis on ± 20 % baseline values of *B. tawa*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. Ranking represents how sensitive the parameter is, 10 being non-sensitive and 1 highly sensitive. Ranking values in bold are the most sensitive.

Tawa					**Abundance**		**Age**		**dbh**		**Height**		**Mean age**		**Mean Basal area**		**Mean height**	
					Ranking		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**		**Ranking**	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.5	0.4	0.6	1	2	3	**1**	**1**	**1**	5	2	9	**1**	5	2	3	**1**	5
Seedling transition	0.04	0.032	0.048	2	3	5	2	4	4	3	3	6	4	2	3	5	4	3
Shade tolerance	0.25	0.2	0.3	5	9	9	10	11	7	6	6	12	8	11	9	9	7	7
Suppression mortality	0.025	0.02	0.03	6	10	12	12	9	12	8	9	8	12	6	10	12	11	8
Suppression tolerance	0.35	0.28	0.42	4	7	4	6	2	11	2	10	**1**	6	4	8	4	12	2
Dispersal	2	1.6	2.4	6	11	10	7	10	8	11	7	10	10	10	12	10	9	12
Reproductive age	20	16	24	5	6	7	11	12	9	10	11	3	11	7	7	8	8	11
Sapling survival	0.7	0.56	0.84	4	5	2	5	5	5	9	5	5	5	12	5	2	5	9
Seed production	1	0.8	1.2	3	4	6	9	6	3	4	4	7	3	3	4	6	3	4
Herbivory	0.8	0.64	0.96	3	**1**	**1**	4	3	6	7	8	4	7	9	**1**	**1**	6	6
Edge effect	0.1	0.08	0.12	2	8	8	3	8	2	**1**	**1**	2	2	**1**	6	7	2	**1**
LDD	0.01	0.008	0.012	6	12	11	8	7	10	12	12	11	9	8	11	11	10	10

Table A2.9 Sensitivity values used in the sensitivity analysis on ± 20 % baseline values of all species for *B. tawa*. *Default values* are the baseline fixed values, *down* represents the default values minus 20 % and *up* represents the default values plus 20 %. We considered state variables (y) with $S_{y,x} > 1$ sensitive to changes in parameter (x).

Tawa					**Abundance**		**Age**		**dbh**		**Height**		**Mean age**		**Mean Basal area**		**Mean height**	
					$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$		$S_{y,x}$	
Parameter	**Default value**	**Down**	**Up**	**Overall rank**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**	**Down**	**Up**
Seedling survival	0.5	0.4	0.6	1	4.40	4.56	0.61	4.56	1.42	0.07	0.03	0.00	1.21	0.05	4.23	4.43	0.94	0.06
Seedling transition	0.04	0.032	0.048	2	3.49	3.26	0.53	0.32	0.58	0.14	0.03	0.00	0.50	0.12	3.32	3.03	0.38	0.10
Shade tolerance	0.25	0.2	0.3	5	0.39	0.37	0.09	0.05	0.04	0.03	0.00	0.00	0.04	0.01	0.35	0.34	0.02	0.02
Suppression mortality	0.025	0.02	0.03	6	0.10	0.01	0.02	0.15	0.01	0.03	0.00	0.00	0.00	0.04	0.08	0.01	0.01	0.02
Suppression tolerance	0.35	0.28	0.42	4	0.84	3.35	0.20	0.74	0.02	0.32	0.00	0.03	0.07	0.11	0.87	3.25	0.00	0.23
Dispersal	2	1.6	2.4	6	0.03	0.19	0.20	0.12	0.03	0.00	0.00	0.00	0.03	0.02	0.00	0.20	0.02	0.00
Reproductive age	20	16	24	5	1.27	1.12	0.07	0.04	0.03	0.00	0.00	0.01	0.02	0.03	1.24	1.11	0.02	0.00
Sapling survival	0.7	0.56	0.84	4	3.05	4.67	0.22	0.31	0.56	0.02	0.01	0.00	0.47	0.01	2.83	4.64	0.38	0.02
Seed production	1	0.8	1.2	3	3.33	2.98	0.14	0.30	0.59	0.13	0.02	0.00	0.53	0.11	3.13	2.78	0.41	0.10
Herbivory	0.8	0.64	0.96	3	5.05	5.31	0.48	0.52	0.07	0.03	0.00	0.01	0.06	0.02	4.93	5.26	0.05	0.02
Edge effect	0.1	0.08	0.12	2	0.71	0.55	0.53	0.25	1.00	1.10	0.03	0.03	0.60	0.67	1.57	1.53	0.76	0.85
LDD	0.01	0.008	0.012	6	0.02	0.04	0.17	0.29	0.03	0.00	0.00	0.00	0.03	0.02	0.01	0.04	0.02	0.01