Urban Restoration Ecology:
Investigating environmental change, ecological function, and enrichment planting

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ABSTRACT

Ecosystems worldwide are being degraded and destroyed by human actions on an unprecedented level. This continues despite growing evidence that intact, functioning ecosystems are critical to human health and well-being. The field of restoration ecology has rapidly developed as a response to ameliorate the damage by investigating how to re-build ecosystems. This branch of science generally posits that replacing lost structure, i.e. re-vegetation, will re-create ecosystems, but there is little empirical evidence supporting this assumption. In ecosystems with long development timelines, such as forests, it is unclear how dynamics change after planting and over the long-term, and hence what best management practices should be used in the decades following initial plantings. This thesis addresses these knowledge gaps through three separate studies on restored urban forests.

The first study investigated whether planted trees will eventually grow into self-regenerating forests that provide suitable conditions for establishment of late-successional plant species. Further, what timeline does this occur along and what specific conditions drive native plant regeneration? To answer these questions a chronosequence of restored urban temperate rainforests aged 3 to 70 years was used in the New Zealand cities of Hamilton and New Plymouth. Various ecosystem properties were measured in the restored forests and compared with the same in remnant and unrestored forests. Structural equation modelling was used to determine which properties were significant drivers of plant regeneration and break point analysis was used to identify thresholds in ecosystem property development over time. Results indicated that unrestored forests had marginally fewer regenerating late-successional plants than remnant forests did. This indicates that restoration actions must take place in these areas to ensure regeneration densities reach natural, desirable levels. The final model indicated it is possible for restored forests to provide suitable conditions for late-successional plant regeneration at 20 years after planting, when basal area has reached ≥ 27 m^2/ha. Further, there are key ecosystem properties that drive native plant regeneration, including formation of a forest canopy that reduces competition from herbaceous exotic weeds and stabilizes the microclimate.

The second study explored the connection between ecological function and forest structure. Specifically, it investigated whether nutrient cycling in the forms of decomposition and denitrification were related to restored forest structural properties and if so, what properties exactly? This is especially important in the New Zealand urban forest, where exotic deciduous trees shed leaves each winter, allowing drastic annual swings in sunlight reaching the forest floor and in leaf litter inputs. This, together with horticultural runoff that causes nitrogen enrichment, disturbs normal nutrient cycling. To understand drivers of decomposition rates and denitrification potential, various ecosystem properties were measured in 27 restored urban temperate rainforests. Structural equation modelling was used to determine whether forest structural attributes were related to the decomposition and denitrification. We found that decomposition rates were indirectly related to the forest canopy but denitrification potential was completely uncoupled from forest structure and instead was driven by edaphic and landscape qualities such as soil texture and drainage patterns.

The third study investigated methods for establishing late-successional tree species under restored urban forest canopies which are invaded by exotic herbaceous weeds. Urban areas are prone to invasion by exotic plants. Throughout much of New Zealand the herbaceous groundcover species *Tradescantia fluminensis* Vell. (Commelinaceae) has invaded forest remnants, forming mats up to 1 m tall that prevent regeneration of native woody species. Without regeneration of late-successional native trees, an initially planted early-successional tree community will lack long-term diversity and resilience. This study used *Beilschmiedia tawa* (A. Cunn.) Kirk (tawa) as a model late-successional tree species to enrich early-successional tree plantings. Seedlings of heights 0.5 m and 1 m were planted into 11 replicate blocks infested with *T. fluminensis* throughout the city of Hamilton, New Zealand. Weeding and mulching were combined in a full factorial design to determine impacts on survival and growth of *B. tawa*. Environmental conditions were also measured to investigate their relationships with *B. tawa* growth and survival. Using ANOVA it was determined that weeding has no impact on *B. tawa* growth and mulching reduces its growth rate. Mulching is typically helpful in early-successional plantings in exposed landscapes but here did not aid tree growth, perhaps because soil moisture was not a limiting factor. Height partially determined growth rates where seedlings that were at least 1 m tall at planting grew faster and were not overgrown by *T. fluminensis*, but shorter seedlings were overtopped and had their growth rates hampered by *T. fluminensis*. Environmental conditions positively related to seedling growth were canopy openness, soil temperature, and air temperature. These results suggest that for maximum establishment success in the presence of aggressive exotic weeds, enrichment trees should be ≥ 1 m tall and planted when the developing forest understory microclimate is suitable.

These studies contribute theoretical and practical advancements to the field of restoration ecology by demonstrating how planted urban forests develop, their best management after initial planting, and relationships between nutrient cycling and forest structure. Results indicate that there are some specific ecosystem properties that are disproportionately key in restored forest succession and nutrient cycling, such as exotic herbaceous weeds and the microclimate. These properties affect a critical goal in restoration, the regeneration of late-successional native plants. Analyses demonstrated that formation of the forest canopy is a key indirect driver of herbaceous weeds, the microclimate, and of decomposition rates. This information is important to ensure initial planting efforts and follow-up management are successful in providing long-lived, resilient restored forests.

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“The acid test of our understanding is not whether we can take ecosystems to bits on paper, however scientifically, but whether we can put them together in practice and make them work.”

- A. D. Bradshaw

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CHAPTER 1

INTRODUCTION

1.1 RESEARCH TOPIC

This thesis presents research about urban forest restoration, with specific focus on forest development after initial plantings. Most studies on urban forest restoration are short-term (< 10 years), far briefer than the multi-decadal time-scale that forest succession dynamics occur on (Shoo et al. 2015, Oldfield et al. 2015, Johnson and Handel 2016, Miller et al. 2016). It is paramount that we understand how urban forests form after initial plantings occur in order to restore effectively for long-term success (Miller et al. 2016).

The earth's ecosystems have been dominated by increasingly intensive human use and are subsequently heavily degraded (Vitousek et al. 1997). Because of this, the field of restoration ecology has received growing attention (Palmer et al. 1997, Aronson and Alexander 2013), with urban areas recently emphasized as important candidates for restoration (Platt et al. 1994, McDonnell 2007, Gaston et al. 2013, Oldfield et al. 2013). There are several important reasons for restoring ecosystems within cities. Urban areas themselves only comprise about 2-3% of land globally (Millenium Ecosystem Assessment 2005) but typically have an actual resource footprint one to two orders of magnitude larger (Rees 1992). It is important to increase size and quality of biome-appropriate green spaces within cities in order to provide ecosystem functions (e.g. nutrient cycling, flooding, microclimate mediation) within the urban matrix itself. Additionally, restoration of urban forests has direct positive impacts on human health and well-being (Alberti 2005), and supports native biodiversity (Burghardt et al. 2009).

In many cases restored forest plantings require multiple interventions during establishment to reach the desired target state (Palmer et al. 1997). Urban green spaces undergoing ecological restoration often suffer strong propagule pressure from invasive exotic plant species (Oldfield et al. 2013). Anthropogenic alterations of the landscape cause habitat fragmentation with disproportional edge habitat, resulting in reduced resistance to invasive introduced species and altered microclimates. Horticultural activities within residential areas increase exotic species’ propagule pressure as well as cause nutrient run-off and nitrogen enrichment that favours weedy plant species (Gilliam 2006). Compared to rural native areas, urban restoration plantings experience greater disturbance and generally unfavourable conditions (Mackay 2006, Alvey 2006). Urban forest restoration must be orchestrated to persist despite these manifold barriers.

1.2 BACKGROUND

This thesis contributes to a growing body of research on how ecologically restored areas change after initial interventions (Zedler and Callaway 1999, Smale et al. 2001, Laughlin et al. 2008, Reid et al. 2016). Evaluations of restoration success have used ecosystem descriptors such as net primary production, species richness, or function (Ehrenfeld and Toth 1997, McDonald et al. 2016). However, abiotic descriptors such as environmental conditions could be important to monitor as well before and during restoration (Palmer et al. 1997, Galatowitsch 2012). This is because environmental conditions such as temperature, sunlight, or soil moisture often constitute a filter which deters or encourages plants based on traits they possess (Keddy 1992, Bradshaw 1983).

Targeted interventions through successional phases or thresholds of restoration may be important to achieve desired end results (Hobbs 1996, Temperton et al. 2004, Hilderbrand et al. 2005). Therefore, environmental conditions and actions taken during these secondary steps (i.e. exotic plant control, enrichment plantings) could set the restoration trajectory (Palmer et al. 1997, Temperton et al. 2004, Suding and Gross 2006), determining the assembly pathway for a restored habitat and influencing long-term community composition (Hobbs and Norton 2004, Suding and Gross 2006).

Evidence indicates that forest properties, especially abiotic conditions such as temperature and humidity, differ depending on restored forest age (Miller 2011, Dean 2013, Bertacchi et al. 2016). These changes in environmental conditions affect important ecosystem processes and have implications for recruitment of important late-successional native tree species that require such specific conditions (Knowles and Beveridge 1982). Soil nutrient dynamics, such as nitrogen availability, are not well understood across forest successional age (Yang et al. 2011), although it is currently thought that total nitrogen increases with time (Knops and Tilman 2000, Robertson and Groffman 2007). For example, soil microbial activities, such as those involved with nitrogen cycling, are often mediated by habitat temperature and moisture (Bergsma et al. 2002), which are conditions that forest canopy cover regulates (McCune and Antos 1982, Chen et al. 1993). Ecosystem properties appear to change through time after restoration, but it is not well understood which ones drive plant regeneration, or if there are distinct thresholds. It is therefore critical to learn more about how restored forest age and forest properties from forestry and old-field succession research, as well as new empirical work.

Chapters two and three in this thesis rely on the use of chronosequences for data collection. This method is considered an acceptable space-for-time substitution in ecological succession (Walker et al. 2010), but there are associated pros and cons. By using this method researchers are able to measure plant community growth at multiple sites where it has been occurring for different lengths of time, on the order of decades. This would be virtually impossible otherwise and lends great insights to changes across long time spans. However, because the sites are spatially separated, drawbacks include potential differences in uncontrolled variables, such as landscape factors, topography, soil type, and environmental conditions. These variables are capable of causing major impacts on the response variables such as plant communities. Because of this, it is important to select chronosequence sites in close proximity to one-another if possible, and measure as many uncontrolled variables as possible so their impact on the response variables can be statistically tested. These precautions have been taken in the research reported in this thesis.

Ruiz-Jaen and Aide (2005) conducted a review of 468 studies that employed seeding or planting techniques for terrestrial restoration and found only 14% evaluated restoration success afterward. The ecosystem attributes were categorized into three categories, diversity, vegetation structure, and ecological processes and the study found that 59% of the time at least two of these attributes were studied post-restoration, usually diversity and vegetation structure but not functional processes. Plant community diversity and structure can be greatly enhanced through restoration work, but establishment of plants does not mean ecological or ecosystem processes will follow (Ehrenfeld and Toth 1997, Wortley et al. 2013). More research is needed on the relationships between restored vegetation structure and ecosystem processes (Tongway and Ludwig 1996, Palmer et al. 1997, Hobbs and Harris 2001). Without functioning ecosystem processes, a restored area may provide good recreational or educational space, but be failing on a greater ecosystem service level. It is important that a “restored ecosystem functions normally for its ecological stage of development” (SER 2004, McDonald, T. 2016).

Urban restoration plantings may require more intensive management and resource manipulation during establishment than plantings in other areas. Increasing survival of late-successional woody species in established restored forest areas, including cities in forest-biomes, is beneficial (Stagoll et al. 2012, Suganuma and Durigan 2015). It is important that this successional group is represented to enhance community stability (SER 2004), resist exotic plant invasion (Elton 1958), and help provide critical ecosystem services (Tilman et al. 1997). Sometimes an established early-successional planting may act as a nursery for late-successional plant species to germinate (Coiffait-Gombault et al. 2012). But without a native propagule source, this cannot occur. Instead, succession may be halted indefinitely as ruderal exotic species continue to dominate (Overdyck and Clarkson 2012).

There are further limitations to naturally occurring late-successional tree establishment in cities and confusions about best management methods. Lack of native late-successional tree species may be due to low seed dispersal, which for large-fruited trees is typically limited by frugivorous bird visits (Powlesland et al. 2011, Wotton and Kelly 2012). This method of late-successional tree dispersal is stifled in many cities throughout New Zealand due to reduced frugivorous bird populations (Clarkson et al. 2007, Fitzgerald and Innes 2013). Further, dispersal issues may be exacerbated by short duration of seed viability in the seed bank, seed predation (Overdyck and Clarkson 2012), herbivory, or limited light (Suganuma and Durigan 2015) and nutrients. Even if these barriers are overcome, late-successional tree seedlings often encounter fierce competition with exotic weeds in the forest ground layer (Standish 2002).

Direct planting of seedlings is often undertaken to circumvent barriers to late-successional tree establishment. In New Zealand, *Beilschmiedia tawa* (A.

Cunn.) Kirk (Tawa) is a common candidate for planting because it is recognized as historically important and abundant North Island forests, but its populations are now decreased due to clearing for agriculture and urban growth. This has occurred to such an extent that reproductive *B. tawa* are greatly reduced and there is poor seedling recruitment (Smale and Kimberley 1983, Carswell et al. 2007, Overdyck and Clarkson 2012). As with long-lived dominant tree species in cities (McCauley et al. 2012), there is probably delayed awareness of decreased generation turnover in *B. tawa* and therefore the extinction debt is already considerable (Tilman et al. 1994). To reverse this and achieve re-establishment of planted late-successional species such as *B. tawa,* we must understand the conditions key to their survival and growth.

This thesis investigates the development of restored urban forests after initial planting, how forest structure is related to nutrient cycling, and how to re-establish late-successional tree species. Results will increase understanding of dynamics within forests undergoing restoration and allow for specific management recommendations. This information is necessary to develop best practices that result in long-term urban forest restoration.

1.3 RESEARCH QUESTIONS

This thesis investigates the following questions:

- how do biotic and abiotic ecosystem properties change over seven decades in restored urban forests?
- what are the key direct and indirect drivers of native tree regeneration and epiphyte colonization in restored urban forests?
- is restoration of forest ecosystem structure related to decomposition rates and denitrification potential?
- what are the key direct and indirect drivers of decomposition and denitrification?
- what management strategies are most effective for promoting enrichment tree establishment in exotic weed-infested restored forests?

1.4 THESIS OBJECTIVES

This thesis aims to:

- measure forest environmental conditions along a restoration age gradient (Chapter 2)
- create a predictive model of environmental conditions dependent on restored forest age (Chapter 2)
- investigate decomposition rates in restored urban forests and whether they are related to restored forest structure (Chapter 3)
- investigate denitrification potential in restored urban forests and whether it is related to restored forest structure (Chapter 3)
- determine key conditions and management approaches that improve *Beilschmiedia tawa* growth when planted into patches of the exotic weed *Tradescantia fluminensis* (Chapter 4)

1.5 THESIS OVERVIEW

The thesis comprises five chapters, three of which are prepared as manuscripts for publication which have been accepted by or are intended to be submitted to scientific journals. Because of this there are some differences in writing style and formatting.

- Chapter 1: provides introduction and background for the entire thesis.
- Chapter 2: has been published in Ecological Applications, a journal of the Ecological Society of America by K. J. Wallace, D. C. Laughlin and B. D. Clarkson.
- Chapter 3: is intended to be submitted to the Journal of Ecology (*in preparation*), a journal of the British Ecological Society.
- Chapter 4: is intended to be submitted to the New Zealand Journal of Ecology (*in preparation*), journal of the New Zealand Ecological Society.
- Chapter 5: synthesises the results of the three main chapters, highlighting the implications for restored urban forest management.

The ideas, research, data analysis and writing were all my own and were conducted under the supervision of Professor Bruce D. Clarkson and Associate Professor Daniel C. Laughlin from the University of Waikato. Specific contributions are acknowledged at the conclusion of each chapter.

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CHAPTER 2

EXOTIC WEEDS AND FLUCTUATING MICROCLIMATE CAN CONSTRAIN NATIVE PLANT REGENERATION IN URBAN FOREST RESTORATION[1]

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2.1 ABSTRACT

Restoring forest structure and composition is an important component of urban land management, but we lack clear understanding of the mechanisms driving restoration success. Here we studied two indicators of restoration success in temperate rainforests: native tree regeneration and epiphyte colonization. We hypothesized that ecosystem properties such as forest canopy openness, abundance of exotic herbaceous weeds, and the microclimate directly affect the density and diversity of native tree seedlings and epiphytes. Relationships between environmental conditions and the plant community were investigated in 27 restored urban forests spanning 3 to 70 years in age and in unrestored and remnant urban forests. We used structural equation modelling to determine the direct and indirect drivers of native tree regeneration and epiphyte colonization in the restored forests. Compared to remnant forest, unrestored forest had fewer native canopy tree species, significantly more light reaching the forest floor annually, and higher exotic weed cover. Additionally, epiphyte density was lower and native tree regeneration density was marginally lower in the unrestored forests. In restored forests, light availability was reduced to levels found in remnant forests within 20 years of restoration planting, followed shortly thereafter by declines in herbaceous exotic weeds and reduced fluctuation of relative humidity and soil temperatures. Contrary to expectations, canopy openness was only an indirect driver of tree regeneration and epiphyte colonization, but it directly regulated weed cover and microclimatic fluctuations, both of which directly drove the density and richness of regeneration and epiphyte colonization. Epiphyte density and diversity were also positively related to forest basal area, as large trees provide physical habitat for colonization. These results imply that ecosystem properties change predictably after initial restoration plantings, and that reaching critical thresholds in some ecosystem properties makes conditions suitable for the regeneration of late successional species, which is vital for restoration success and long-term ecosystem sustainability. Abiotic and biotic conditions that promote tree regeneration and epiphyte colonization will likely be present in forests with a basal area $\geq 27\ \mathrm{m}^2/\mathrm{ha}$. We recommend that urban forest restoration plantings be designed to promote rapid canopy closure to reduce light availability, suppress herbaceous weeds, and stabilize the microclimate.

Key words: restoration targets, indicators, temperate rainforest, urban ecology, tree regeneration, structural equation modeling, epiphytes, microclimate, non-native species, introduced species.

2.2 INTRODUCTION

Forest ecosystems undergo complex successional dynamics (Oliver and Larson 1990), and management actions must mimic these natural dynamics to be successful at restoring degraded forests (Walker et al. 2007, Reid et al. 2016). However, our understanding of the dynamics that occur in restored forests over decadal time scales is limited by a lack of long-term monitoring and the fact that most forest restoration projects have only started within the past few decades (Shoo et al. 2015, Oldfield et al. 2015, Johnson and Handel 2016, Ruiz-Jaen and Aide 2005, Miller et al. 2016). Improving our understanding of the mechanisms that determine the success of long-term forest restoration is a high research priority (Bullock et al. 2011, Suding 2011).

Two indicators of successful restoration of temperate rainforests are regeneration of long-lived, shade-tolerant trees (Suganuma and Durigan 2015, Johnson and Handel 2016) and colonization by epiphytes (Oishi and Doei 2015, Reid et al. 2016). Spontaneous dispersal and recruitment of these indigenous, late successional plants into a forest undergoing restoration is an indication that conditions have become suitable for natural forest dynamics to occur without additional management actions (Bertacchi et al. 2016, Shoo et al. 2015, Robinson and Handel 1993, Boudreault et al. 2000). However, the factors that influence regeneration and colonization and the time it takes for conditions to become suitable are unclear in urban forests, which are often fragmented, invaded by aggressive exotic plants, and are constrained by limited seed dispersal and germination (Overdyck et al. 2013, Lehvävirta and Rita 2002, McCauley et al. 2012, Overdyck and Clarkson 2012). Identifying the environmental conditions that promote successful regeneration of native trees and epiphyte colonization in forests will clarify processes driving succession (Brown 1993) and will also directly inform restoration practice (Walker et al. 2007, Bertacchi et al. 2016).

Urban ecosystems differ from rural ecosystems (Groffman et al. 2016, Dobbs et al. 2011) and therefore present unique restoration challenges. However, the benefits of ecologically intact urban forest are worth the effort of restoration (Pickett et al. 2011). Research over the past few decades suggests that aside from providing wildlife habitat (Threlfall et al. 2016, Burghardt et al. 2009), urban forests provide economically valuable ecosystem services such as flooding and climate mitigation (Pickett et al. 2011, Dobbs et al. 2011) and pollutant filtering (Pickett et al. 2011). Additionally, urban forests provide a space in which humans re-connect with nature and enjoy individual health and societal benefits (Groffman et al. 2016). Therefore, urban forest is now prioritized in city planning (Groffman et al. 2016, Threlfall et al. 2016) and practitioners need information about the best practices for successful long-term forest restoration (Dobbs et al. 2011).

Theories of forest dynamics and succession provide the context for understanding how to restore ecosystems that feature plant species that will only establish in mature vegetation, such as shade-tolerant trees (Smale et al. 2001, Laughlin et al. 2008, Zedler and Callaway 1999, Palmer et al. 1997) and vascular epiphytes (Reid et al. 2016, Shono et al. 2006). Urban forest restoration is typically initiated by removing undesirable plants and planting early successional native tree species (Johnson and Handel 2016) that will develop into a structurally complex, diverse native forest. Subsequent responses of vegetation structure, composition, and function are only sometimes monitored (Wortley et al. 2013, Ehrenfeld and Toth 1997), and while these metrics are important for assessing if a restoration target has been achieved, they do not necessarily identify the mechanisms propelling forest succession toward that target.

Abiotic and biotic ecosystem properties constrain restoration success (Suding and Hobbs 2009), and may respond to restoration actions in different ways during ecosystem recovery (Hobbs and Harris 2001, Hobbs and Norton 1996, Suding et al. 2004). Some ecosystem properties reach restoration targets rapidly, whereas others demonstrate linear, lagged, or threshold responses (Fig. 2.1). Ecosystem properties may also fail to reach targets altogether by falling short of targets or later reverting to an unrestored state (Fig. 2.1).

Some ecosystem properties reach thresholds during ecological succession that trigger shifts in other ecosystem properties (Temperton et al. 2004). For example, abiotic properties such as microclimate and light availability are key drivers of regeneration in the forest understory (Brown 1993, Tilman 1985, Shono et al. 2006, Sporn et al. 2010, Neufeld and Young 2014, Palmer et al. 1997) (Fig. 2.2). Recognizing these relationships and how they change through time can be crucial for improving management decisions and facilitating desired plant community assembly (Suding and Gross 2006, Temperton et al. 2004, Palmer et al. 1997, Laughlin 2014).

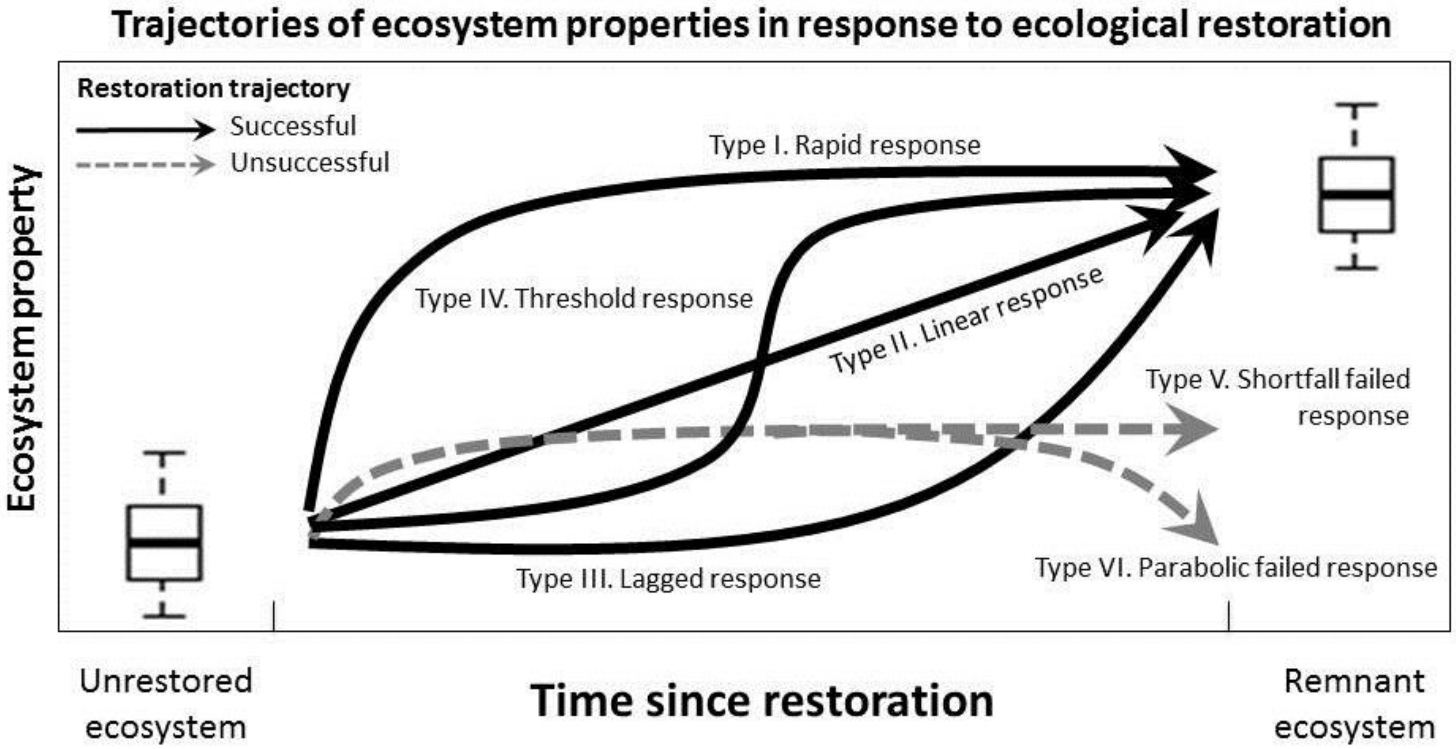
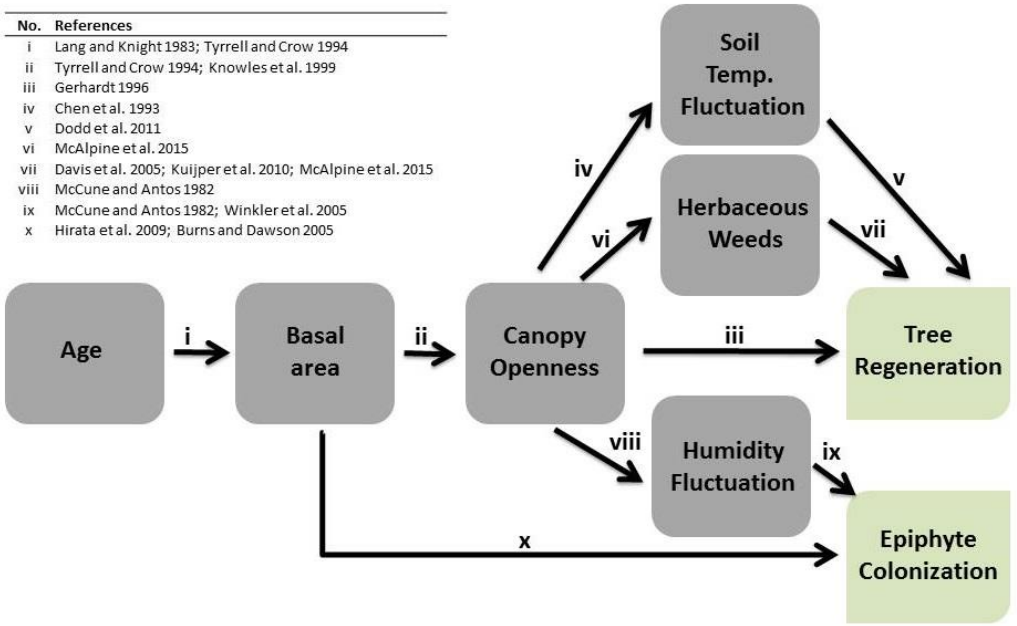


Figure 2.1 Conceptual diagram illustrating multiple possible trajectories of ecosystem properties to restoration efforts over time since restoration (Hobbs and Harris 2001, Hobbs and Norton 1996, Suding et al. 2004). The four solid arrows represent successful trajectories that a property may follow from an unrestored level to reach the target level of remnant ecosystems: I) rapid response, II) linear response, III) lagged response, or IV) threshold response. The response shape may depend on the nature of the property itself or could be affected by management actions. All solid response curves eventually reach values found in remnant ecosystems, but I), II) and IV) display marked thresholds where the rate of change is drastically altered. The two dashed arrows represent unsuccessful trajectories where target levels are never attained: V) shortfall failed response, and VI) parabolic failed response, where restoration efforts were only temporarily effective. This conceptual diagram arbitrarily displays unrestored ecosystem values as low and remnant ecosystem values as high, but the inverse may be true depending on the ecosystem property.

Biotic thresholds include the loss of native species and the invasion of exotic species, which can also affect the abiotic conditions of a site (Hobbs et al. 2009). Sometimes succession is arrested in an alternative stable state (Hobbs and Norton 1996) or re-directed because the microclimate favors invasive exotic species (Suding and Gross 2006, Johnson and Handel 2016, Standish et al. 2001). Because urban forests are fragmented, small, and contain high edge-to-area ratios (Overdyck and Clarkson 2012, Smale and Gardner 1999), they are particularly overwhelmed by strong propagule pressure from invasive exotic plant species.

Many degraded urban forests in New Zealand are invaded by exotic deciduous trees. Unlike the native evergreen tree species, these exotics senesce leaves in autumn causing an increase in light availability and larger fluctuations of soil temperatures throughout the winter. These biota-driven changes in environmental conditions facilitate growth of invasive herbaceous plants (McQueen et al. 2006), which would normally go dormant but instead flourish through the mild winters. These herbaceous weeds prevent the regeneration of native tree species (Standish et al. 2001). By restoring a native evergreen canopy, the microclimate may fluctuate less and light availability will be reduced, thereby allowing native shade-tolerant trees and epiphytes to colonize the developing forest.

Our overall objective in this study was to determine the environmental drivers that promote native tree regeneration and epiphyte colonization in restored urban temperate forests (Fig. 2.2). Forest restoration research often focuses solely on plant community change after planting; here, our objective was to identify the conditions driving that change. To achieve this, we substituted space-for-time and established a unique chronosequence of forests representing 70 years of forest development following an initial restoration planting. We measured abiotic environmental conditions as well as biotic plant community structure and composition and used structural equation modelling to assess which variables were key drivers of native tree and epiphyte regeneration. Specifically, we asked the following questions: 1) how do biotic and abiotic ecosystem properties change over seven decades in restored urban forests?, and 2) what are the key direct and indirect drivers of native tree regeneration and epiphyte colonization?



No.	References
i	Lang and Knight 1983; Tyrrell and Crow 1994
ii	Tyrrell and Crow 1994; Knowles et al. 1999
iii	Gerhardt 1996
iv	Chen et al. 1993
v	Dodd et al. 2011
vi	McAlpine et al. 2015
vii	Davis et al. 2005; Kuijper et al. 2010; McAlpine et al. 2015
viii	McCune and Antos 1982
ix	McCune and Antos 1982; Winkler et al. 2005
x	Hirata et al. 2009; Burns and Dawson 2005

Figure 2.2 Hypothesized *a priori* structural equation model (SEM) illustrating how restored forest properties might influence native tree regeneration and epiphyte colonization. Support for causal relationships are listed by pathway number in the top left. The indicators of restoration success, native tree regeneration and epiphyte colonization, are light green and their drivers are dark grey.

2.3 MATERIALS AND METHODS

2.3.1 Study sites

Our study took place on New Zealand’s North Island, which was historically 75% covered in temperate rainforest but 66% of which is now cleared for agriculture and silviculture (Nicholls 1980). Data were collected from restored urban forest patches in two cities, Hamilton, population 160,000 (37.7870° S, 175.2793° E) and New Plymouth, population 60,000 (39.0556° S, 174.0752° E), about 200 km apart (Appendix 2.1). Hamilton has an annual mean precipitation of 1,110 mm with mean daily minima and maxima temperatures of of 8.7 °C and 18.9 °C, respectively (CliFlo), and 2.1% indigenous forest cover (Clarkson et al. 2007a). New Plymouth has an annual mean precipitation of 1,400 mm with mean daily minima and maxima temperatures of 10 °C and 17.5 °C, respectively (CliFlo), and 8.5% indigenous forest cover (Clarkson et al. 2007b) of a composition similar to Hamilton. Urban forest patches averaged 2.9 ha (± 2.4 ha SD) in size and were 147 m (± 197.97 m SD) from the nearest forest patch > 0.1 ha (Appendix 2.1).

Data was collected from three types of urban forest: unrestored (n = 6), restored (n = 27), and remnant forest (n = 6). Restored sites formed a chronosequence from 3-70 years since initial restoration plantings; 36 sites were public and three were private. Chronosequences are space-for-time substitutions that are useful for understanding the long-term processes of ecological succession (Walker et al. 2010). Unrestored urban forest was defined as a forested area subjected to severe anthropogenic disturbance (e.g. clear-felling or sand mining) before 1960 without further major disturbance or any restoration since, and is now dominated by exotic trees. Remnant forest was defined as a surviving urban fragment of old-growth native forest currently protected from major anthropogenic disturbance. Each urban forest site encompassed three randomly located 10 x 10 m^2 plots, with the constraints that plot edges were never < 1 m from each other or the edge of the site, or on slopes > 10 degrees. At 12 out of 39 sites at least one plot had to be placed within 1 m of the forest edge due to the small size or steepness of the forest patch. Five permanent 1 m^2 subplots were established in each plot.

2.3.2 Data collection

Woody plants ≥ 2.5 cm (single and multi-stemmed individuals) diameter at breast height (DBH; 1.4 m) in all three plots at each site were identified to species, classified as native or exotic and the DBH of each stem was recorded. We used these data to compute the basal area of each species in each site. Only native trees were used to compute canopy species richness. Regenerating tree species, defined as trees < 2.5 cm DBH, but mature beyond the cotyledon stage, were identified, classified as native or exotic, and tallied by species in one randomly chosen quarter of each plot. Forest community successional status (e.g. early vs. late for each tree species was assigned according to information found in the restoration plan for Waiwhakareke Natural Heritage Park, a 60 ha New Zealand urban forest restoration project listed in Oldfield et al. (2013).

Herbaceous species were assessed within the subplots by identifying every species rooted within and estimating percent cover by species. Total percent cover could exceed 100% due to plant overlap in three-dimensional space.

Epiphytes were defined as any vascular plant growing on a tree rooted within a plot. Epiphytes were identified to species using binoculars and tallied by number of host trees they occurred on (Suganuma and Durigan 2015). Total native epiphytes and obligate native epiphytes were used in the analyses; obligate epiphytes are those which must grow on trees (Kirby 2014). A comprehensive list of plants identified in the study is listed in Appendix 2.1.

Atmospheric relative humidity (RH) was measured every four hours for 12 months using hygrochrons (iButton dataloggers model DS1923, Maxim Integrated, San Jose, CA, U.S.A). Hygrochrons (one per site) were hung in radiation shields 2 m above the center subplot in the central plot at each urban forest site. Soil temperature at 10 cm depth was measured every four hours for 12 months at the center subplot in the outermost two of the three plots at each urban forest site using thermochrons (iButton dataloggers model DS1921G-F5, Maxim Integrated, San Jose, CA, U.S.A.) (Hubbart et al. 2005). For both RH and soil temperature we computed the standard deviation over one year to represent the temporal fluctuations in these abiotic conditions at each site.

Canopy openness was measured four times (once per season) by taking hemispherical photos of the canopy from 1 m above the ground in each plot. Resulting images were analyzed with the software Gap Light Analyzer v. 2.0 (Institute of Ecosystem Studies, Millbrook New York, U.S.A.). The average value across the three plots and four seasons was used to quantify site-level canopy openness, an index of light availability.

We also measured a variety of ecosystem properties that were non-impacting, i.e. did not differ between unrestored and remnant forests, did not change over time in the restored forests, and were not related to tree regeneration or epiphyte colonization. For completeness, we list and describe methods and results for these variables in Appendix 2.2.

2.3.3 Statistical analyses

Change in forest ecosystem properties over time

First, we inspected bivariate plots and fitted generalized linear regression models to evaluate the relationships between restored forest age and either environmental conditions (canopy openness, soil temperature fluctuation and humidity fluctuation) or plant community attributes (tree basal area, canopy species richness, herbaceous weed cover, native tree regeneration and epiphyte colonization). We compared environmental conditions and plant community attributes between remnant forests and unrestored forests using Welch’s unequal variances *t*-tests ($\alpha = 0.05$). Prior to these tests, canopy openness and humidity were log-transformed. We used the ‘segmented’ package in R (Muggeo 2003) to find breakpoints in the relationships between ecosystem properties and time to test for critical transitions in trajectories of ecosystem properties.

Second, we used non-metric multidimensional scaling (NMDS) ordination in the ‘vegan’ package in R (Oksanen et al. 2015) to quantify differences in plant community composition among unrestored, restored, and remnant forests. Composition was assessed in four vegetation strata: canopy species composition (basal area: m^2/ha), native regeneration composition (stems/ha), herbaceous weed composition (% cover), and epiphytes (host trees/ha). One outlier had a very different plant community because it was the only restored site in a salty coastal habitat; this was removed from all NMDS analyses. Prior to fitting the ordination models, species abundance data were square root transformed and standardized using a Wisconsin double relativization (Gauch 1982). Environmental variables were log transformed and illustrated as vectors on the NMDS plots if they were significantly correlated with the ordination axes ($\alpha = 0.05$). We tested for differences in plant community composition between unrestored and remnant forests with PERMANOVA (Anderson 2001), using the ‘vegan’ package in R (Oksanen et al. 2015).

Constraints on tree regeneration and epiphyte colonization

We used structural equation modelling with the R package ‘piecewiseSEM’ (Lefcheck 2015) to determine the direct and indirect drivers of native tree regeneration and epiphyte colonization. This multivariate approach tests hypothesized relationships among a system of state variables. Using theory and empirical data, we developed an *a priori* model that we believed to be the most plausible causal structure of the factors that constrain native tree regeneration and epiphyte colonization in restored forests (Fig. 2.2).

We hypothesized that age and basal area would be indirect drivers of native tree regeneration and obligate epiphyte colonization (Lang and Knight 1983, Tyrrell and Crow 1994) and that basal area would mediate the indirect effect of age on canopy openness (Knowles et al. 1999, Tyrrell and Crow 1994). We predicted that canopy openness would have direct effects on native tree regeneration (Gerhardt 1996, Olesen and Madsen 2008, Bertacchi et al. 2016), soil temperature fluctuation

(Chen et al. 1993), humidity fluctuation (McCune and Antos 1982), and herbaceous weed cover (McAlpine et al. 2015). Our model hypothesized that soil temperature fluctuation (Dodd et al. 2011) and herbaceous weed cover would directly constrain native tree regeneration (Davis et al. 2005, Kuijper et al. 2010, Overdyck and Clarkson 2012, McAlpine et al. 2015, Yelenik 2016, Dodd et al. 2011), while basal area (Hirata et al. 2009, Burns and Dawson 2005) and humidity fluctuation (Callaway et al. 2002, Zotz and Bader 2009, Winkler et al. 2005, McCune and Antos 1982) would directly constrain epiphyte colonization.

Prior to analysis, variables were log transformed to linearize relationships, except for standard deviation of soil temperature and standard deviation of humidity. All variables were also scaled to unit variance, except for epiphyte density and richness, which were Poisson distributed. We fit two models using the same *a priori* model structure (Fig. 2.2): one for the density of tree regeneration and epiphyte colonization, and one for species richness of tree regeneration and epiphyte colonization. We used a Gaussian distribution to model regeneration density and richness, but we used a quasipoisson distribution to model epiphyte density and richness because these Poisson-distributed variables were over-dispersed (Wells and O'Hara 2013). Because the model included both Gaussian and Poisson error distributions, we only report the unstandardized coefficients. Model fit was assessed using Fisher’s C statistic (Grace 2006, Lefcheck 2015), where good-fitting models yield small C statistics and P-values > 0.05. Poor fitting models were improved by removing nonsignificant pathways and variables that were not significantly related to the response variables.

We tested whether the effects of direct drivers of native plant regeneration differed between the two cities by fitting separate ANCOVA models. We added city as a fixed effect to test for differences in the direct effects of microclimate, weeds, and basal area on plant regeneration. For example, tree regeneration density was modelled as a function of weed cover, city, and a weed cover × city interaction, where the main effect of city tests for a shift in intercept, whereas the interaction tests for a difference in slope between cities.

2.4 RESULTS

Change in forest ecosystem properties over time

Unrestored forests contained marginally less tree basal area than remnant forests (36 m^2/ha vs. 93 m^2/ha, $t_{6.0}$ = -2.1664, P = 0.0734, Fig. 2.3A) and although they contained less than half the basal area of remnant forests on average, high variability by site meant this difference was not significant. Unrestored forests had higher canopy openness than remnant forests (13% vs. 3%, $t_{9.3}$ = 5.9372, P = 0.0002, Fig. 2.3B). In restored forests, tree basal area increased linearly over the 70 year timespan of the chronosequence (Fig. 2.3A), contrasting with canopy openness, which dropped rapidly (Fig. 2.3B). A breakpoint in canopy openness occurred at approximately 18 years (Appendix 2.3), when light transmittance decreased to levels detected in remnant forests.

There was no difference in humidity fluctuation in unrestored and remnant forests ($t_{7.0}$ = 1.9312, P = 0.0945), while in restored forests, fluctuations in humidity decreased rapidly with age (Fig. 2.3C). A breakpoint in humidity fluctuation occurred at approximately 23 years (Appendix 2.3), after which humidity levels were consistently more stable. Unrestored forest soil temperatures fluctuated marginally more than remnant forest soils ($t_{8.5}$ = 2.1387, P = 0.0626, Fig. 2.3D). In restored forests, soil temperature fluctuations lessened with age, and became consistently stable at approximately 21 years (Appendix 2.3).

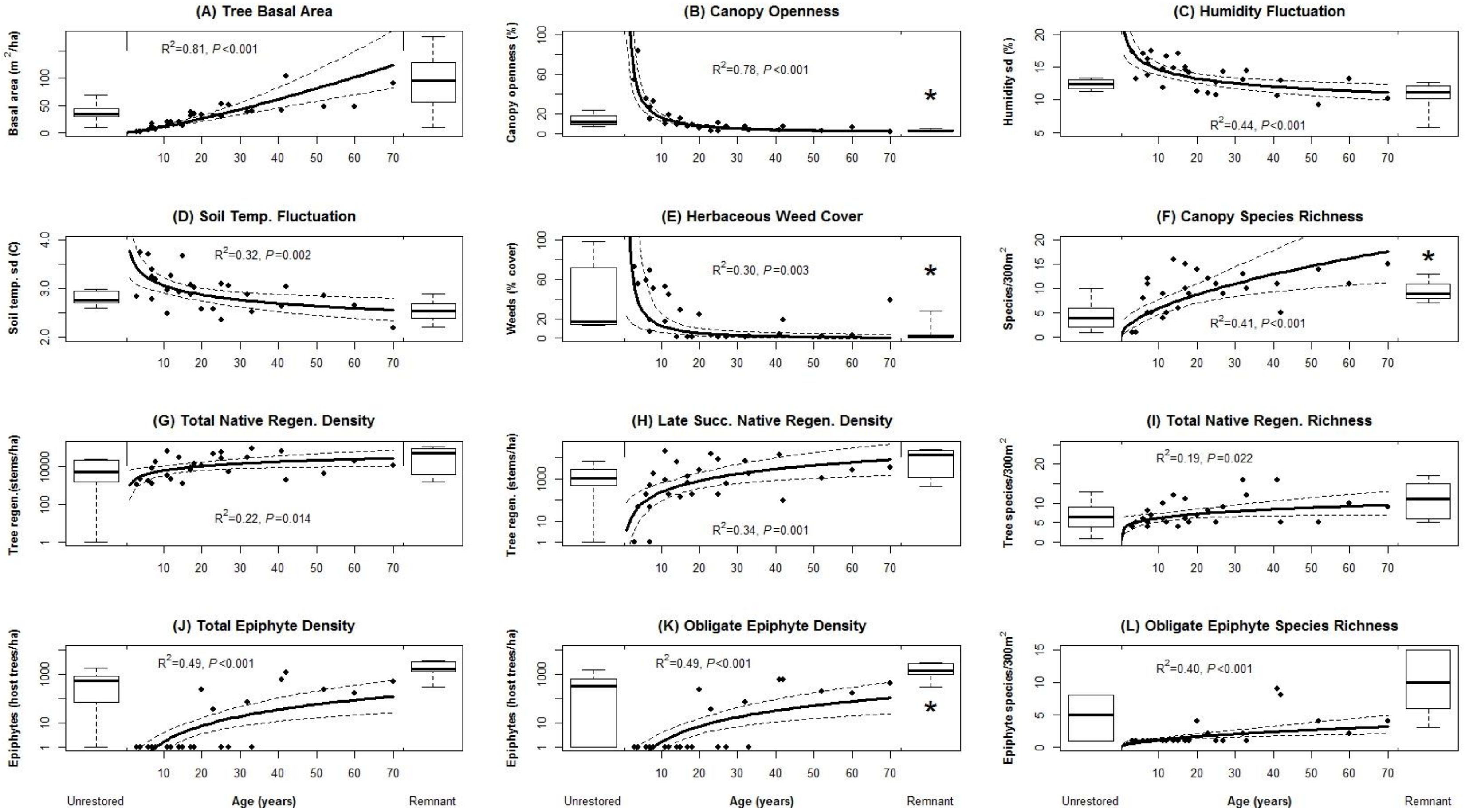


Figure 2.3 Environmental conditions and plant community attributes in restored forests over time (central section of each bivariate plot), compared with unrestored and remnant forests (boxplots to left and right, respectively). Total native tree species regeneration, late successional tree regeneration density, total epiphyte density, and obligate epiphyte density have y-axes shown in log-scale. Boxplots represent 25th, 50th, and 75th percentiles and whiskers extend to data extremes. Scatterplot points represent restored sites; the solid lines represent the fitted values from a linear regression model on log-transformed data, and the dashed lines represent 95% confidence intervals. Asterisks indicate a significant difference between unrestored and remnant forests ($\alpha = 0.05$).

Herbaceous weed cover in unrestored forests was greater than in remnant forests (37% vs. 5%, $t_{8.7} = 3.8366$, $P = 0.0042$, Fig. 2.3E). Weed cover in restored forests declined rapidly from 75% in the youngest planting to 1% at approximately 18 years, where a breakpoint occurred (Appendix 2.3). Herbaceous weed community composition differed between unrestored and remnant forests (PERMANOVA, $F_{10,1} = 3.1103$, $P = 0.016$, Appendix 2.4). Restored forest weed compositions were least similar to one-another between six and eleven years post-planting.

Canopy species richness differed significantly between unrestored and remnant forests ($t_{8.9} = -3.0812$, $P = 0.0133$), and increased linearly over time in restored forests (Fig. 2.3F). By 70 years after restoration the restored forest canopy had twice as many tree species than unrestored forest (14 vs. 7.3, Fig. 2.3F). Canopy composition differed between unrestored and remnant forests (PERMANOVA, $F_{10,1} = 1.9676$, $P < 0.005$, Appendix 2.4). The oldest restored forests had canopy compositions most similar to remnant forest.

There was a marginal difference in total native tree regeneration density between unrestored and remnant forests, with five times more native trees regenerating in remnant forests (9,422 stems/ha vs. 50,244 stems/ha, $t_{5.5} = -2.190$, $P = 0.0749$, Fig. 2.3G). Total native tree regeneration density in restored forests increased over time, becoming similar to remnant forests within the first few decades (Fig. 2.3G). Regeneration density of late successional native trees followed a similar pattern and was marginally greater in remnant forest than in unrestored forest ($t_{5.6} = -2.3636$, $P = 0.0591$, Fig. 2.3H), however it was generally much lower than total regeneration density, and comprised little of the total regeneration in the youngest restored forests (Fig. 2.3G and H, Appendix 2.5). Total native tree regeneration species richness was not different between unrestored and remnant forest ($t_{9.8} = -1.6051$, $P = 0.14$), but did increase with restoration age (Fig. 2.3I). Native tree regeneration in unrestored forests had a different composition to those of remnant forests (PERMANOVA, $F_{10,1} = 1.7149$, $P = 0.043$; Appendix 2.4). Only 29% of tree species regenerating in unrestored forest were late successional species, compared with 58% in remnant forest, where environmental conditions were more stable. A comprehensive list tree species identified and their successional statuses is available in Appendix 2.5.

Total epiphyte density was marginally greater in remnant forests compared with unrestored forests ($t_{7.5}$ = -2.2761, *P* = 0.0545, Fig. 2.3J). Epiphytes were absent in young restored forests, but colonization began at approximately 20 years after restoration and total densities subsequently appeared to be similar to remnant site levels by approximately 40 years (Fig. 2.3J). Obligate epiphyte density was significantly greater in remnant forest than unrestored ($t_{7.7}$ = -2.3275, *P* = 0.04976, Fig. 2.3K) and obligate epiphyte species richness was marginally greater in remnant forest ($t_{8.6}$ = -2.0521, *P* = 0.0717, Fig. 2.3L). Obligate epiphyte species were also absent in sites < 20 years old, but after that there were on average 2.3 species growing in restored forest sites (Fig. 2.3L). Epiphyte community composition in remnant forest was dissimilar to that of unrestored forests (PERMANOVA, $F_{10,1}$ = 3.9031, *P* = 0.005; Appendix 2.4).

Constraints on tree regeneration and epiphyte colonization

The *a priori* structural equation model of native tree regeneration and epiphyte density did not fit the data well (Fisher's *C* = 53.99, *df* = 36, *P* = 0.027, Fig. 2.2). We removed the nonsignificant pathway from canopy openness to native tree regeneration (pathway *iii*, Fig. 2.2). This new model fit the data well (Fisher's *C* = 50.46, *df* = 38, *P* = 0.085, Fig. 2.4A), explaining 40% of the variation in native tree regeneration density and 64% of the variation in epiphyte colonization density. The final model also explained significant variation in herbaceous weed cover (31%), soil temperature fluctuation (58%), humidity fluctuation (53%), canopy openness (77%), and basal area (81%) (Fig. 2.4A).

The final plant density model indicates that native tree regeneration densities were highest where herbaceous weed cover and soil temperature fluctuation were lowest (Fig. 2.4A). Importantly, native tree regeneration density was not directly related to canopy openness, but rather was indirectly related to canopy openness through the mediating factors of herbaceous weed cover and soil temperature fluctuation. High epiphyte density was related to smaller fluctuations in humidity and greater tree basal area.

The *a priori* structural equation model of native tree regeneration and epiphyte species richness did not fit the data well (Fisher's *C* = 65.18, *df* = 36, *P* = 0.002; Fig. 2.2). We removed the nonsignificant pathway from canopy openness to native tree regeneration (pathway *iii*, Fig. 2.2) and removed herbaceous weed cover from the model. This new model fit the data well (Fisher's $C = 31.67$, $df = 28$, $P = 0.288$; Fig. 2.4B) and explained significant variation in tree regeneration species richness (20%) and species richness of epiphytes (60%) (Fig. 2.4B).

The final species richness model indicates that native tree regeneration richness was highest where soil temperature fluctuation was lowest, which was related to canopy openness (Fig. 2.4B). High epiphyte richness was related to smaller fluctuations in humidity and greater tree basal area.

Direct effects on native plant regeneration did not differ substantially between the two cities (Appendix 2.6). We detected minor differences for a few relationships, such as a shift in intercept or a shift in both intercept and slope between the two cities in the relationships between epiphytes and tree basal area (Appendix 2.6), but all other relationships remained unchanged. Importantly, the sign and meaning of the relationships were the same across both cities, and the effects of microclimate and weeds remained significant.

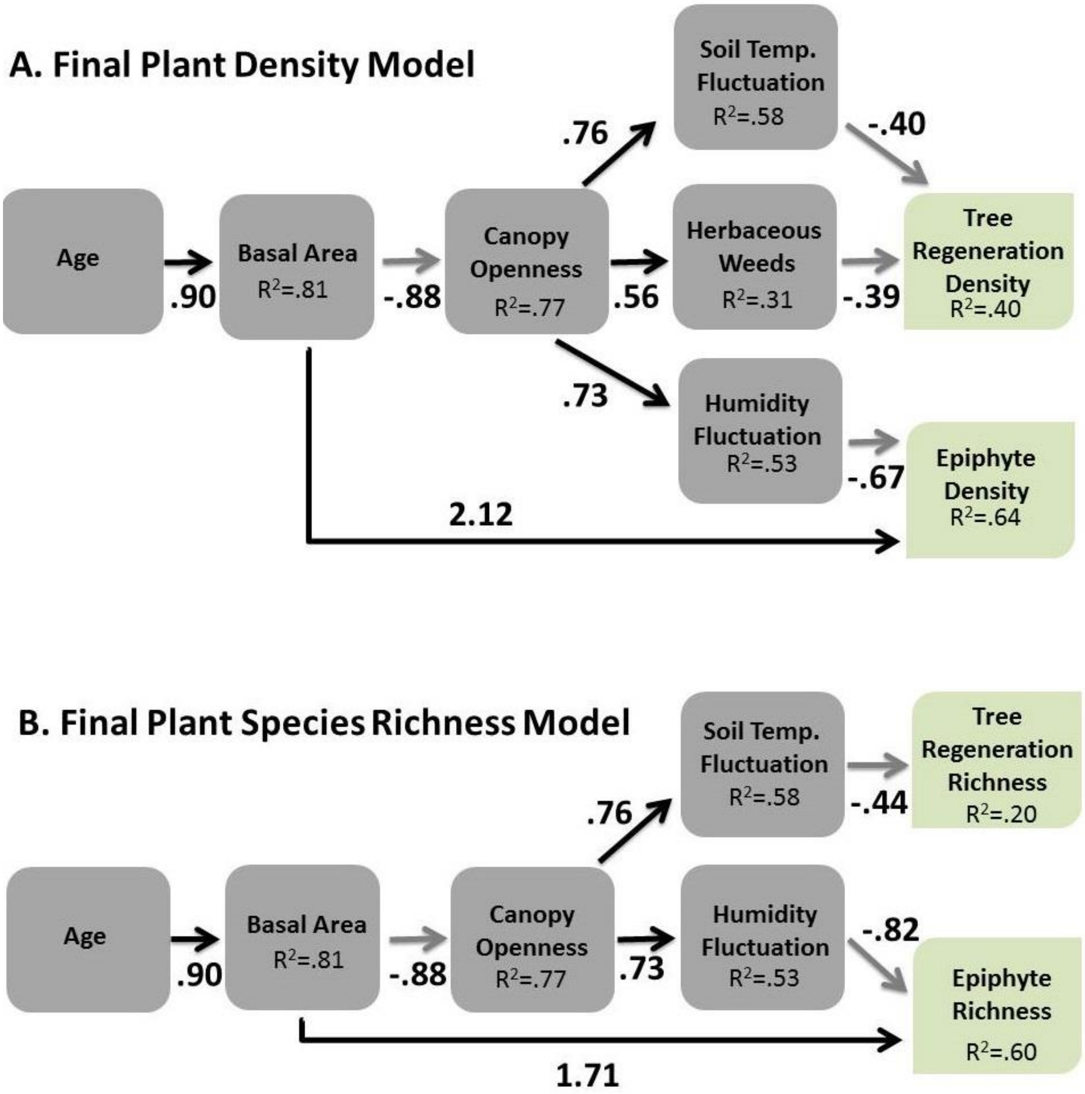


Figure 2.4 The two final structural equation models (SEMs), illustrating drivers of native tree regeneration and epiphyte colonization. The top model (A) illustrates drivers of plant density and the lower model (B) illustrates drivers of plant species richness. The indicators of restoration success, native tree regeneration and epiphyte colonization, are shown in light green, and their drivers in dark grey. Values by arrows are unstandardized path coefficients. An R^2 value is shown in the box of each response variable. For clarity positive pathways are black and negative pathways are grey.

2.5 DISCUSSION

The results of this restoration chronosequence improve our understanding of the temporal dynamics that occur in restored forests over decadal time scales. We found that many ecosystem properties change over time as restored forests mature, and a few key properties drive restoration success. Specifically, our structural equation model (SEM) demonstrated that two indicators of successful forest restoration, native tree regeneration and epiphyte colonization, were constrained by fluctuating microclimate and exotic herbaceous weeds. These factors were functions of changes in forest structure and light availability, both of which changed predictably as the forests aged. A critical threshold was reached at approximately 20 years after the initial restoration planting, when conditions became suitable for the spontaneous regeneration of native trees and epiphytes.

Ecosystem properties of restored forests followed different recovery trajectories (Fig. 2.1). The historic expectation in terrestrial habitat management is a linear response to system perturbation, and threshold responses are not yet well understood (Suding and Hobbs 2009). We observed linear rates of change, rapid changes that plateaued quickly, and threshold responses. Understanding the nature of these responses is important for management because restored forest properties are inexorably linked (Dodd et al. 2011). Importantly, we observed that reaching a threshold in one ecosystem property can trigger sudden changes in other conditions that promote natural processes, such as regeneration, that are necessary for long-term forest development.

Many critical changes occurred at approximately 20 years of forest development, when basal area increased to an average 27 m^2/ha (± 2.8 SE). Trajectories of four ecosystem properties in particular were altered at this level of basal area: light availability reached a low point, herbaceous weed cover was reduced, atmospheric relative humidity beneath the canopy was stabilized, and soil temperature was stabilized (Appendix 2.3). Forest structure and composition can be dynamic during this early stand initiation phase of forest dynamics (Oliver and Larson 1990). Time since restoration is a main driver of success (Crouzeilles et al. 2016), and recent research suggests that critical changes in restored ecosystem conditions occur within 15-20 years after the initiation of forest restoration. For example, Johnson and Handel (2016) found significantly more native regeneration and more complex forest structure in 15-20 year old temperate forest restored sites than in unrestored sites. Shoo et al. (2015) found that species richness increased within 20 years in tropical rainforest restoration plantings and the richness included important elements of forest structure such as vines and epiphytes. Structural complexity and native regeneration increase biodiversity (Burghardt et al. 2009, Threlfall et al. 2016), which increases resilience to perturbation (Dodd et al. 2011, Walker 1995, Oakley and Knox 2012), thereby minimizing the need for further restoration intervention. Isolation of urban forest patches may have hindered seed dispersal of some native plant species (Overdyck and Clarkson 2012, Taylor and Burns 2015). Such isolation could ultimately limit regeneration success regardless of whether the required set of environmental conditions arise within the developing forests (Robinson and Handel 1993, Lehvävirta and Rita 2002). In cases of extreme seed dispersal limitation in some urban forests, propagules will need to be introduced by practitioners to promote native plant colonization.

In our study, the key direct drivers of native tree regeneration were herbaceous weeds and microclimatic fluctuations. Herbaceous weeds limit the establishment and survival of native tree seedlings (George and Bazzaz 2014, Overdyck and Clarkson 2012, McAlpine et al. 2015, Yelenik 2016, Davis et al. 2005). Many exotic weeds are nutrient-demanding and will compete for below-ground resources in forests (Yelenik 2016, Peltzer et al. 2009, Gilliam 2006). Some also have specific symbiotic mycorrhizae that can cause advantage in uptake capability (Cornelissen et al. 2001) or have antifungal exudates that disrupt native tree mycorrhizal associations (Stinson et al. 2006). Whether shade-tolerant or light-demanding, exotic herbaceous weeds compete for light reaching the forest floor (Neufeld and Young 2014). Despite a significant decrease in weed cover as sites grew older, our oldest site contained unexpectedly high cover (38%) of a shade-tolerant weed (*Tradescantia fluminensis* Vell.), which has been known to reduce native tree regeneration if present in great enough biomass (Standish et al. 2001).

Native tree regeneration was also directly regulated by temperature fluctuations in the soil. Soil temperatures can play a pivotal role in both tree regeneration density and diversity by triggering germination (Vázquez-Yanes and Orozco-Segovia 1982) and dictating growth rate (Heninger and White 1974). Both soil frost (Goulet 1995) and excessive heat (Lopushinsky and Max 1990) can cause seedling mortality. Tree seedlings differ by species in their optimal soil temperature for growth (Heninger and White 1974). Early successional species are adapted to larger fluctuations in conditions (Bazzaz 1979), explaining why they comprise the majority of seedlings early in the chronosequence. The difference between unrestored and remnant forest regeneration composition suggests that a subset of species, likely many late successional native trees, cannot tolerate conditions found in unrestored forests.

Epiphyte colonization was triggered by reaching critical thresholds in microclimatic stability and substrate availability (Fig. 2.1). Taylor and Burns (2015) proposed three stages of epiphyte community development: *i*) host trees are devoid of epiphytes due to lack of sufficient architectural characteristics, *ii*) adult host trees acquire epiphytes and continue to do so into maturity, and *iii*) epiphyte communities experience decline due to host tree mortality. We observed the first two stages within the chronosequence we studied. Stage one lasted for approximately 20 years, and stage two was triggered when epiphytes began to colonize forests with basal area of ca. 27 m^2/ha and when humidity stabilized under the forest canopy.

Epiphytes can be particularly sensitive to desiccation because their roots are exposed as they cling to their host trees (León-Vargas et al. 2006, Palmer et al. 1997). Epiphyte species stratify themselves along a ground to canopy gradient, where those that are more sensitive to evaporative water loss colonize closer to the shaded forest floor (Hietz and Briones 1998, Sporn et al. 2010). The development of the tree canopy creates an increasing range of suitable conditions for epiphytes, facilitating greater species diversity, especially high in the canopy (León-Vargas et al. 2006, Reid et al. 2016). Additionally, as epiphytes accumulate, their own biomass creates further microclimatic buffering, facilitating greater epiphytic colonization (Reid et al. 2016). This mechanism is likely to occur in other groups, as plant density increases in general, e.g. with tree seedlings. Other studies have found that restored forests often support greater diversity and density of epiphytes compared to unrestored or spontaneously regenerated forests (Kanowski et al. 2003, Reid et al. 2016). In our study, greater density and richness was found in stands with smaller fluctuations in humidity and the largest trees (Burns 2008, Hirata et al. 2009, Burns and Dawson 2005).

Management actions promoting the conditions that allow for native plant regeneration are required to ensure that initial planting efforts lead to resilient and enduring forests. Our results suggest that late successional plant establishment in restored urban forests is constrained by herbaceous weeds and microclimatic instability, both of which are driven by light availability. The relationships we observed between direct drivers and native plant regeneration were qualitatively similar between the two cities (Appendix 2.6). We expect to observe natural variation in the strength and importance of some of these relationships across different cities and regions, but the overall patterns should be robust and, within reason, can be generalized to other global contexts. To succeed in restoring urban forests to a point where native plant regeneration occurs, we recommend management actions that promote rapid canopy closure. For example, given a finite supply of native tree seedlings, it is better to plant seedlings at high densities over small areas rather than low densities across large areas. Many ecosystem properties change predictably over time as canopies develop, allowing management decisions to be planned on decadal timescales. Given the timescales at which forest dynamics operate, local governments that manage urban forests should adopt long-term planning strategies similar to those of forestry operations. This will be challenging given the rapid turnover of political offices.

Initial restoration plantings are often followed by further site management, such as enrichment planting of late successional species. These enrichment plantings are undertaken to hasten forest development after the initial planting (Martínez-Garza and Howe 2003, Schulze 2008), but more work is needed to evaluate the survival of enrichment seedlings that are planted early on, given that the conditions in the chronosequence were not optimal until 20 years after planting. Microclimate conditions are difficult to manipulate directly, but tree seedling survival could be enhanced by coinciding enrichment planting with herbaceous weed control until the canopy is sufficiently closed.

Some indicators of long-term forest restoration success, such as colonization of the canopy by epiphytes, will be constrained by the size of the trees (Hirata et al. 2009, Burns and Dawson 2005). A minimum target basal area of 27 m^2/ha could provide guidance for where to cultivate tree seedlings or epiphytes, especially in urban sites that are chronically limited by adequate propagule dispersal (Overdyck and Clarkson 2012). The restoration of natural areas within cities is a critically important objective for urban land managers to reconnect people to the ecosystems that sustain life on Earth (Standish et al. 2013, Pickett et al. 2011), and our results provide guidance for how to restore resilient urban forests efficiently and successfully.

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2.8 APPENDICES

APPENDIX 2.1 - Table 1. Urban forest patch site name, location, age, size, and distance to nearest forest > 0.1 ha.

Site	City	Age	Size	Distance to forest
Airport	New Plymouth	23	1.85	494
Avalon	Hamilton	7	0.80	62
Barrett	New Plymouth	155	1.13	10
Berkley	Hamilton	205	6.16	10
Brymer	Hamilton	17	0.99	282
Camden	New Plymouth	55	4.21	22
Claudelands	Hamilton	112	6.50	501
Cowling	New Plymouth	70	3.96	10
Edgar	Hamilton	42	2.90	10
Featherstone	Hamilton	12	0.10	32
Hamilton Lake Old	Hamilton	60	1.84	23
Hamilton Lake Young	Hamilton	14	1.07	23
Hammond	Hamilton	174	7.87	120
Herekawe	New Plymouth	11	1.84	132
Huatoki mature	New Plymouth	174	2.95	10
Huatoki restored	New Plymouth	41	1.19	10
Hukanui	Hamilton	7	3.28	15
Living Legends	New Plymouth	4	0.84	282
Minogue	Hamilton	33	5.71	591
Mooney	Hamilton	17	0.77	433
Morris	Hamilton	32	3.21	15
Munro	Hamilton	27	3.42	337
Peringa Park	New Plymouth	7	2.18	104
Sandford Restored	Hamilton	15	0.99	28
Sandford Unrestored	Hamilton	42	9.94	28
Seeleys	Hamilton	52	4.66	644
Sheppards Bush	New Plymouth	174	2.76	57
Swampy Creek	Hamilton	48	8.28	158
Tauhara	Hamilton	25	0.66	28
Te henui 1	New Plymouth	6	0.73	15
Te henui 2	New Plymouth	8	0.47	10
Te henui 3	New Plymouth	29	4.75	18
Te henui 4	New Plymouth	20	0.72	18
Te henui 5	New Plymouth	39	0.85	9
Tills	Hamilton	18	2.17	504
Totara	Hamilton	58	2.07	513
Waipu	New Plymouth	25	5.99	150
Waiwhakareke Old	Hamilton	11	1.20	30
Waiwhakareke Young	Hamilton	3	1.84	30

APPENDIX 2.1 – Figure 1. Study site locations in the New Zealand cities of Hamilton and New Plymouth. Orange, yellow and green pins are unrestored, restored, and remnant sites, respectively.

APPENDIX 2.1 - Table 2. All plant species identified in this study, along with growth form and nativity.

Scientific name	Growth form	Nativity
acacia melanoxylon	tree	nonnative
acer buergerianum	tree	nonnative
acer cappadocicum	tree	nonnative
acer palmatum	tree	nonnative
achillea millefolium	herb	nonnative
agapanthus praecox	herb	nonnative
agathis australis	tree	native
agrostis stolonifera	herb	nonnative
albizia julibrissin	tree	nonnative
alectryon excelsus	tree	native
allium triquetrum	herb	nonnative
alternanthera sp.	herb	unk
anagallis arvensis	herb	nonnative
anthoxanthum odoratum	herb	nonnative
aristotelia serrata	tree	native
arthropteris tenella	epiphyte	native
asparagus scandens	herb	nonnative
asplenium bulbiferum	epiphyte	native
asplenium flaccidum	epiphyte	native
asplenium oblongifolium	epiphyte	native
asplenium polyodon	epiphyte	native
astelia hastata	epiphyte	native
astelia solandri	epiphyte	native
banksia serrata	tree	nonnative
banksia sp.	tree	nonnative
beilschmiedia tarairi	tree	native
beilschmiedia tawa	tree	native
berberis darwinii	tree	nonnative
berberis glaucocarpa	tree	nonnative
blechnum chambersii	epiphyte	native
blechnum filiforme	epiphyte	native
briza maxima	herb	nonnative
bromus diandrus	herb	nonnative
calystegia sepium	herb	native
calystegia soldanella	herb	native
camellia japonica	tree	nonnative
carex dissita	herb	native
carex geminata	herb	native
carex secta	herb	native
carex sylvatica	herb	nonnative
carex uncinata	herb	native
carex virgata	herb	native
carpodetus serratus	tree	native
cenchrus caliculatus	herb	native
cerastium glomeratum	herb	nonnative
cirsium vulgare	herb	nonnative
clematis paniculata	vine	native
clematis vitalba	herb	nonnative
conyza canadensis	herb	nonnative
conyza sp.	epiphyte	unk
conyza sumatrensis	herb	nonnative
coprosma acerosa	tree	native
coprosma areolata	tree	native
coprosma grandifolia	tree	native
coprosma repens	tree	native
coprosma rhamnoides	tree	native
coprosma rigida	tree	native
coprosma robusta	tree	native

Scientific name	Growth form	Nativity
coprosma robusta x propinqua	epiphyte	native
coprosma rotundifolia	tree	native
coprosma spathulata	tree	native
coprosma tenuicaulis	tree	native
cordyline australis	tree	native
corokia cotoneaster	tree	native
corynocarpus laevigatus	tree	native
cotoneaster franchetii	tree	nonnative
cotoneaster microphyllus	tree	nonnative
crepis capillaris	herb	nonnative
crocosmia crocosmiiflora	herb	nonnative
cryptomeria japonica	tree	nonnative
cyathea dealbata	treefern	native
cyathea medullaris	treefern	native
cyathea smithii	treefern	native
cyperus congestus	herb	nonnative
cyperus eragrostis	herb	nonnative
cytisus scoparius	tree	nonnative
dacrycarpus dacridioides	tree	native
dacrydium cupressinum	tree	native
dactylis glomerata	herb	nonnative
dianella nigra	herb	native
dicksonia squarrosa	treefern	native
dodonaea viscosa	tree	native
drymoanthus adversus	epiphyte	native
dysoxylum spectabile	tree	native
earina autumnalis	epiphyte	native
elaeocarpus dentatus	tree	native
erechtites valerianifolia	herb	nonnative
euonymus europaeus	tree	nonnative
euonymus japonicus	tree	nonnative
euphorbia peplus	herb	nonnative
fagus sylvatica	tree	nonnative
fallopia japonica	herb	nonnative
fatsia japonica	tree	nonnative
festuca rubra	herb	nonnative
foeniculum vulgare	herb	nonnative
freycinetia banksii	tree	native
fuchsia excorticata	tree	native
fumaria muralis	herb	nonnative
galium aparine	herb	nonnative
geniostoma ligustrifolium	tree	native
geranium robertianum	herb	nonnative
grass sp	herb	unk
griselinia littoralis	tree	native
griselinia lucida	epiphyte	native
hebe stricta	tree	native
hedera helix	epiphyte	nonnative
hedycarya arborea	tree	native
hoheria populena	tree	native
hoheria sextylosa	tree	native
holcus lanatus	herb	nonnative
hymenophyllum demissum	epiphyte	native
hymenophyllum dilatatum	epiphyte	native
hymenophyllum sanguinolentum	epiphyte	native
hymenophyllum species	epiphyte	native
hypericum androsaemum	herb	nonnative
hypochaeris glabra	herb	nonnative
hypochaeris radicata	herb	nonnative
jasminum polyanthum	vine	nonnative
juglans ailantifolia	tree	nonnative
juncus effusus	herb	nonnative
knightia excelsa	tree	native

Scientific name	**Growth form**	**Nativity**
kunzea ericoides	tree	native
lactuca virosa	herb	nonnative
lamium purpureum	herb	nonnative
laurelia novae-zelandiae	tree	native
leontodon taraxacoides	herb	nonnative
leptospermum scoparium	tree	native
ligustrum lucidum	tree	nonnative
ligustrum sinense	tree	nonnative
lindsaea viridis	epiphyte	native
linum bienne	herb	nonnative
litsea calicaris	tree	native
lonicera japonica	epiphyte	nonnative
lotus pedunculatus	herb	nonnative
lupinus arboreus	tree	nonnative
machaerina rubiginosa	herb	native
magnolia sp	tree	nonnative
melicope simplex	tree	native
melicytus micranthus	tree	native
melicytus ramiflorus	tree	native
metrosideros diffusa	epiphyte	native
metrosideros excelsa	tree	native
metrosideros fulgens	epiphyte	native
metrosideros perforata	tree	native
metrosideros sp.	tree	nonnative
microlaena stipoides	herb	native
microsorum pustulatum	epiphyte	native
microsorum scandens	fern	native
modiola caroliana	herb	nonnative
muehlenbeckia australis	vine	native
muehlenbeckia axillaris	epiphyte	native
muehlenbeckia complexa	vine	native
myosotis arvensis	herb	nonnative
myrsine australis	tree	native
nandina domestica	tree	nonnative
nestegis cunninghamii	tree	native
nhotogrammitis angustifolia	epiphyte	native
no herbs	herb	none
no native saplings present	tree	none1
no nonnative saplings	tree	none
no trees present in the subunit	tree	none
notogrammitis billardierei	epiphyte	native
olearia lineata	tree	native
olearia paniculata	tree	native
olearia solandri	tree	native
olearia traversiorum	tree	native
olearia virgata	tree	native
oxalis dillenii	herb	nonnative
oxalis vallicola	herb	nonnative
ozothamnus leptophyllus	tree	native
parsonsia heterophylla	vine	native
paspalum dilatatum	herb	nonnative
pennantia corymbosa	tree	native
phlegmariurus varius	epiphyte	native
phoenix canariensis	tree	nonnative
phormium cookianum	herb	native
phormium tenax	herb	native
phyllocladus trichomanoides	tree	native
phytolacca octandra	herb	nonnative
piper excelsum	tree	native
pittosporum crassifolium	tree	native
pittosporum eugenioides	tree	native
pittosporum tenuifolium	tree	native
plagianthus regius	tree	native

Scientific name	**Growth form**	**Nativity**
plantago lanceolata	herb	nonnative
platanus acerifolia	tree	nonnative
poa annua	herb	nonnative
poa trivialis	herb	nonnative
podocarpus cunninghamii	tree	native
podocarpus totara	tree	native
polyphlebium endlicherianum	epiphyte	native
potentilla anglica	herb	nonnative
prumnopitys ferruginea	tree	native
prumnopitys taxifolia	tree	native
prunella vulgaris	herb	nonnative
prunus serotina	tree	nonnative
prunus sp	tree	nonnative
pseudopanax arboreus	tree	native
pseudopanax colensoi	tree	native
pseudopanax colensoi x crassifolius	tree	native
pseudopanax crassifolius	tree	native
pseudopanax laetus	tree	native
pseudopanax lessonii	tree	native
pseudopanax sp.	tree	native
ptisana salicina	fern	native
pyrrosia eleagnifolia	epiphyte	native
ranunculus repens	herb	nonnative
raphanus raphanistrum	herb	nonnative
rhopalostylis sapida	tree	native
ripogonum scandens	vine	native
robinia pseudoacacia	tree	nonnative
robinia sp.	tree	nonnative
rubus fructicosus	vine	nonnative
rumex acetosa	tree	nonnative
rumex crispus	herb	nonnative
rumex obtusifolius	herb	nonnative
rumex sagittatus	herb	nonnative
rumex sp.	herb	unk
salix cinerea	tree	nonnative
salix fragilis	tree	nonnative
schedonorus arundinaceus	herb	nonnative
schefflera digitata	tree	native
selaginella kraussiana	herb	nonnative
senecio bipinnatisectus	herb	nonnative
senecio quadridentatus	herb	native
sequoia sempervirens	tree	nonnative
silene gallica	herb	nonnative
solanum chenopodioides	tree	nonnative
solanum mauritianum	tree	nonnative
solanum nigrum	herb	nonnative
solanum sp.	herb	unk
sonchus oleraceus	herb	nonnative
sophora microphylla	tree	native
sophora prostrata	tree	native
sophora tetraptera	tree	native
stachys arvensis	herb	nonnative
stachys sylvatica	herb	nonnative
stellaria media	herb	nonnative
streblus banksii	tree	native
streblus heterophyllus	tree	native
syzygium maire	tree	native
syzygium smithii	tree	nonnative
taraxacum officinale	herb	nonnative
tilia cordata	tree	nonnative
tmesipteris elongata	epiphyte	native
tmesipteris species	epiphyte	native
tmesipteris tannensis	epiphyte	native

Scientific name	Growth form	Nativity
trachycarpus fortunei	tree	nonnative
tradescantia fluminensis	herb	nonnative
trifolium micranthum	herb	nonnative
trifolium repens	herb	nonnative
tropaeolum majus	herb	nonnative
ulex europaeus	tree	nonnative
viburnum sp	tree	nonnative
vicia sativa	herb	nonnative
vicia sp.	herb	unk
vitex lucens	tree	native
zantedeschia aethiopica	herb	nonnative

APPENDIX 2.2 Methods and results for ecosystem properties that were non-impacting.

This is a detailed description of methods for non-impacting ecosystem properties, i.e. that either did not differ between unrestored and remnant forests, were not significantly affected by restoration efforts, or were not important drivers of tree regeneration or epiphyte colonization.

Soil samples were collected by removing leaf litter and coring to 15 cm in three subplots per plot, totaling 9 cores per urban forest site. The resulting nine cores per site were homogenized, air dried, and used for all soil analyses. Prior to total carbon (C) and total nitrogen (N) analysis, samples were sieved (2 mm sieve), fine roots removed, and samples finely ground with mortar and pestle. Soil C and N was determined using an Elementar vario EL cube (Elementar Ananysensysteme GmgH, Germany).

Prior to particle size analysis, soil samples underwent hydrogen peroxide digestion to remove organic material and were then processed with a Malvern Mastersizer 2000 (Malvern, U.K.). Olsen P was measured using molybdenum blue colorimetery on the Olsen extraction. Total P was determined by a nitric/hydrochloric digestion followed by inductively coupled plasma-optical emission spectroscopy (ICP-OES) and reported on a dry weight basis. Calcium (Ca) and Potassium (K) were assessed via 1M neutral ammonium acetate extraction followed by ICP-OES. Soil pH samples were made into slurries (1:2 soil:water) followed by potentiometric determination(Blakemore et al. 1987).

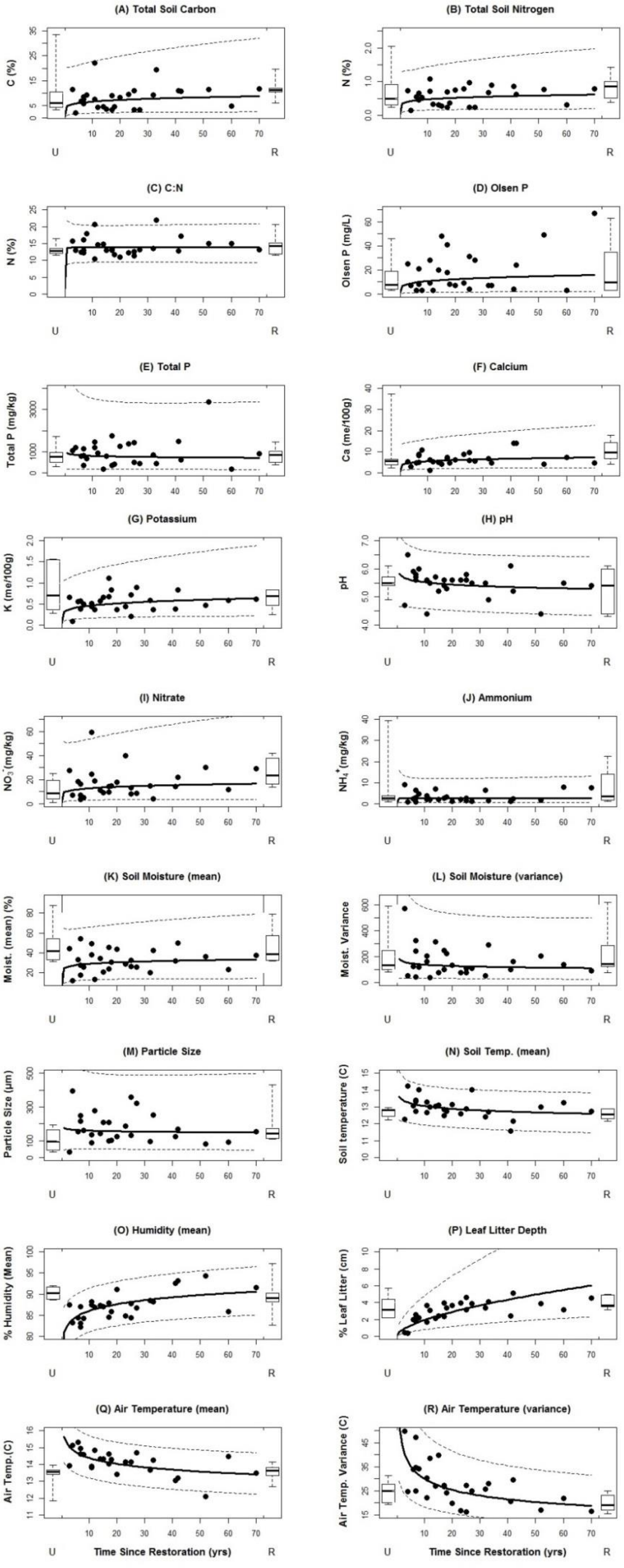
We measured ammonium (NH_4^+) and nitrate (NO_3^-) twice (March and December 2015) because they are labile forms of N and levels can fluctuate. We averaged results from the two sampling periods. Coring protocol was the same as other soil sampling except only to depths of 8 cm and soil was kept refrigerated and moist until tested within 3 days. Ammonium and nitrate were extracted with 2M KCl using a 1:10 soil:extractant ratio and a 1 hour end-over-end shake followed by filtration (Blakemore et al. 1987). Ammonium was determined colorimetrically using the indophenol reaction with sodium salicylate and hypochlorite (Lachat Instruments 1998a) and NO_3 by Cd reduction and NEDD colorimetry (Lachat Instruments 1998b), both using a QuikChem 8500 flow injection analyser.

Soil moisture was measured monthly for 12 months in the center subplot using a time domain water reflectometer probe (Hydrosense CS 620 Campbell Scientific, Logan, Utah, U.S.A.). An annual mean and variance for soil moisture at each site was calculated. Leaf litter depth was measured in each subplot monthly for 12 months.

Air temperature was measured every four hours for 12 months using hygrochrons (iButton dataloggers model DS1923, Maxim Integrated, San Jose, CA, U.S.A). Hygrochrons (one per site) were hung in radiation shields 2 m above the center subplot in the central plot at each urban forest site. We computed the variance over one year to represent the temporal fluctuation in this abiotic condition at each site.

APPENDIX 2.2 - TABLE 1. Summaries of the non-impacting ecosystem properties and associated data collection methodologies.

Ecosystem Property	**Methodology**	**Sampling Freq.**
Total C	Elemental analysis	Once
Total N	Elemental analysis	Once
Total C:N	Elemental analysis	Once
Particle size	Mastersizer particle analyser	Once
Olsen P	Olsen extraction	Once
Total P	Nitric/hydrochloric digestion	Once
Ca & K	Ammonium acetate extraction	Once
pH	Potentiometric determination	Once
NO_3^- and NH_4^+	KCl extraction	Twice
Moisture ($\bar{x}$) and (σ^2)	Time domain reflectometer	Monthly
Leaf litter depth	Ruler	Monthly
Air Temperature ($\bar{x}$) and (σ^2)	Hygrochron ibutton	Every 4 hrs (for 12 mos)


(A) Total Soil Carbon
C (%)
(B) Total Soil Nitrogen
N (%)
(C) C:N
N (%)
(D) Olsen P
Olsen P (mg/L)
(E) Total P
Total P (mg/kg)
(F) Calcium
Ca (me/100g)
(G) Potassium
K (me/100g)
(H) pH
pH
(I) Nitrate
NO_3^-(mg/kg)
(J) Ammonium
NH_4^+(mg/kg)
(K) Soil Moisture (mean)
Moist. (mean) (%)
(L) Soil Moisture (variance)
Moist. Variance
(M) Particle Size
Particle Size (µm)
(N) Soil Temp. (mean)
Soil temperature (C)
(O) Humidity (mean)
% Humidity (Mean)
(P) Leaf Litter Depth
% Leaf Litter (cm)
(Q) Air Temperature (mean)
Air Temp.(C)
(R) Air Temperature (variance)
Air Temp. Variance (C)
U
R
10
20
30
40
50
60
70
Time Since Restoration (yrs)

APPENDIX 2.2 - Figure 1. Non-impacting ecosystem properties in restored forests over time (central section of each bivariate plot) compared with unrestored (U) and remnant (R) forests (boxplots to left and right, respectively). Boxplots represent 25th, 50th, and 75th percentiles and whiskers extend to data extremes. Scatterplot points represent restored sites; the solid lines represent the fitted values from a linear regression model on log-transformed data, and the dashed lines represent the 95% confidence intervals. There were no significant differences between unrestored and remnant site values ($\alpha = 0.05$).

APPENDIX 2.2 LITERATURE CITED

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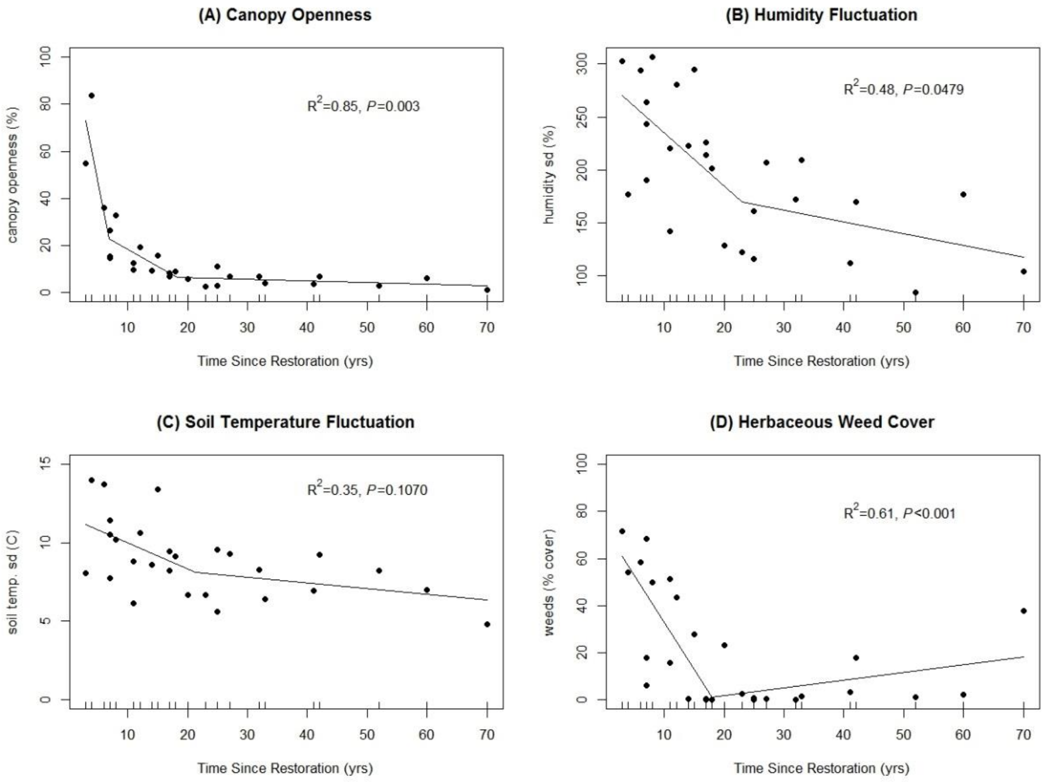
Lachat Instruments. 1998a. Quick Chem Method 12-107-04-1-B. Milwaukee, WI, U.S.A.

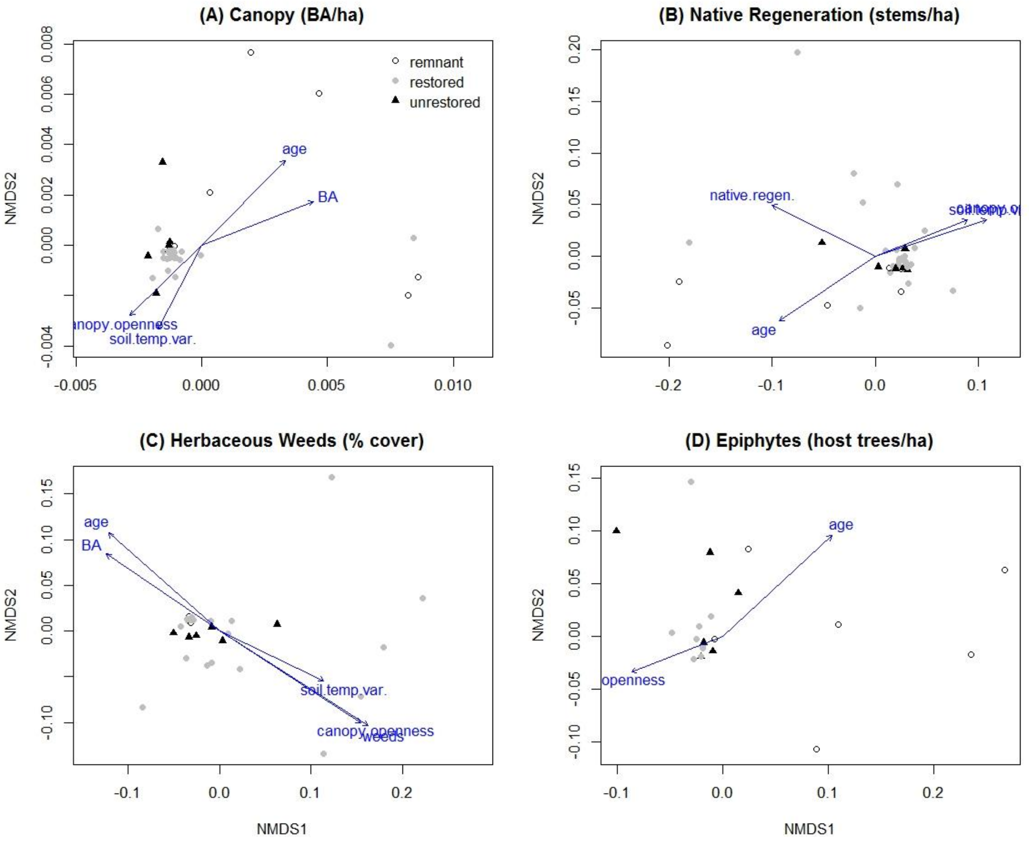
Lachat Instruments. 1998b. Quick Chem Method 12-107-06-3-A. Milwaukee, WI, U.S.A.

APPENDIX 2.3. Breakpoints of key ecosystem properties.



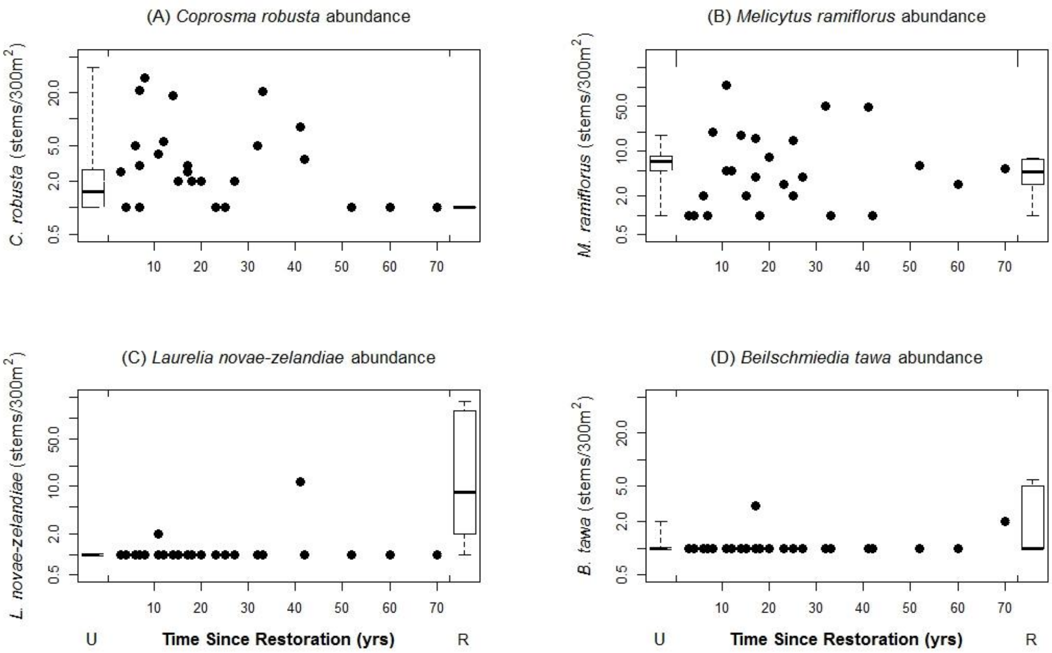
APPENDIX 2.3 - Figure 1. Breakpoints of ecosystem properties that either indirectly or directly affected native tree regeneration and epiphyte colonization in the restored forest chronosequence. Thresholds all occurred approximately 20 years after restoration planting. (A) Canopy openness had two thresholds, occurring at 7.0 and 18.1 years, (B) humidity fluctuation had a threshold point at 23.1 years (C) soil temperature fluctuation at 21.3 years and (D) herbaceous weed cover at 17.9 years.

APPENDIX 2.4. NMDS ordination plots illustrating forest plant community composition.



APPENDIX 2.4 - Figure 1. Plant communities were analyzed by forest strata: A) forest canopy (basal area: m^2/ha), B) native tree regeneration (stems/ha), C) herbaceous weeds (% cover) and D) epiphytes (host trees/ha). Urban forest types are represented by different symbols (each point is a site). Vectors illustrate directions of significantly correlated site properties ($\alpha = 0.05$), the properties that were tested are those properties shown in the *a priori* SEM (Fig. 2.1). Length of vector arrow is proportional to its correlation with the ordination. Final NMDS stresses were A) 0.0992, B) 0.1085, C) 0.1019 and D) 0.0494.

APPENDIX 2.5. Regenerating native tree densities of two early and two late successional species.



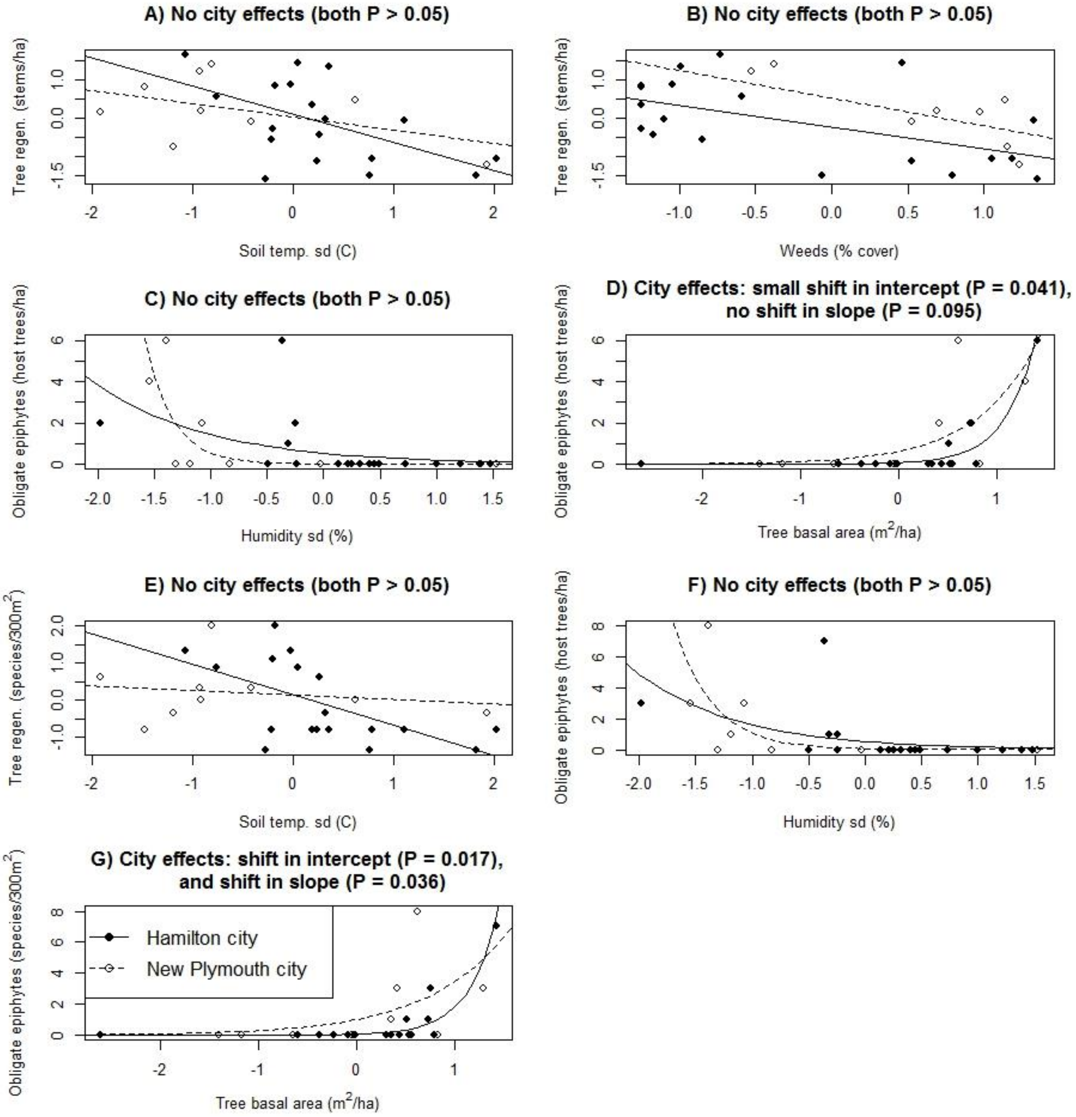
APPENDIX 2.5 - Figure 1. Regenerating native trees shown by species in unrestored (U), restored (central section of each plot) and remnant (R) forests. (A) and (B) are generally considered early successional species and tend to be more prevalent in unrestored or younger sites while (C) and (D) are considered late successional and rarely appear in the first 70 years, but are abundant in remnant forests (where environmental conditions are more suitable). All data were natural log transformed and y-axes are shown log scale. Plant naming conventions follow Landcare Research Nga Tipu o Aotearoa – NZ Plants (http://nzflora.landcareresearch.co.nz/).

APPENDIX 2.5 – Table 1. Regenerating native woody seedlings identified accross all plots and their assigned successional categories according to information found in the restoration plan for Waiwhakareke Natural Heritage Park, a 60 ha New Zealand urban forest restoration project listed in Oldfield et al. (2013). Listed here by six letter codes, see Appendix 2.1, Table 2 for full species names.

Species	Early succession	Mid succession	Late succession
aleexc	early	mid	none
ariser	early	mid	none
beitar	none	mid	late
beitaw	none	none	late
copace	early	mid	none
copare	early	mid	late
copgra	none	mid	late
coprep	early	mid	none
coprha	early	none	none
coprig	early	none	none
coprob	early	none	none
coprot	early	mid	none
copspa	none	mid	none
copten	early	mid	none
coraus	early	none	none
corcot	early	none	none
corlae	early	mid	none
dacdac	early	none	none
dysspe	none	mid	late
freban	none	mid	late
fucexc	early	mid	none
genlig	none	mid	late
grilit	early	mid	none
hebstr	early	mid	none
hedarb	early	mid	none
hohpop	early	none	none
hohsex	early	none	none
kniexc	early	none	none
kuneri	early	none	none
launov	late	none	none
lepsco	early	none	none
litcal	none	mid	late
melmic	none	mid	late
melram	early	mid	late
melsim	none	mid	late
myraus	early	none	none
nescun	none	mid	late
olepan	early	mid	none
olesol	early	none	none
ozolep	early	none	none
pencor	none	mid	late
phytri	early	mid	late
pipexc	none	mid	none
pitcra	early	none	none
piteug	early	none	none
pitten	early	none	none
plareg	early	mid	none
podcun	none	mid	none
podtot	none	mid	none
prufer	none	mid	none
prutax	none	mid	none
psecol	early	none	none

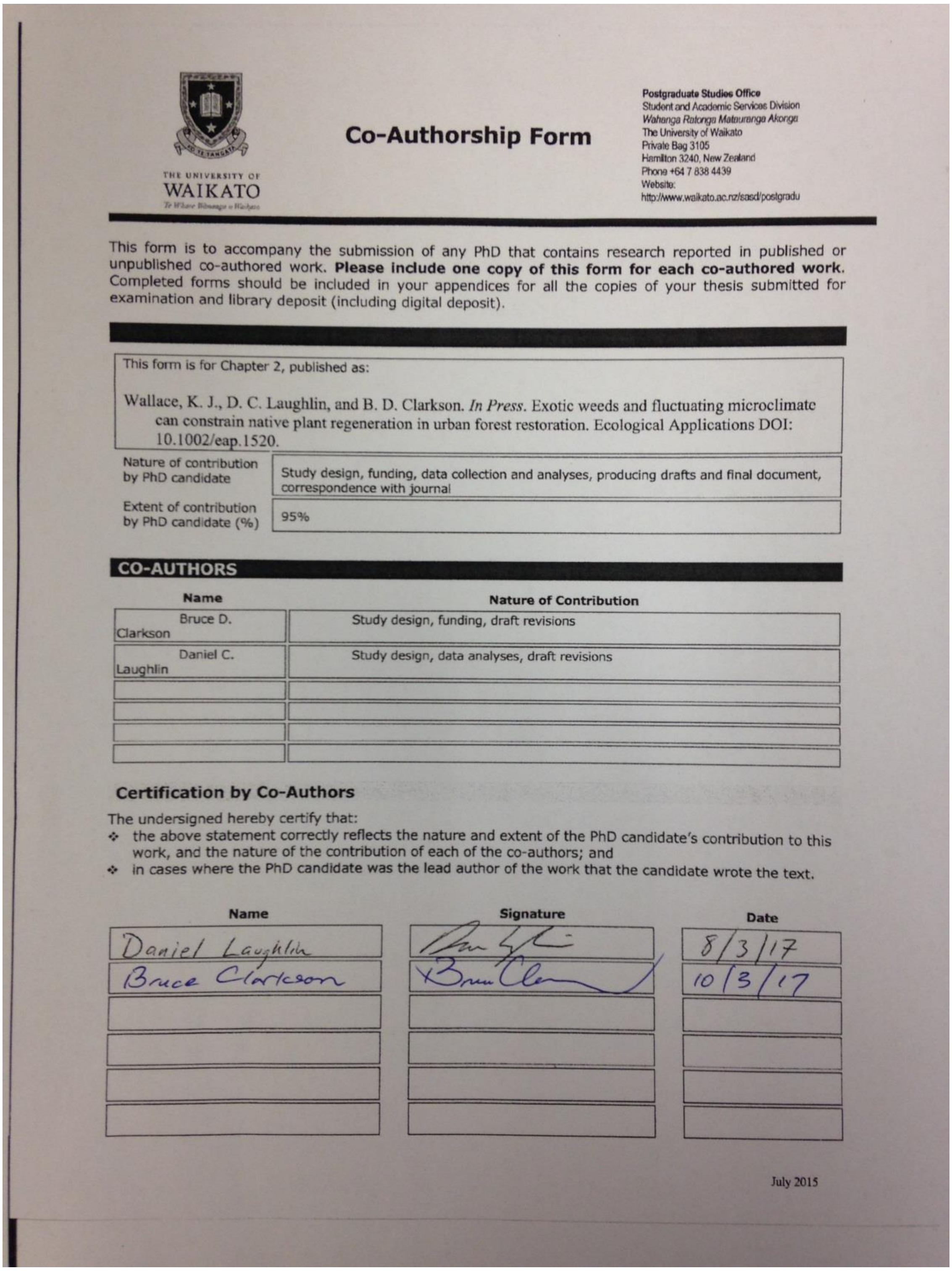
Species	Early succession	Mid succession	Late succession
psecolxcra	early	none	none
psecra	early	mid	none
pselae	early	mid	none
pseles	early	none	none
psespp	early	none	none
rhosap	none	mid	late
schdig	none	mid	late
sopmic	early	none	none
soppro	early	none	none
soptet	early	mid	none
strhet	none	mid	none
syzmai	none	mid	late
vitluc	none	mid	late

APPENDIX 2.6. Comparison of direct effects on plant regeneration between the two cities.



APPENDIX 2.6 - Figure 1. Bivariate scatterplots of direct effects in the SEMs, where relationships are illustrated for each city. We used ANCOVA to test whether the relationships differed between the two cities. In cases where neither the main effect of city nor the interaction effect with city is significant, we note that there were “No city effects (both *P* > 0.05)”.

APPENDIX 2.7. University of Waikato publication co-authorship form



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This form is for Chapter 2, published as:

Wallace, K. J., D. C. Laughlin, and B. D. Clarkson. *In Press*. Exotic weeds and fluctuating microclimate can constrain native plant regeneration in urban forest restoration. Ecological Applications DOI: 10.1002/eap.1520.

Nature of contribution by PhD candidate	Study design, funding, data collection and analyses, producing drafts and final document, correspondence with journal
Extent of contribution by PhD candidate (%)	95%

CO-AUTHORS

Name	Nature of Contribution
Bruce D. Clarkson	Study design, funding, draft revisions
Daniel C. Laughlin	Study design, data analyses, draft revisions

Certification by Co-Authors

The undersigned hereby certify that:

- the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and
- in cases where the PhD candidate was the lead author of the work that the candidate wrote the text.

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CHAPTER 3

URBAN FOREST RESTORATION HAS OPPOSING EFFECTS ON LITTER DECOMPOSITION AND HAS NO EFFECT ON DENITRIFICATION

3.1 ABSTRACT

Forest restoration is commonly recommended as a way to recover degraded ecosystem functions. As restored forest canopies develop, they may indirectly impact ecosystem functions by altering the abiotic conditions that control them. Here we measured litter decomposition and denitrification potential, two critical steps in forest nutrient cycling that are often compromised by anthropogenic activities. When exotic deciduous trees invade evergreen forests, decomposition rates may be accelerated due to the faster breakdown of the deciduous leaves. Additionally, excessive runoff from gardens and agricultural settings can inflate nitrogen availability in urban forests to detrimental levels, increasing the need for N removal through denitrification, the microbial conversion of nitrogen from mineral to gaseous forms. We hypothesized that forest canopy openness, topography (e.g. gullies or ridgetops), and soil sand content would indirectly affect decomposition and denitrification by regulating the forest microclimate, herbaceous plant layer, soil chemistry and soil moisture. Relationships between these properties and decomposition and denitrification were investigated in 27 restored urban temperate rainforests using structural equation modelling to determine direct and indirect drivers of the ecosystem functions. We found that decomposition was indirectly related to forest structure but denitrification was not related to forest structure at all. Ecosystem properties that were related to faster litter decomposition rates included higher herbaceous plant cover and increased humidity, both of which were associated with canopy openness, but canopy openness increased herbaceous weeds and decreased humidity. Gully environments contained moister soil, which increased both decomposition and denitrification. Denitrification was indirectly related to soil sand content, which was independent of forest structure. Finally, higher soil pH was associated with slower denitrification rates. These results indicate that the restoration of urban forest has offsetting indirect effects on litter decomposition rates that cancel each other out: a closed canopy suppresses herbaceous weeds, which leads to lower decomposition rates, but increases relative humidity, which leads to higher decomposition rates. Denitrification rates are not affected by forest restoration, but instead are driven by abiotic landscape factors.

Key words: forest restoration, decomposition, denitrification, ecological function, urban restoration, ecosystem function, structural equation modelling.

3.2 INTRODUCTION

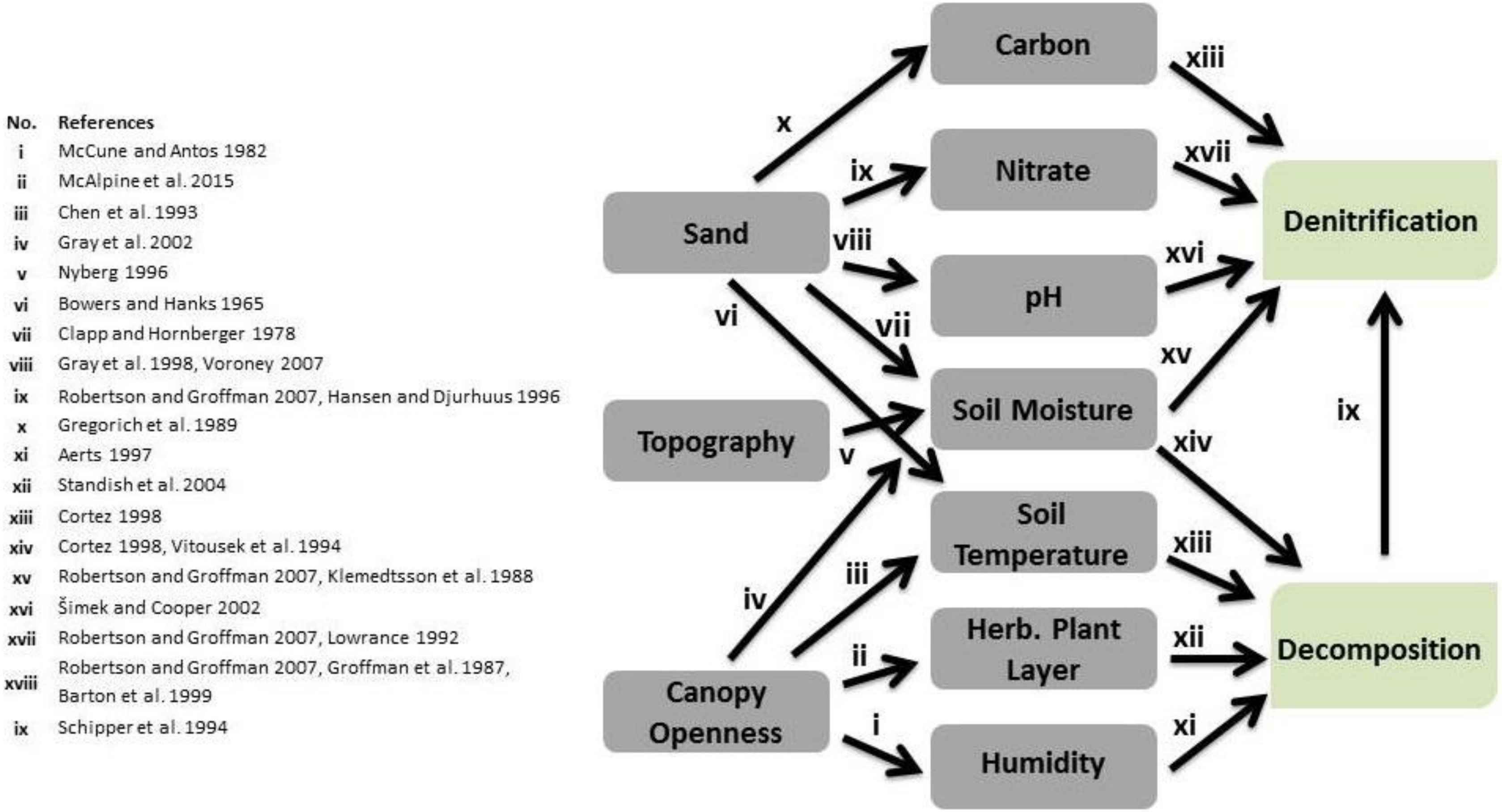
Our understanding of how restoration affects forest ecosystem functioning lags behind our understanding of how it drives changes in forest structure and composition (McKee and Faulkner 2000, Wortley et al. 2013, Suding 2011). Until recently, the common assumption in restoration practice claimed that ecosystem functions would be restored following the restoration of ecosystem structure, but this has been shown to be a simplification (Bradshaw 1983, Ehrenfeld and Toth 1997, Zedler and Callaway 1999, Ruiz-Jaen and Aide 2005, Derhé et al. 2016). Moreover, in the few studies where ecosystem processes have been evaluated following restoration, the specific mechanisms driving those processes are often not identified (Wortley et al. 2013). By enhancing our understanding of these relationships we can improve the restoration of forest ecosystem functions (Guariguata and Ostertag 2001, Stanturf et al. 2014, Thackway and Freudenberger 2016).

Two important ecosystem processes involved in carbon (C) and nutrient cycling include decomposition (Harmon et al. 1999, Swift et al. 1979) and denitrification (Van Der Heijden et al. 2008). However, the rates at which decomposition and denitrification occur in urban forests and the factors that drive them are unclear (Reisinger et al. 2016, Pouyat et al. 1997), making management of these processes difficult. Often many factors jointly influence ecosystem functioning so that determining the main drivers is complicated. Clarity of how aboveground-belowground linkages, such as those in nutrient cycling, occur in restored forests will improve management approaches (Kardol and Wardle 2010).

The introduction of exotic deciduous tree species into historically evergreen urban forests has likely changed nutrient cycling dynamics. Deciduous trees often have less substantial leaves which break down more readily, speeding the rate of decomposition to rates that plants in the native ecosystem are not accustomed to. Nutrient pollution in the form of nitrogen (N) runoff is known to alter urban forest composition by benefitting N-demanding exotic weed species (Gilliam 2006). Therefore, altered decomposition and denitrification rates can have far-reaching implications for the urban forest ecosystem.

The main factors thought to control rates of litter decomposition include atmospheric relative humidity (Aerts 1997), the herbaceous plant layer (Standish et al. 2004), and soil temperature and moisture (Cortez 1998, Vitousek et al. 1994). These factors can be indirectly controlled by forest structure, landscape topography, and soil texture (Fig. 3.1). Standish et al. (2004) found that decomposition rates of tree leaves doubled beneath mats of the herbaceous exotic weed *Tradescantia fluminensis* Vell. and they attributed this to a more favourable microclimate and an improved habitat for the decomposer community. Plant litter decomposition rates can control the speed of tree seed germination and establishment (Xiong and Nilsson 1999), so by understanding factors controlling decomposition we will better predict future forest composition.

Denitrification is the anaerobic process by which N is converted by soil microbes into nitrate (NO_3^-) and then the nitrogenous gases NO, N_2O and N_2 (Robertson and Groffman 2007). This conversion is instrumental in ameliorating N pollution, which is an environmental concern due to the vast quantities of N applied as horticultural and agricultural fertilizer and produced by fossil fuel combustion (Vitousek et al. 1997, Galloway et al. 2003). Inflated quantities of soil N may negatively impact plant communities (Prober et al. 2005, Prober and Wiehl 2011) by facilitating exotic weeds that outcompete regenerating native trees, causing long-term changes in forest composition. Inflated N deposition causes soil acidification (Tian and Niu 2015), and can leach into ground water and contaminate surface water bodies, causing eutrophication (Galloway et al. 2003, Hall et al. 2009). Eutrophication often causes algal blooms and subsequent fish die-offs, and acidic soil typically reduces plant growth and species diversity.



No.	References
i	McCune and Antos 1982
ii	McAlpine et al. 2015
iii	Chen et al. 1993
iv	Gray et al. 2002
v	Nyberg 1996
vi	Bowers and Hanks 1965
vii	Clapp and Hornberger 1978
viii	Gray et al. 1998, Voroney 2007
ix	Robertson and Groffman 2007, Hansen and Djurhuus 1996
x	Gregorich et al. 1989
xi	Aerts 1997
xii	Standish et al. 2004
xiii	Cortez 1998
xiv	Cortez 1998, Vitousek et al. 1994
xv	Robertson and Groffman 2007, Klemedtsson et al. 1988
xvi	Šimek and Cooper 2002
xvii	Robertson and Groffman 2007, Lowrance 1992
xviii	Robertson and Groffman 2007, Groffman et al. 1987, Barton et al. 1999
ix	Schipper et al. 1994

Figure 3.1 Hypothesized *a priori* structural equation model (SEM) illustrating how restored forest properties might influence the ecosystem functions of decomposition and denitrification. Support for causal relationships are listed by pathway number on left. The functions are light green and their drivers are dark grey. The *a priori* structural equation model of decomposition and denitrification did not fit the data well (Fisher's $C = 136.56$, $df = 88$, $P = 0.001$).

Denitrification is controlled by the availabilities of oxygen, nitrate, and carbon (Knowles 1982). Therefore, the most important driver of denitrification is soil moisture (Robertson and Groffman 2007, Klemedtsson et al. 1988) because microbes will only use the denitrification process to produce energy when oxygen is unavailable. Both soil C (Robertson and Groffman 2007, Groffman et al. 1987, Barton et al. 1999) and the mineral forms of N (Robertson and Groffman 2007, Lowrance 1992) are required for denitrification activity. Denitrifying microbes produce energy by reducing mineral N through use of C as an electron donor. Soil pH is also known to govern denitrification, and denitrification is typically higher in alkaline soils (Šimek and Cooper 2002). Restoration of urban forest could improve conditions for denitrification by increasing C inputs through production of evergreen leaves and other C-rich plant matter.

Restoration research too often focuses exclusively on either plant community structure or diversity, without considering functional processes (Montoya et al. 2012). The objective of this study was to assess whether forest structural development following restoration can affect two ecosystem functions related to C and N cycling: decomposition and denitrification. To do this we measured rates of leaf litter decomposition and denitrification within 27 restored temperate rainforests and used structural equation modelling to determine which factors most strongly regulate these processes. Specifically, we asked 1) is restoration of forest ecosystem structure related to rates of decomposition and denitrification?, and 2) what are the key direct and indirect drivers of decomposition and denitrification?

3.3 MATERIALS AND METHODS

3.3.1 Study sites

Our study took place on New Zealand's North Island, which was historically 75% covered in temperate rainforest but 66% of which is now cleared for agriculture and silviculture (Nicholls 1980). Data were collected from restored urban forest patches in two cities, Hamilton, with a population of 160,000 (37.7870° S, 175.2793° E) and New Plymouth, with a population of 60,000 (39.0556° S, 174.0752° E), which are about 200 km apart. Hamilton has an annual mean precipitation of 1,110 mm with mean daily minimum and maximum temperatures of 8.7 °C and 18.9 °C, respectively (CliFlo), and 2.1% indigenous forest cover

(Clarkson et al. 2007a). New Plymouth has an annual mean precipitation of 1,400 mm with mean daily minimum and maximum temperatures of 10 °C and 17.5 °C, respectively (CliFlo), and 8.5% indigenous forest cover (Clarkson et al. 2007b) of a composition similar to Hamilton. The restored urban forest patches used in the study averaged 2.05 ha (± 1.6 ha SD) in size and were 159.7 m (± 201.4 m SD) from the nearest forest patch > 0.1 ha.

Data was collected from restored urban forests (n = 27) aged from 3-70 years since initial planting. Each urban forest site encompassed three randomly located 10 x 10 m^2 plots, with the constraints that plot edges were never < 1 m from each other or the edge of the forest patch, or on slopes > 10 degrees. Five permanent 1 m^2 subplots were established in a stratified manner, equidistant from each other in each plot.

3.3.2 Data collection

Canopy openness was measured four times (once per season) by taking hemispherical photos of the canopy at 1 m above the ground in each plot. Resulting images were analysed with the software Gap Light Analyzer v. 2.0 (Institute of Ecosystem Studies, Millbrook New York, U.S.A.). The average value across the three plots and four seasons was used to quantify site-level canopy openness, an index of light availability. The herbaceous plant layer was assessed by within the subplots by estimating percent cover of all plants together, which could exceed 100% due to plant overlap in three-dimensional space.

We calculated the topographic index following methods in McNab (1993), by standing in the central plot at each site and measuring the gradient, in percent, from the plot centre to the horizon at 8 equidistant compass directions, and computing the average gradient for each site. Low averaged topographic index values represent plots in flat areas and on ridges, high values represent those in gullies. Soil samples for assessing sand content, total carbon (C), and pH measurements were collected by removing leaf litter and coring to 15 cm in three subplots per plot. The resulting nine cores per site were homogenized, air dried, and analyzed. Prior to C analysis, samples were sieved (2 mm sieve), fine roots removed, and samples finely ground with mortar and pestle. Soil C was determined using an Elementar vario EL cube (Elementar Ananysensysteme GmgH, Germany). Prior to particle size analysis to determine percent sand, soil samples underwent hydrogen peroxide digestion to remove organic material and were then processed with a Malvern Mastersizer 2000 (Malvern, U.K.). Soil pH samples were made into slurries (1:2 soil:water) followed by potentiometric determination (Blakemore et al. 1987).

We measured nitrate (NO_3^-) twice (March and December 2015) because it is a labile form of N and levels can fluctuate. We averaged results from the two sampling periods. The coring protocol was the same as for sand content, C, and pH, except was only to depths of 8 cm and soil was kept refrigerated and moist until analysis occurred within 3 days. Nitrate was extracted with 2M KCl using a 1:10 soil:extractant ratio and a 1 hour end-over-end shake followed by filtration (Blakemore et al. 1987) and determined by Cd reduction and NEDD colorimetry (Lachat Instruments 1998a), both using a QuikChem 8500 flow injection analyser (Lachat Instruments, Loveland Colorado, U.S.A.).

Soil moisture was measured monthly for 12 months in the center subplot of all three plots using a time domain water reflectometer probe (Hydrosense CS 620, Campbell Scientific, Logan, Utah, U.S.A.). Soil temperature at 10 cm depth was measured every four hours for 12 months in the centre subplot in the outermost two of the three plots using thermochrons (iButton dataloggers model DS1921G-F5, Maxim Integrated, San Jose, CA, U.S.A.) (Hubbart et al. 2005). Atmospheric relative humidity was measured every four hours for 12 months using hygrochrons (iButton dataloggers model DS1923, Maxim Integrated, San Jose, CA, U.S.A). Hygrochrons (one per site) were hung in radiation shields 2 m above the centre subplot in the central plot. For soil temperature, moisture, and relative humidity, we computed the mean over one year to represent these conditions at each site.

Decomposition rate at each site was quantified using the leaf litter bag method (Wieder and Lang 1982, Harmon et al. 1999, Bocock and Gilbert 1957). Litter bags were 20 × 20 cm in size and constructed of both coarse and fine mesh of UV-resistant high-density polyethylene shadecloth (Cosio Industries Ltd., Auckland NZ). The coarse mesh side (1×2 mm pores) was placed facing skywards, and the finer mesh (<1 mm pore size) rested on the ground. Larger pores provide access for meso and macrofauna and smaller pores prevented loss of small leaf pieces. Litterbags were stitched together with nylon thread (Bocock and Gilbert 1957, Harmon et al. 1999) and filled with leaves of *Beilschmiedia tawa* (A. Cunn.) Kirk., a native lowland tree species chosen as a standard material for use in all sites to determine the potential decomposition rate at each site.

Beilschmiedia tawa was not present in the restored forest site canopies except for one, where it represented only 0.23% of total basal area. This meant that a specialist decomposer community adapted to *B. tawa* leaf litter was unlikely to already be present at any sites and present a confounding variable. Naturally senesced, recently dropped *B. tawa* leaves sourced from the forest floor of rural forest fragments surrounding Hamilton were collected for use in litter bags. Leaves were oven dried at 60 °C for one week and approximately 5 g of dry leaves were placed in each litter bag. This mass was chosen to mimic naturally occurring leaf litter abundance on a 20 × 20 cm area of mature reference forest floor.

Litterbags were stapled closed with stainless steel staples. One litter bag was placed in each of three subplots to total 9 litter bags per site. Litterbags were placed on the forest floor substrate to mimic natural litter fall and secured with stainless steel pegs. All litter bags were retrieved after 14 months and contents carefully cleaned to remove soil. Remaining litter was oven dried at 60 °C for one week and weighed to obtain end dry mass. Proportion mass loss was calculated for each bag and we computed the average across the nine bags for analyses at the site level. Litter decomposition rates were only monitored in Hamilton.

Microbial denitrification potential in the forest soils was ascertained through denitrification enzyme activity (DEA) assays using the acetylene inhibition method (Groffman et al. 2006) under optimal conditions in anoxic N and C amended slurries (Bruesewitz et al. 2011). A DEA assay estimates the maximum potential capacity of denitrifying enzymes in soil microbes to convert nitrate into the gaseous forms of N. Specifically, as nitrate is converted to the gaseous form N_2O, acetylene is used to inhibit the usual reduction of N_2O to N_2. Measuring N_2O rather than N_2 is more indicative of nitrogen conversion, since N_2O is comparatively sparse in the atmosphere.

DEA assay protocol generally followed Bruesewitz et al. (2011). To conduct the assays, a soil core (10 cm depth) was taken from each subplot, these five cores were homogenized by plot, and chilled at 2-4 °C to minimize microbial activity until the assay took place. Soil was used in assays within three days of collection by mixing 60 mL of field moist soil with 54 mL distilled water in a glass jar to form a slurry (n = 3 replicates per site). The slurry was amended with chloramphenicol to halt additional microbial enzyme protein synthesis and the jar was evacuated for 4 minutes and then flushed with N_2 for ten minutes. Assays were amended with C (30 mgL^{-1} C as glucose) and nitrate (10 mgL^{-1} N as KNO_3) (Smith and Tiedje 1979). Acetylene was added as 10% of the headspace volume to prevent conversion of N_2O to N_2 and jars were placed on shakers and incubated at 20° C with headspace gas samples taken at t=10, 30, 60 and 120 minutes. We then detected N_2O gas produced using gas chromatography (Varian CP3800 Gas Chromatograph equipped with a CTC Analytics Auto-Sampler, and an Electron Capture Detector, the Netherlands), and assumed N_2O was a proxy of denitrification enzyme activity taking place in the soil samples. The denitrification rate was calculated from the linear increase in N_2O concentration over the 120 minutes (Smith and Tiedje 1979). Denitrification rates were corrected by dividing by grams of oven dry soil contained in 60 mL of field moist soil from each plot. The mean denitrification rate was then calculated using the values of the three plots in each forest site.

3.3.3 Statistical analyses

Relationships between ecosystem structure and function

We inspected bivariate plots and fitted generalized linear regression models to evaluate the relationships between either decomposition or denitrification and ecosystem attributes that we hypothesized were indirectly or directly related to these functions (Fig. 3.1). For decomposition this included canopy openness, the topographic index, soil sand content, soil moisture, soil temperature, the herbaceous plant layer and humidity. For denitrification this included canopy openness, the topographic index, soil sand content, soil carbon, soil nitrate, soil pH, and soil moisture. These variables were always analysed using their mean values across the three plots at each site.

Drivers of decomposition and denitrification

We used structural equation modelling with the R package ‘piecewiseSEM’ (Lefcheck 2015) to determine the direct and indirect drivers of decomposition and denitrification. This multivariate approach tests hypothesized relationships among a system of state variables. Using theory and empirical data, we developed an *a priori* model that we believed to be the most plausible causal structure of the factors driving decomposition and denitrification in restored forests (Fig. 3.1).

We hypothesized that decreased canopy openness would indirectly increase decomposition by creating moister soil conditions, (Gray et al. 2002, Cortez 1998, Vitousek et al. 1994), warmer soil temperatures (Chen et al. 1993, Cortez 1998, Wallace et al. 2017) and higher relative humidity (McCune and Antos 1982, Aerts 1997, Wallace et al. 2017) as well as suppressing the herbaceous plant layer (McAlpine et al. 2015, Standish 2004, Wallace et al. 2017).

We also hypothesized that soil sand content and topography would indirectly control decomposition and denitrification. We predicted increased sand content would indirectly affect decomposition by increasing the soil temperature (Bowers and Hanks 1965) and decreasing both decomposition and denitrification rates by decreasing soil moisture (Clapp and Hornberger 1978, Groffman et al. 1987, Groffman and Tiedje 1989). We predicted denitrification rates to increase in moister soil conditions within gully environments (Nyberg 1996). We also predicted that higher soil sand content would indirectly reduce denitrification because of N loss through nitrate leaching (Robertson and Groffman 2007, Lowrance 1992, Hansen and Djurhuus 1996), and decreased C availability (Gregorich et al. 1989, Robertson and Groffman 2007, Groffman et al. 1987). Soil sand content can have variable effects on soil pH depending on the study system, but we expected that denitrification rates would be higher in alkaline soils (Voroney 2007, Šimek and Cooper 2002, Gray et al. 1998). Finally, we predicted faster decomposition rates would be positively associated with high denitrification rates (Schipper et al. 1994).

Prior to analysis, all variables except sand, pH and soil moisture were log transformed to linearize relationships. Topographic index was square root transformed. All variables were scaled to unit variance. Model fit was assessed using Fisher's *C* statistic (Grace 2006, Lefcheck 2015), where good-fitting models yield small *C* statistics and *P*-values > 0.05. Poor fitting models were improved by removing nonsignificant pathways and variables that were not significantly related to the response variables.

3.4 RESULTS

Relationships between ecosystem structure and function

Decomposition had a significant positive relationship with soil moisture ($R^2 = 0.40$, $P = 0.0063$, Fig. 3.2D) and cover of the herbaceous plant layer ($R^2 = 0.32$, $P = 0.0179$, Fig. 3.2F), but not with any other ecosystem attributes (Fig. 3.2).

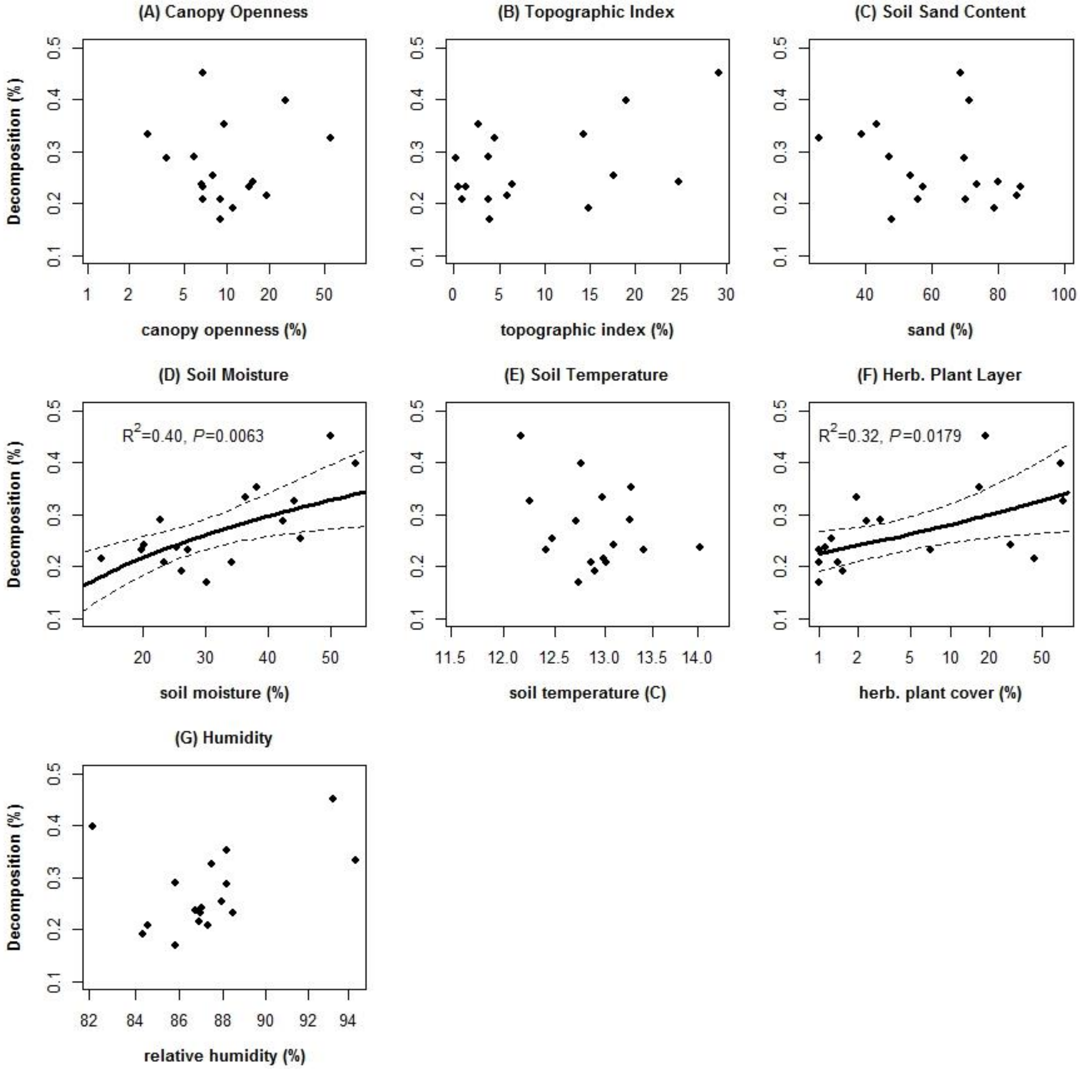


Figure 3.2 Decomposition (proportion of mass loss) and forest ecosystem attributes in restored forests. Points represent restored forest sites. Significant relationships are shown with solid lines representing the fitted values from a linear regression model, with dashed lines representing 95% confidence intervals. Ecosystem attribute values shown on the x-axis are displayed log scale if they were log transformed for the SEM.

Denitrification was significantly related to four of the ecosystem attributes we investigated (Fig. 3.3). Denitrification decreased with soil sand content (R^2 = 0.24, *P* = 0.0089, Fig. 3.3C), but increased with soil C (R^2 = 0.23, *P* = 0.0107, Fig. 3.3D). As soil pH increased denitrification rates decreased (R^2 = 0.32, *P* = 0.0021, Fig. 3.3F), and as soil moisture increased so did denitrification (R^2 = 0.59, *P* <0.0001, Fig. 3.3G).

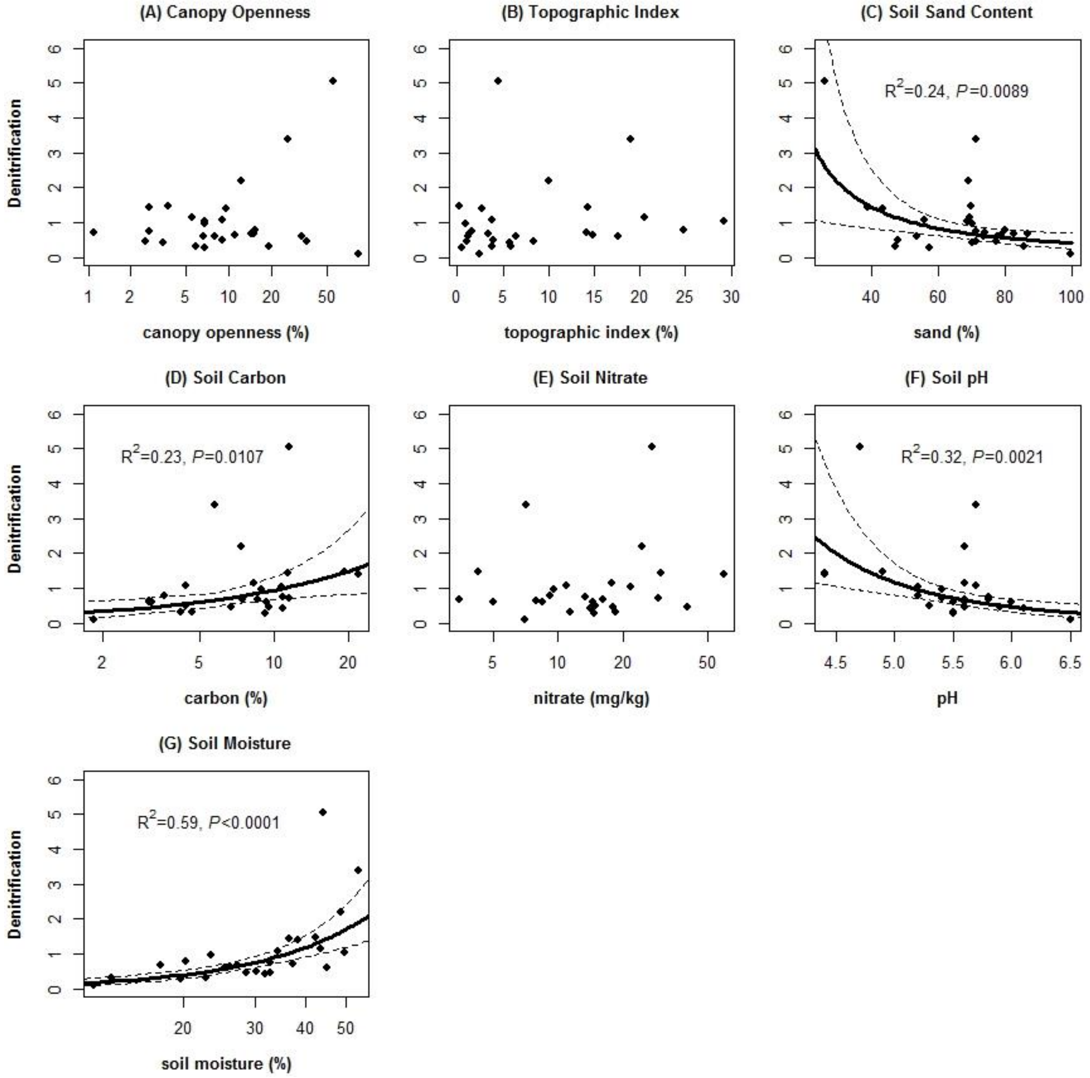


Figure 3.3 Denitrification (μg N_2O/hr/g soil) and forest ecosystem attributes in restored forests. Points represent restored forests. Significant relationships are shown with solid lines representing the fitted values from a linear regression model, with dashed lines representing 95% confidence intervals. Ecosystem attribute values shown on the x-axis are displayed log scale if they were log transformed for the SEM.

Drivers of decomposition and denitrification

The *a priori* structural equation model of decomposition and denitrification did not fit the data well (Fisher's C = 136.56, df = 88, P = 0.001; Fig. 3.1). We removed the nonsignificant pathways from decomposition to denitrification and from canopy openness to soil moisture (pathways *ix* and i*v* respectively, Fig. 3.1) and removed soil temperature, carbon and nitrate from the model because they did not explain significant variation in any response (despite some significant bivariate relationships). This new model fit the data well (Fisher's C = 59.96, df = 46, P = 0.081; Fig. 3.4) and explained significant variation in decomposition (74%) and denitrification (70%). The final model also explained variation in the herbaceous plant layer (31%), humidity (36%), soil moisture (38%) and pH (47%) (Fig. 3.4).

The final model indicates that decomposition was highest under greater herbaceous plant layer cover, higher humidity, and moister soil (Fig. 3.4). Interestingly, the bivariate relationship between forest structure, i.e. canopy openness, and decomposition is not significant (Fig. 3.2A) because canopy openness has opposing effects on the herbaceous plant layer and humidity, such that they offset one-another. In other words, initially the open canopy increases decomposition through greater herbaceous plant cover, but there is generally low humidity. As restored forests age and canopy closure occurs, herbaceous plant cover dwindles and instead it is humidity levels that positively drive decomposition.

Forest structural attributes had no effect on denitrification. Instead, denitrification was controlled by abiotic properties and was highest when soil moisture was highest and pH lowest. Soil sand content increased soil pH and decreased soil moisture, and large topographic index scores (i.e. gully landscapes) increased soil moisture.

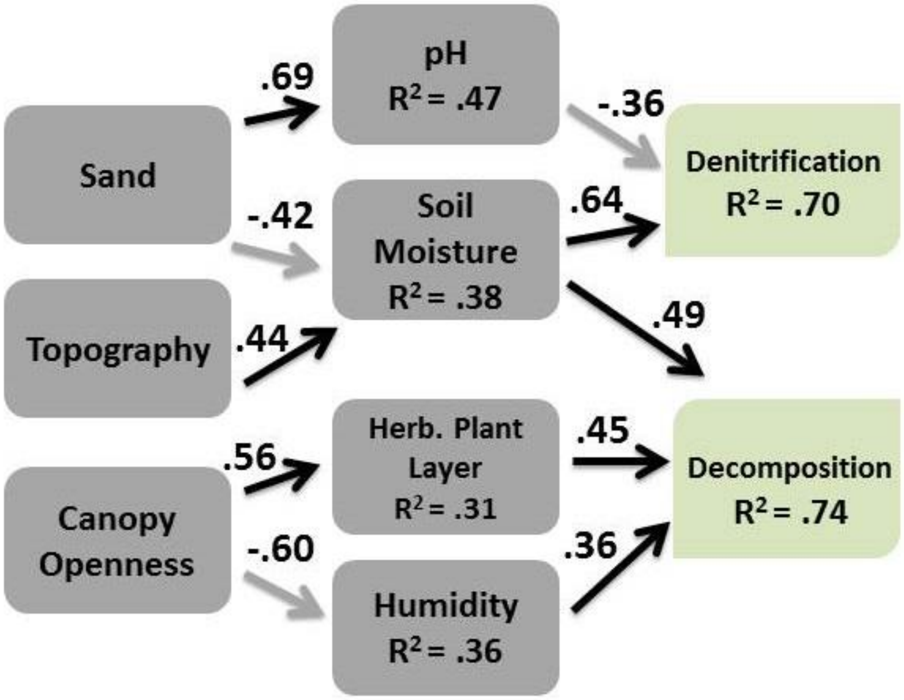


Figure 3.4 The final structural equation model (SEM), illustrating drivers of decomposition and denitrification. The ecosystem functions of decomposition and denitrification are shown in light green, and their drivers in dark grey. Values by arrows are unstandardized path coefficients. An R^2 value is shown in the box of each response variable. For clarity positive pathways are black and negative pathways are grey. This SEM fit the data well (Fisher's *C* = 59.96, *df* = 46, *P* = 0.081).

3.5 DISCUSSION

Our results expand current understanding of how restored forest structure affects decomposition and denitrification, two critical steps in C and N cycling. We observed that forest structure can be indirectly related to decomposition, but denitrification is independent of forest structure and is instead driven by the abiotic attributes of topography and soil texture. Importantly, the structural equation model illustrated that an ecosystem attribute may be a significant indirect driver of a given function, but this relationship is not readily apparent because influence occurs through two direct drivers that are offsetting one-another. Our model demonstrates that decomposition is directly driven by the ecosystem attributes of soil moisture, relative humidity and the herbaceous plant layer while denitrification is driven strictly by the belowground, abiotic properties of soil pH and soil moisture.

The offsetting of two ecological properties that are both controlled by another single ecosystem property may occur often in ecosystems, but can be difficult to identify without appropriate analysis (Grace et al. 2010). Regression analyses alone can be misleading and cause researchers to disregard important ultimate causal forces. Using regression analyses, Hall et al. (2009) found that the fraction of agricultural and urban land could predict nitrate uptake in streams, but further analysis using structural equation modelling revealed land use as an indirect driver of nitrate uptake which mediated the offsetting forces of nitrate concentration and gross primary production. It is important for researchers and practitioners alike to consider whether ecosystem attributes in their study systems may be offsetting one another. Our findings indicate that when the forest canopy is young and sparse, the flourishing herbaceous plant layer fosters decomposition, perhaps because it provides structural habitat and suitable microclimate for decomposing invertebrates and fungi (Standish et al. 2004). However, as forest canopy cover increases and herbaceous plant cover declines (Wallace et al. 2017), higher humidity develops and this instead positively drives decomposition rates. Therefore, the indirect effects of canopy cover on decomposition are mediated through offsetting effects that cancel each other out, such that the total net effect is null.

An exotic deciduous canopy could alter decomposition dynamics (Vivanco and Austin 2008) substantially by producing pulsed inputs of leaf litter and seasonal swings in sunlight levels that cause fluctuations in humidity (Wallace et al. 2017) and support a permanent herbaceous plant layer. This is concerning as the herbaceous plant layer in New Zealand forests is primarily exotic and could have long-term impacts on soil properties (Peltzer et al. 2009) and forest composition (Davis et al. 2005, Standish et al. 2001) if enabled to persist. Additionally, change in forest structure, such as a newly closed canopy and subsequent decline of the herbaceous plant layer, can affect fauna inhabiting the ecosystem. In maturing evergreen forests, a transition in the specialist decomposer community can occur when herbaceous plants senesce and instead ligneous, evergreen tree detritus sits on the forest floor (Gartner and Cardon 2004). Without restoration to native evergreen trees, this will not occur, adding to the long-term consequences for invaded forests.

Denitrification was not driven by forest structure but instead by the indirect abiotic controls of soil sand content and topography. Soil sand content regulated two direct controls of denitrification: soil pH and soil moisture. Although the negative relationship between soil pH and denitrification was somewhat unexpected, the relationship between pH and denitrification is not well understood and has many mediating factors (Šimek et al. 2002). Our results reflect the major influence that edaphic conditions and topography have on denitrification, something that should be considered on a landscape scale when making management decisions (Quesada et al. 2012).

In summary, our model suggests that restoration of urban forest structure has offsetting effects on decomposition, and no effect on denitrification. We expected that a closed canopy would foster moist soil conditions by preventing evaporation through solar irradiation, but our results illustrate that establishing canopy cover cannot be used as a technique for soil nitrogen removal. Instead, denitrification is influenced by local abiotic factors and probably large-scale drainage patterns and therefore to counter excess nitrogen resulting from anthropogenic activities we should set aside or engineer landscape features where denitrification can occur, e.g. low-lying areas with fine soil textures such as gullies and wetlands or bioreactors (Long et al. 2011). Such a targeted approach will allow imbalances in nutrient cycling to be addressed with success, and emphasizes how specific ecosystem functions can be produced by only the appropriate landscape type.

Land managers and policy makers should recognize that a range of ecosystems must be protected or restored to provide various ecosystem functions. Knowing which areas to protect can only be determined by linking specific ecosystem properties to the desired ecosystem function. Our results demonstrate that this is possible, and further, by using structural equation modelling we can uncover direct and indirect drivers and offsetting effects. Through careful assessment, it is possible to be effective in managing ecosystem functions for more resilient and healthy urban forests (Millenium Ecosystem Assessment 2005).

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CHAPTER 4

GROWTH RATES OF *BEILSCHMIEDIA TAWA* SEEDLINGS IN COMPETITION WITH AN EXOTIC WEED ARE DRIVEN BY SEEDLING HEIGHT, MULCH, AND CANOPY OPENNESS

4.1 ABSTRACT

Successful establishment of late-successional trees in restored forests is paramount to ensuring diverse and resilient forest communities. However, newly-formed restored forests often possess ground layers invaded by exotic weeds that prevent tree establishment even when light levels and microclimate are suitable. Enrichment of restored forests by planting tall seedlings can limit overgrowth by weeds, mulching provides a physical barrier to retain soil moisture while restricting weed re-growth, and removing weeds eliminates direct competition. Therefore, we hypothesized that planting seedlings at least 1 m tall and managing exotic weeds by weeding and mulching would promote tree seedling growth and survival. We also hypothesized that tree growth would depend on canopy openness, which determines light availability and microclimate in the understorey. Specifically, we predicted that trees would grow best under higher light availability, higher humidity, and warmer soil and air temperatures. We planted short (0.5 m) and tall (1 m) seedlings of the species *Beilschmiedia tawa* into mono-specific patches of the groundcover weed *Tradescantia fluminensis* and applied mulching and weeding treatments in a full factorial design with 11 blocks in six different patches of urban forest. To determine effects of management treatments and planting height on enrichment tree establishment after two years, we measured tree growth, number of leaves, mortality, and percent overgrowth by *T. fluminensis*. We also measured soil moisture, carbon, and nitrogen to see if management treatments indirectly affected plant growth by altering these properties.

Contrary to our hypothesis, weeding had no direct impact on seedlings and mulching reduced seedling growth rates. Mulch increased soil C:N, but C:N had no relationship with tree growth rates. Soil moisture was not affected by mulching or weeding, and was negatively related to seedling growth. Short seedlings had slower growth rates that were related to how overgrown they were by *T. fluminensis.* Tall seedlings grew faster, were less overgrown by *T. fluminensis,* and their growth rates were not affected by how overgrown they were by *T. fluminensis*. Seedling growth rates were positively related with canopy openness, soil temperature, and air temperature. These results indicate that for enriching forests undergoing restoration, the establishment of planted late-successional tree seedlings into *T. fluminensis* invasions is not aided by weeding or mulching, but is best facilitated by planting trees > 1 m into understoreys with appropriate microclimatic conditions.

Key words: *Tradescantia fluminensis,* forest restoration, enrichment planting, exotic weeds *Beilschmiedia tawa,* urban ecology.

4.2 INTRODUCTION

Forests undergoing restoration often require planting of late-successional tree species after formation of an early-successional tree canopy (Bertacchi et al. 2016, Overdyck et al. 2013, Suganuma and Durigan 2015, Ramos and del Amo 1992). Achieving late-successional tree establishment in restored forests signifies the crossing of an important threshold in forest dynamics (Oliver and Larson 1990). However, barriers to this step include inadequate light levels and microclimatic conditions and exotic weed dominance in the understorey (Wallace et al. 2017, Suganuma and Durigan 2015, Standish et al. 2001). Urban forests are particularly prone to microclimatic fluctuation and weed invasion that suppresses late-successional woody plant survival and diversity (Overdyck and Clarkson 2012). It is not clear which management strategies are most effective at promoting native seedling establishment over the long-term in the presence of competitive, exotic weeds (Reid et al. 2009, Cutting and Hough-Goldstein 2013).

Beilschmiedia tawa (A. Cunn.) Kirk (tawa) is recognized as a historically important and abundant tree in New Zealand North Island forests (Ogden 1985, Knowles and Beveridge 1982), but its low-altitude populations are now drastically reduced, especially in urban settings. *Beilschmiedia tawa* exhibits the classic characteristics of late-successional tree species, including a slow growth rate, extreme shade-tolerance (Carswell et al. 2012, Knowles and Beveridge 1982), need for a stable understorey microclimate (Clarkson and McQueen 2004) and provision of dense shading at maturity. Despite the necessity of an established canopy to protect *B. tawa* from frosts and desiccation while young, it grows faster with indirect light provided through small canopy gaps (Knowles and Beveridge 1982), which warm the air and soil slightly. With a reduced tree population and avian dispersal agents in decline (McEwen 1978), successful establishment techniques are needed to ensure recruitment into developing restored forests.

These obstacles are compounded by exotic herbaceous weeds, which have been shown to limit tree seedling recruitment in developing restored forests even when other conditions are appropriate (Wallace et al. 2017). The herbaceous weed *Tradescantia fluminensis* Vell. (Commelinaceae) was introduced unintentionally to New Zealand from South America in 1910 and has become a significant problem in forest understoreys (Kelly and Skipworth 1984a, Fowler et al. 2013, Esler 1962). No naturally occurring insects or pathogens in New Zealand use *T. fluminensis* (Fowler et al. 2013) and consequently the weed displays the monocultures and heightened competition typical under enemy escape (Standish et al. 2001). This exotic weed invades recovering forests and suppresses regeneration of native plants by forming a dense mat to 90 cm in height (Standish 2002), often climbing over neighbouring plants less than 0.5 m tall (Kelly and Skipworth 1984b, Esler 1962).

Control of *T. fluminenis* has been attempted with a variety of methods. Herbicides are somewhat successful (Standish 2002), but drawbacks include non-target damage and considerable expense and application issues (Kelly and Skipworth 1984b). *Tradescantia fluminensis* can regenerate from a small portion of stem material, so eradication through repeated weeding often fails (Standish 2002). The most successful approach found to limit *T. fluminensis* growth long-term is via dense overhead shading (Maule et al. 1995, Standish 2002).

Managing *T. fluminensis* populations by mulching could be successful for several reasons. To prevent competition, weeds surrounding *B. tawa* are often removed, but it is possible that clearing *T. fluminensis* from around *B. tawa* has a desiccating effect on the soil and roots. *Beilschmiedia tawa* prefers humid conditions during early growth and can experience high mortality during droughty summer periods that cause low soil moisture (Knowles and Beveridge 1982, Burrows 1999). Desiccation after weeding may be compounded as small urban forest patches have lower humidity than larger rural tracts (Miller 2011). Mulch may maintain soil moisture (Iles and Dosmann 1999, Sullivan et al. 2009) while also creating a physical barrier to weed growth (Skroch et al. 1992). Mulching may also alter soil carbon (C) and nitrogen (N), by increasing C inputs through decomposition, thus increasing the soil C:N ratio. An increased soil C:N ratio could benefit the slow-growing *B. tawa* over the nutrient-demanding *T. fluminensis* (Knowles and Beveridge 1982, Maule et al. 1995).

In this experiment, we investigated impacts of weed management treatments, tree planting height, and microclimatic conditions on *B. tawa* enrichment plantings under restored urban forest canopies. We hypothesized that planting taller trees in sites that have been both mulched and weeded would increase *B. tawa* growth rates and survival, and that greater diffuse light from canopy gaps, higher soil and air temperatures, and more humid conditions would increase *B. tawa* growth rates.

4.3 MATERIALS AND METHODS

Study Sites

Our study took place on New Zealand's North Island, which was historically 75% covered in temperate rainforest but 66% of which is now cleared for agriculture and silviculture (Nicholls 1980). Sites were located in restored urban forest patches in Hamilton, population 160,000 (37.7870° S, 175.2793° E). Hamilton has an annual mean precipitation of 1,110 mm with mean minimum and maximum temperatures of 8.7 °C and 18.9 °C, respectively (CliFlo), and 2.1% indigenous forest cover (Clarkson et al. 2007). We established 11 replicate blocks in six different restored urban forest patches that all exhibited closed canopies comprised of at least half native tree species, as estimated from % canopy cover. Ground slope was < 10 degrees at all sites and an established *T. fluminensis* infestation existed on the forest floor of each block location. The six experimental plots in each block were 1 x 1 m in size (Appendix 4.1).

Experimental Seedlings

Experimental seedlings were grown from *B. tawa* seeds all sourced from a single private bush patch off Bellevue Road in Matangi, New Zealand. Seeds were germinated together and grown in three nurseries under different conditions and care regimes. As a result, the seedlings varied distinctly in planting height and formed two groups: a short height type (n = 124, height = 40.5 ± 8.4 cm, mean ± SD) and tall height type (n = 74, height = 95.9 ± 23.9 cm, mean ± SD). All tree seedlings were hardened off together in a shade house for seven weeks before planting in October 2013, 2.5 years after germination. A random selection of one tall and two short *B. tawa* seedlings were planted in each plot, all equidistant from each other and at the same, equal distances from the plot edge.

Weed Management Treatments

The full factorial design included all combinations of two factors: weeding (unweeded, initial weeding, repeated weeding), and mulching (no mulch, mulch) (Table 4.1). The resulting six treatment combinations were applied separately to six different plots which were grouped into a block. This was replicated 11 times. Plots with initial and repeated *T. fluminensis* weeding were raked initially to clear the weed and then repeated weeding plots were hand-weeded every three months in year one and every six months in year two. Other plants besides *T. fluminensis* were also removed if they grew in the repeated weeding treatment plots. Fresh eucalyptus wood mulch was applied at the beginning of year one and fresh poplar mulch at the beginning of year two, to four cm depth each time. Mulch was held in place with netting. All plots were supplemented with nine litres of water each on once occasion during a severe drought in mid-summer of 2014.

Canopy Openness and Microclimate

Canopy openness and microclimate conditions were measured at the block level to determine impacts on tree growth. Canopy openness was measured four times (once per season) by taking hemispherical photos of the canopy from one meter above the ground in the centre of each block. Since plots were 0.5 -3 m from each other at most, it was not considered necessary to take a photo from each individual plot as the canopy would be virtually the same. Resulting images were analysed with the software Gap Light Analyzer v. 2.0 (Institute of Ecosystem Studies, Millbrook New York, U.S.A.). The average value across the four seasons was used to quantify block-level canopy openness, an index of light availability.

Soil temperature at 10 cm depth was measured every four hours for 12 months at two points equidistant from one another and the block edges using thermochrons (iButton dataloggers model DS1921G-F5, Maxim Integrated, San Jose, CA, U.S.A.) (Hubbart et al. 2005). Because of the close proximity of the plots it was not considered necessary to measure in each plot individually. Atmospheric relative humidity (RH) and air temperature (C) were measured every four hours for 12 months using hygrochrons (iButton dataloggers model DS1923, Maxim Integrated, San Jose, CA, U.S.A). Hygrochrons (one per block) were hung in radiation shields 2 m above the forest floor in the centre of each block. For RH, air temperature, and soil temperature we computed an annual mean value for each block.

Table 4.1 Variables with sampling methodologies and frequencies.

Independent Variables		
MANAGEMENT TREATMENTS	**METHODOLOGY**	**FREQUENCY**
Mulching	Two levels: mulch, no mulch	Mulch applied once annually
Weeding	Three levels: unweeded, initial weeding, repeated weeding	Repeated weeding every three mos in year one, every six mos in year two
Beilschmiedia tawa initial height	Two levels: (tall, short)	At planting
CANOPY OPENNESS & MICROCLIMATE (block-level)		
Canopy openness	Hemispherical photography	Quarterly (seasonal)
Soil temperature	Thermochron ibutton	Every four hrs (for twelve mos)
Air temperature	Thermochron ibutton	Every four hrs (for twelve mos)
Relative Humidity	Hygrochron ibutton	Every four hrs (for twelve mos)
Dependent Variables		
Beilschmiedia tawa diameter	Callipers	Two years after planting
Beilschmiedia tawa height	Measuring stick	Two years after planting
Beilschmiedia tawa leaf number	Tally clicker	Two years after planting
Beilschmiedia tawa mortality	Visual assessment	Two years after planting
Tradescantia fluminensis % overgrowth	Visual assessment, percent cover estimate	Two years after planting
Tradescantia fluminensis height	Measuring stick	Two years after planting
Carbon:Nitrogen	Elemental analysis	Two years after planting
Soil moisture	Time domain reflectometer	Every three months in year one, every six months in year two

Plant and Soil Responses

Following *B. tawa* seedling planting and application of management treatments, we monitored responses of the seedlings and *T. fluminensis*, as well as soil moisture, C, and N (Table 4.1). *Beilschmiedia tawa* stem diameter was measured at soil level with callipers and we recorded height for both *B. tawa* and *T. fluminensis*. Tree height measurements were taken without physically manipulating plants even when trees were bent sideways by *T. fluminensis* growth. Leaves on *B. tawa* trees were counted if they were green and the leaf was at least 50% intact. Trees were considered mortalities if they had no green leaves and therefore the height, diameter, and number of leaves were not measured. The percent overgrowth of *T. fluminensis* over each *B. tawa* tree was assessed from directly above the plot and was always estimated by the same person. *Tradescantia fluminensis* height was measured in the centre of each plot.

Soil samples for C and N analysis were collected by removing leaf litter and coring to 15 cm in the centre of each $1m^2$ plot. The sample was homogenized, air dried and then sieved (2 mm mesh sieve). Fine roots were then removed and samples finely ground with mortar and pestle. Soil C and N was determined using an Elementar vario EL cube (Elementar Ananysensysteme GmgH, Germany).

Soil moisture was measured at the 1 m^2 plot level using a time domain water reflectometer probe (Hydrosense CS 620 Campbell Scientific, Logan, Utah, U.S.A.). An annual mean for soil moisture in each plot was calculated.

Statistical Analysis

Using diameter and height measurements, a relative growth rate (RGR) was calculated for each living *B. tawa* seedling:

$$RGR = \frac{[\ln(D_2^2 * H_2) - \ln(D_1^2 * H_1)]}{(t_2 - t_1)}$$

where D_1 and D_2 are stem diameter at t_1 (decimal years at planting) and t_2 (decimal years at two years) respectively, and H_1 and H_2 are shoot height at t_1 and t_2 respectively (Martin et al. 2011). Rate of change in number of leaves was calculated for each tree seedling:

$$leaves = \frac{[\ln(L_2) - \ln(L_1)]}{(t_2 - t_1)}$$

where L_1 and L_2 are the number of leaves at t_1 (decimal years at planting) and t_2 (decimal years at two years) respectively. Treatment and canopy openness effects were analysed using plot-level means of the dependent variables.

First, we used two-way ANOVA to investigate mulching and weeding effects on *B. tawa* growth rate, number of leaves, mortality, *T. fluminensis* height and growth over seedlings, and soil qualities (C:N and moisture) after two years, this analysis was conducted at the plot level, n=66. To improve understanding of what affected *B. tawa* growth rates we included the environmental measurements of canopy openness, soil and air temperature, and humidity as covariates in the ANOVA model. If a factor was significant we investigated it further using a Welch's unequal variances *t*-test. All analyses were undertaken using the software

R (version 3.3.1) and considered significant at α = 0.05. We used the packages 'plotrix' (Lemon 2006) for standard error calculations.

Second, to explore relationships between the *B. tawa* growth rate and its potential drivers, we inspected bivariate plots and fitted generalized linear regression models. Potential drivers included three variables indicated in prior research to be affected by mulch presence: the soil C:N ratio (Bollen and Lu 1957), weed height, and soil moisture (Maggard et al. 2012). Prior to analysis the soil C:N ratio was natural log transformed to linearize the relationship. We also plotted light and microclimate covariates which were found to be significant in the factorial ANOVA. This analysis was conducted at the plot level, n=66.

Third, we investigated impacts at the individual tree level to see whether height-type at planting (short or tall) affected *B. tawa* growth rate. We did this by using Welch's unequal variances *t*-tests (α = 0.05). We also tested whether the proportion of a tree seedling overgrown by *T. fluminensis* affected seedling growth rate. To evaluate the relationship between *T. fluminensis* weed overgrowth and *B. tawa* growth rates we fitted separate generalized linear regression models for the short and tall height types. This analysis was conducted at the individual tree level, n=198.

4.4 RESULTS

Weeding was not a significant factor affecting *B. tawa* growth and survival, but it did reduce *T. fluminensis* height ($F_{[2,60]}$ = 146.13, $P < 0.0001$) and percent overgrowth ($F_{[2,60]}$ = 48.43, $P < 0.0001$), especially in the repeated weeding treatment. The mulch factor only impacted two responses: *B. tawa* growth rates, such that trees in unmulched plots grew marginally faster (Fig. 4.1) and soil C:N ($F_{[1,60]}$ = 4.930, P = 0.0302) where soil from mulched plots had higher values ($t_{[63.96]}$ = 2.238, P = 0.0287). There was no significant interaction between the mulch and weeding factors, or any differences in leaf numbers. The *B. tawa* mortality rate was 10.6%, and not significantly affected by either weeding or mulching.

Growth rates of *B. tawa* were not related to soil C:N or *T. fluminensis* height (Fig. 4.2A & 4.2B). However, they were negatively related to soil moisture ($F_{[1,51]}$ = 4.732, P = 0.0343, Fig. 4.2C) and positively related to canopy openness ($F_{[1,51]}$ = 9.204, P = 0.0038, Fig. 4.2D), soil temperature ($F_{[1,51]}$ = 5.779, P = 0.0199, Fig 4.2E), and marginally to air temperature ($F_{[1,51]}$ = 3.498, P = 0.0672, Fig. 4.2F).

Canopy openness ranged from approximately 4% - 17%, which enabled observation of both *B. tawa* and *T. fluminensis* responses under differing light availability.

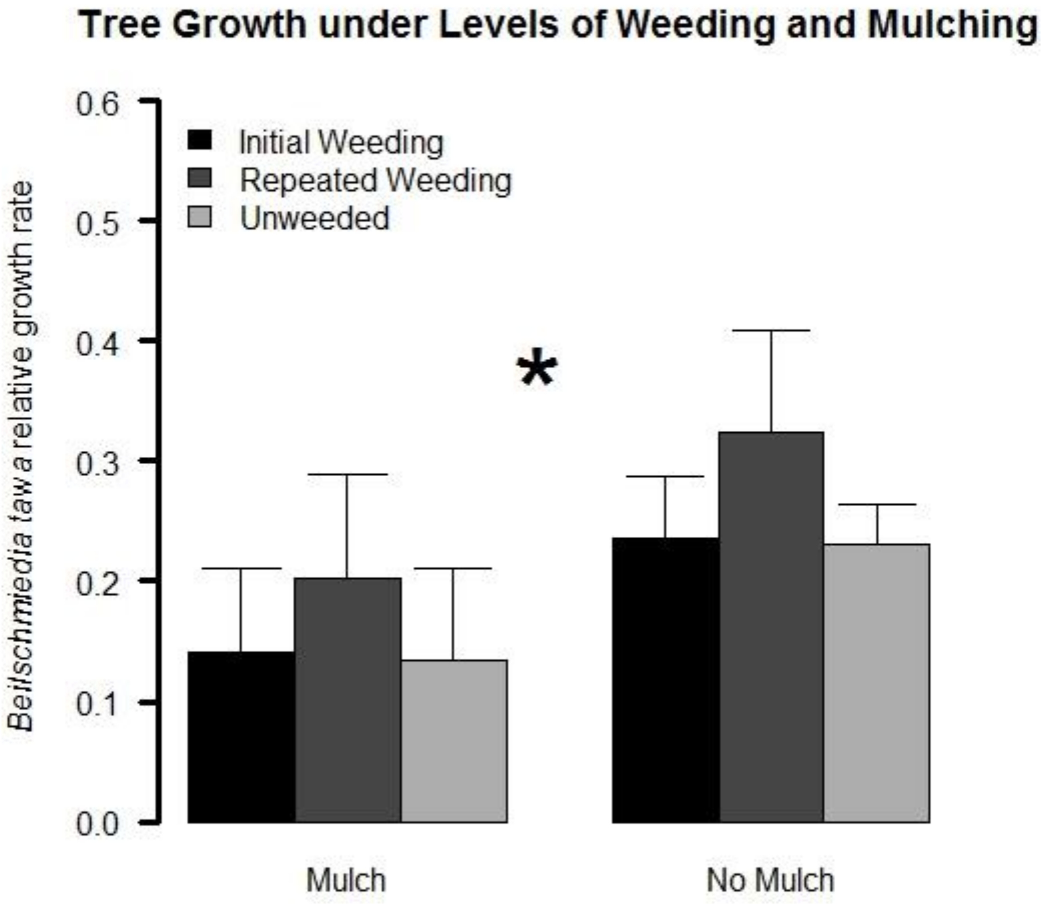

Figure 4.1 Relative growth rates of *Beilschmiedia tawa* seedlings in the full factorial treatment combinations of weeding and mulching. The growth rate was not impacted by weeding treatments ($F_{[2,55]}$ = 1.130, *P* = 0.3306), but was by mulching treatments ($F_{[1,55]}$ = 4.481, *P* = 0.0388) such that growth rates were marginally reduced in the presence of mulch ($t_{[59.23]}$ = -1.850, *P* = 0.0693). Error bars represent standard errors.

The height of the seedlings at the time of planting was significantly related to both their growth rate and what proportion of them was covered in *T. fluminensis* after two years. Trees of the tall type grew faster (Fig. 4.3A) and were less overgrown by *T. fluminensis* (Fig. 4.3B). Only the short seedlings had growth rates correlated with how overgrown by weeds they were (Fig. 4.3C).

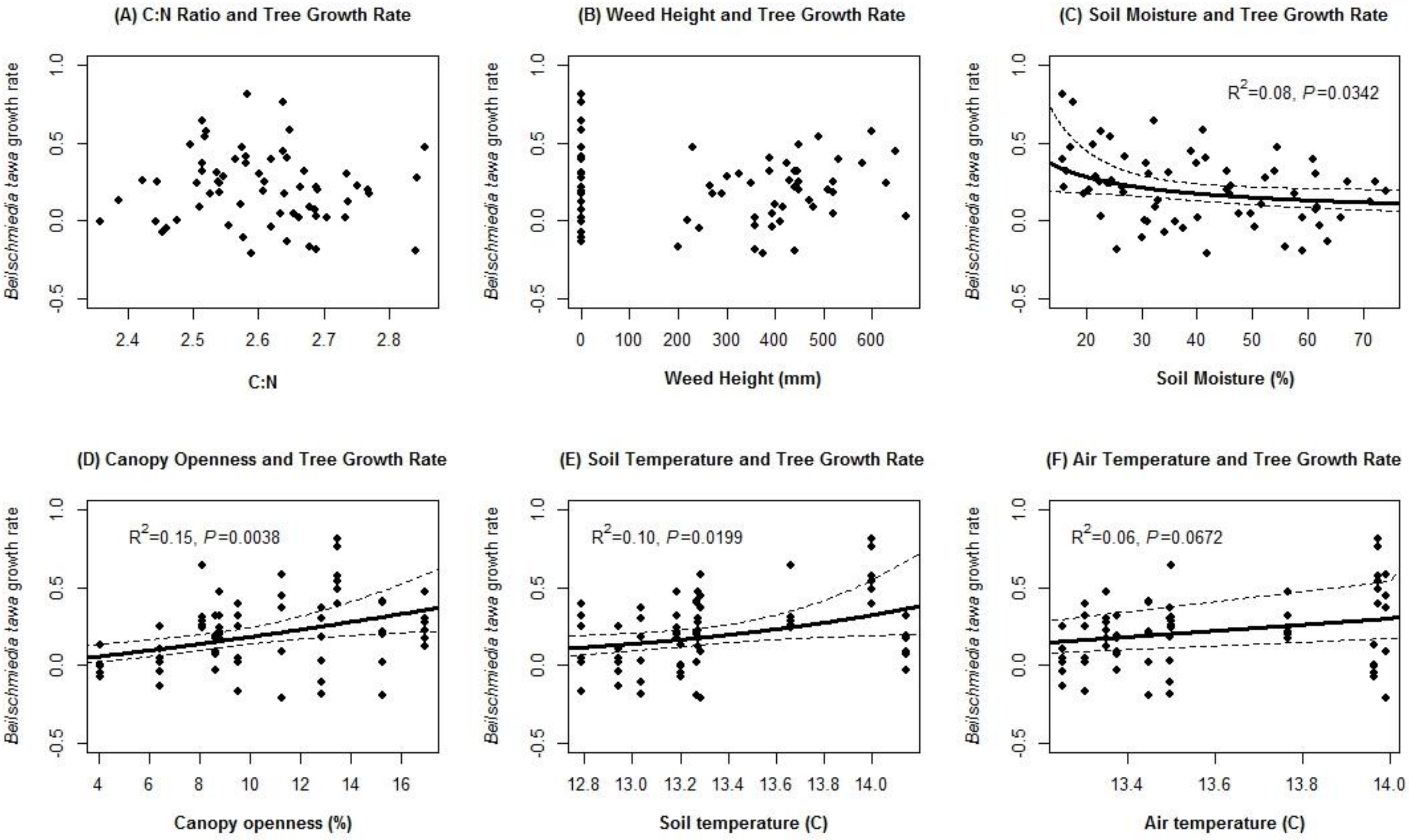

Figure 4.2 Relationships between *Beilschmiedia tawa* growth and its potential drivers, n=66. Significant relationships are illustrated with solid lines representing the fitted values from a linear regression model, and dashed lines represent 95% confidence intervals. The soil C:N ratio data is displayed log scale because it was log transformed for the analysis.

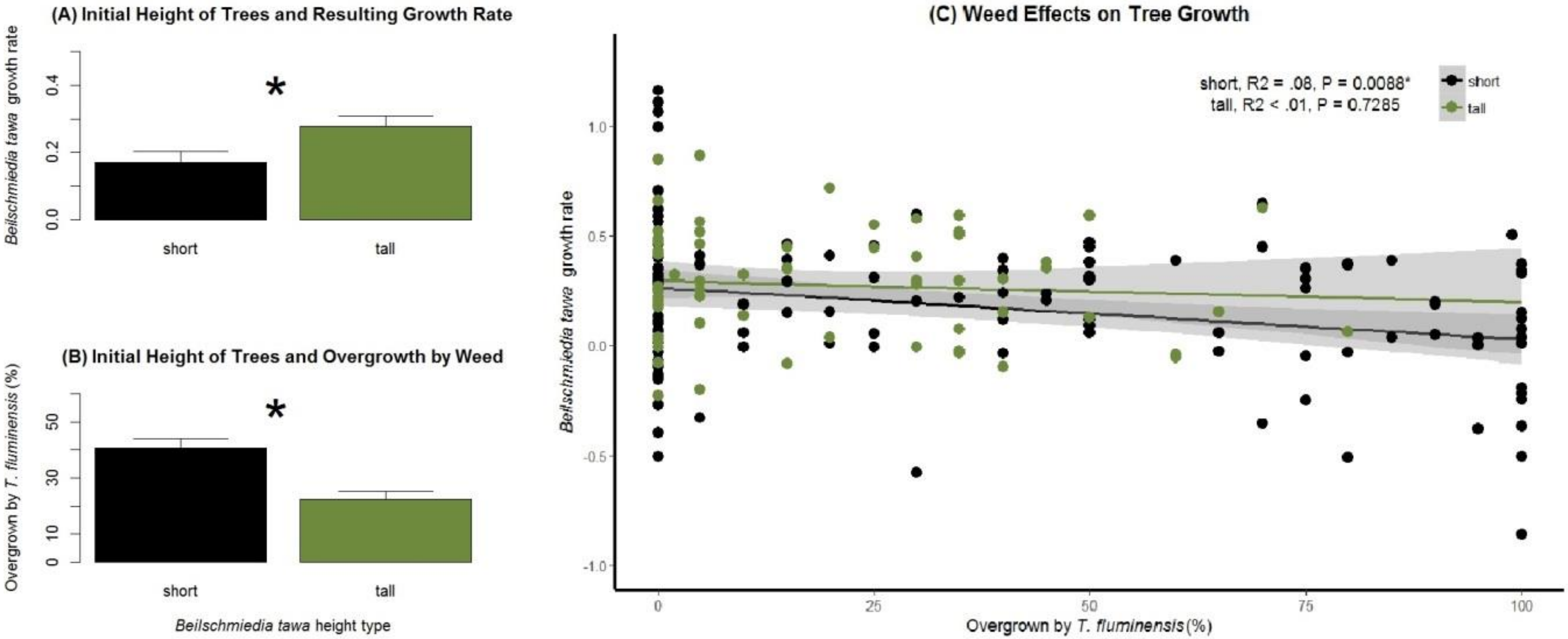

Figure 4.3 Importance of height at planting for *Beilschmiedia tawa*. (A) The tall (green) height type of *B. tawa* had a faster growth rate than the short (black) height type ($t_{71.0}$ = -7.45, *P* < 0.0001) and (B) the tall height type were less overgrown by the exotic weed *Tradescantia fluminensis* ($t_{187.9}$= 3.93 , *P* = 0.0001). (C) The short (black) *B. tawa* growth rates were negatively related to the proportion they were covered by *Tradescantia fluminensis*, while no such relationship existed for tall *B. tawa* seedlings. Error bars in (A) and (B) are standard error, the solid lines in (C) are fitted linear regression models for each *B. tawa* height type, with shaded zones indicating 95% confidence intervals.

4.5 DISCUSSION

Outcomes of this study on planting late-successional tree seedlings to enrich restored forests help increase our understanding of tree establishment and drivers of growth rates. We found that the use of mulch and weed removal did not have the hypothesized effects of increasing tree seedling growth and that, surprisingly, mulched trees grew more slowly. Growth was instead primarily driven by canopy openness and was positively related to three main properties it mediates: light, soil temperatures, and air temperatures. Additionally, results indicated that initial planting height of enrichment trees is important, and that taller trees > 1 m are beyond the reach of *T. fluminensis* and can therefore attain faster growth rates.

Standard practice in forest restoration is to control weeds after planting late-successional native tree seedlings to limit competitive interactions (McAlpine et al. 2015, Davis et al. 2005, Ramos and del Amo 1992). However, our results indicate that weeding made no difference to *B. tawa* growth rates. Similarly, Standish (2002) employed two levels of *T. fluminensis* weeding (none vs. initial) and found no effect on planted native shrub and tree seedling survival after 2.5 years. It is possible that a longer time scale may be needed to observe effects on *B. tawa* because of its slow growth (Knowles and Beveridge 1982). Alternatively, competition for nutrients and resulting *B. tawa* root growth differences may have occurred below-ground such that weeding effects were not quantified (Carswell et al. 2012). Our results allow inference about planting establishment responses of *B. tawa* trees that were already 2.5 years old at planting. Even though weeding had no effect on their growth or survival, results may be poor if attempts were made to germinate the trees from seed in the *T. fluminensis* infestation (Standish et al. 2001).

Surprisingly, mulch slowed *B. tawa* growth rates, which is contrary to other research which found mulching may increase plant survival in initial restoration plantings (Cornes et al. 2008). However, these observations were made on early-successional plantings exposed to direct sun and wind, not late-successional plantings under the shelter of canopies on moist gully slopes and bottoms. Our results may also have occurred because the mulch was too deep, which can harm newly planted trees by deterring water supply during drought and encouraging root girdling of the trunk (Gilman and Grabosky 2004). Soil from mulched plots had a higher C:N ratio, which can limit nutrient availability to plants by enabling microbial uptake of N (Robertson and Groffman 2007). However, our data rule out this possible mechanism because we found no relationship between soil C:N and *B. tawa* growth. It is also possible that either or both of the mulches used had allelopathic effects (Duryea et al. 1999). The mechanism for why mulch slowed growth rates is unclear.

Canopy openness is directly related to light availability, which plays an important role in growth of trees in the understorey (Wyckoff and Clark 2005, Berdanier and Clark 2016, Kobe 1999), even more than N availability (Finzi and Canham 2000). Bertacchi et al. (2016) found that native tree seedling growth in restored forest understoreys was hindered by lack of light availability in older restored forests compared with younger ones. *B. tawa* trees, like other late-successional species, survive in and tolerate deep shade, but minimal or no growth occurs in these situations (Bellingham and Richardson 2006). Greater canopy openness increased seedling height growth of three late-successional tree species in New Zealand montane rain forest (Bellingham and Richardson 2006). There is evidence that *B. tawa* has a very plastic growth rate response depending on light availability (Knowles and Beveridge 1982). In a stand where dominating understorey trees were removed to increase light availability, *B. tawa* growth rates changed from 5-10 cm/yr to 20-30 cm/yr (Knowles and Beveridge 1982).

Light is also a primary driver of exotic herbaceous weed growth, including *T. fluminensis* (Standish 2002). Weeds can capitalize on high light availability to outcompete neighbouring native woody species of a similar height (Ramos and del Amo 1992). Therefore, light availability and *B. tawa* growth may be positively related only to a point, and will reach a threshold where this relationship breaks down in weed-infested, high-light situations. Beyond this threshold *B. tawa* growth rates may plateau as “cheap” herbaceous weed growth overtops young trees or *B. tawa* may reach its maximum photosynthetic rate (Bazzaz 1979). While *B. tawa* growth is positively correlated with light, there are important lower and upper bounds for optimal light levels that facilitate maximum growth when trees are competing with exotic weeds.

Canopy openness also regulates forest understory microclimate conditions such as soil and air temperature (Pinheiro et al. 2013, Holl 1999, Wallace et al. 2017). We found that tawa growth was positively related to both soil and air temperatures, a relationship that is generally the case for woody plants (Lopushinsky and Max 1990, Weih and Karlsson 2001). Lemenih et al. (2004) found that canopies that were more open, in the range of 10%-20% canopy openness increased understorey soil and air temperatures, resulting in greater richness and density of colonizing woody species. Wallace et al. (2017) found soil temperature stability at around 13 °C is an important condition for late-successional tree regeneration in restored forests. Understanding the microclimate in forests undergoing enrichment planting of late-successional species will help predict whether growth will occur.

Finally, we found that the height of seedlings at planting was important when planting into exotic herbaceous weed infestations. Initial seedling height determined how overgrown by *T. fluminensis* a seedling would become as well as subsequent growth rates of a seedling. Tree size is a known predictor of growth rate (Wyckoff and Clark 2005) so it is expected that taller trees will grow faster. Our data demonstrate the advantage of planting trees at least as tall as the weeds for two reasons. First, when seedlings are the same height as weeds at planting, growth rates are greater, and second, this greater growth rate confers the ability to stay above the weeds and out of direct above-ground competition.

Our findings can be applied to improve enrichment tree establishment and growth in exotic weed-infested urban forests undergoing restoration. We conclude that the weed management treatments of weeding and mulching do not aid enrichment tree growth under established canopies. Instead, our results suggest that enrichment tree establishment success can be achieved by planting tall seedlings > 1 m into forest understoreys with appropriate light levels and microclimatic conditions. Our results indicate this to be in the range of 10% - 20% canopy openness with stable soil and air temperatures approximately 13^{o}-15^{o} C. Other work suggests (Wallace et al. 2017) that this level of canopy openness develops by about 15-20 years after initial planting in temperate forests. Since canopy openness and microclimate are difficult to manipulate, this emphasizes the importance of enrichment planting timing, when restored forest canopies are generally formed but still allow some diffuse light. At this point enrichment species should survive and grow, and may also take advantage of any early-successional tree senescence and the associated canopy gaps.

4.6 ACKNOWLEDGEMENTS

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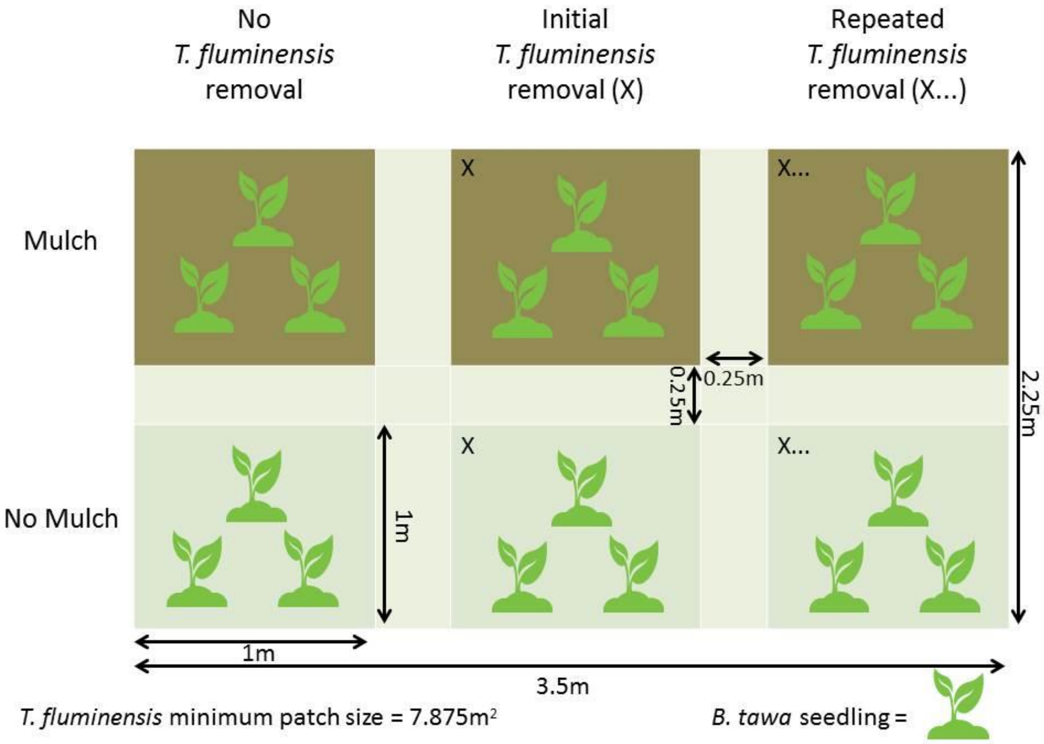
4.8 Appendix 4.1

Figure 1. The experimental design of a single block (i.e. replicate). The ground in all blocks selected for the study was covered in a pre-existing mono-specific mat of *T. fluminensis*. Two short and one tall *B. tawa* seedling were planted in each plot.



CHAPTER 5

THESIS SYNTHESIS

5.1 DISCUSSION

This thesis broadens our understanding of how restored urban forests develop after initial plantings and provides practical applications for continued management. It describes how ecosystem properties in restored lowland temperate rainforests in New Zealand change over 70 years and identifies important specific drivers and their relationship with native late-successional plant regeneration (Chapter 2). This thesis also describes relationships between nutrient cycling and restored forest structure by measuring decomposition and denitrification potential (Chapter 3). The final experiment (Chapter 4) furthers our understanding of how to effectively re-establish late successional tree seedlings in restored urban forests invaded with the exotic herbaceous weed *Tradescantia fluminensis*. Together, these three chapters emphasize the importance of restoring the canopy of urban forests and monitoring changing forest ecosystem properties over the long-term so that appropriately timed management actions can take place.

Chapter 2 demonstrated the importance of canopy openness, i.e. light availability, and its mediation of two main drivers of late-successional plant regeneration: abundance of exotic weeds and microclimatic stability. Approximately 20 years following restoration plantings canopy openness was similar to that of remnant forests, and weed cover was reduced while humidity and soil temperatures fluctuated less. Time since restoration is a major driver of success (Crouzeilles et al. 2016), and the 20-year mark has been identified in other temperate and tropical forest restoration studies (Overdyck 2014, Johnson and Handel 2016, Shoo et al. 2015), indicating it may be a generally important milestone in forest development. This chapter highlights the importance of restored forest temporal dynamics and demonstrates that some ecosystem properties have a non-linear response to restoration (Suding and Hobbs 2009). Understanding the nature of responses to restoration is crucial for management because ecosystem properties are inexorably linked (Dodd et al. 2011) such that a change in one property will trigger changes in others.

Formation of the restored forest canopy played an important role in the ecological function of nutrient cycling (Chapter 3). Canopy openness drove the decomposition rate by mediating herbaceous weed cover and humidity. When canopy openness was high, herbaceous weeds flourished and increased decomposition rates. But when canopy openness was low, humidity under the canopy was generally higher and this also increased decomposition rates. This demonstrates the importance of the canopy in addition to how a single ecosystem property may have offsetting effects on a response variable (Hall et al. 2009) by affecting intermediate variables in a counteracting manner. This dynamic would not be obvious in a regression analysis, and therefore emphasizes the necessity of appropriate statistical approaches, such as structural equation modelling (Grace et al. 2010), to understand ecosystem-wide relationships.

Chapter 3 also demonstrates that restoration of forest structure does not affect all ecological functions. Decomposition rates were affected, but denitrification potential was not, and was instead driven by abiotic landscape factors. Therefore, denitrification must be provided through engineering of landscape features like wetlands or bioreactors (Long et al. 2011). Land managers and policy makers should recognize that a variety of landscape and ecosystem types will need to be conserved or restored to provide the full array of ecosystem services needed for human health and well-being.

The degree of canopy openness and its relationship with forest microclimate continued to be a common, important theme for forest restoration when considering the growth of planted late-successional tree seedlings (Chapter 4). Tree seedlings grew at a faster rate under a small degree of canopy openness, i.e. diffuse light availability. This ranged from a relative growth rate of 0.3% - 81.2% in canopies with 4.1% - 16.9% openness, respectively. They also grew faster under warmer soil and air temperatures, all finding consistent with other research (Lopushinsky and Max 1990, Weih and Karlsson 2001). These environmental conditions dictated enrichment seedling growth while the management treatments of weeding and mulching did not. While mulching has been found helpful in establishment of early-successional species plantings in exposed conditions (Cornes et al. 2008), it may not be beneficial in more sheltered landscapes such as under the forest canopy.

Height at planting of planted late-successional seedlings was important in the presence of exotic herbaceous weeds. Tree height is typically a predictor of growth rate (Wyckoff and Clark 2005), so under weed competition it is a major factor to consider. Trees that measured 0.5 m at planting were often overtaken by weeds and had slower growth rates, but trees that were 1 m or taller stayed above the weeds and grew faster. Chapter 4 of this thesis reports the two-year results of an enrichment planting experiment but three-year measurements will be included in the intended manuscript prepared for publication.

In conclusion, this thesis addresses a gap in the literature on how to restore urban forests for the long-term. It provides novel empirical evidence that broadens understanding of how ecosystem properties of restored forests change through time. Management decisions based on information in this thesis can effectively guide ecosystem recovery toward values found in reference remnant forests. The restoration of natural areas within cities is a critically important objective for urban land managers to reconnect people to the ecosystems that sustain life on Earth (Standish et al. 2013, Pickett et al. 2011).

5.2 IMPLICATIONS FOR MANAGEMENT

This research has the following implications for urban forest management:

- In New Zealand, restoration of native evergreen urban forest is necessary to ensure exotic deciduous trees do not increase canopy openness each winter. An evergreen canopy will reduce light availability adequately to stabilize the microclimate, reduce weed growth and allow regeneration of native plant species.
- All efforts should be made to achieve rapid canopy closure of early successional plantings to encourage abiotic and biotic conditions that promote late-successional plant regeneration. This can be expected at approximately 20 years after initial plantings and at a forest basal area ≥ 27 m^2/ha. Efforts to facilitate canopy closure may include high-density plantings or weed control to maximize tree growth.

- Budgets should provide for monitoring and management for as long as possible after initial plantings so that managers are aware of changes in key ecosystem properties that constrain plant regeneration. This will allow for an adaptive management approach and most appropriate care of the restored forest, e.g. timing of enrichment plantings.
- Relationships between different ecosystem properties in developing restored forests need to be fully understood for successful management. Therefore, ecosystem properties should be monitored post-restoration and analysed appropriately, i.e. structural equation modelling, to reveal how properties affect each other and how management can be improved.
- Policy makers and managers should recognise that forest structure only affects some ecological functions, like decomposition. The function of denitrification is not related to restored forest structure or plantings in any way, and must be provided instead through conservation of low-lying, poorly drained landscapes like unmodified gullies and wetlands. This function can also be provided through creation of engineered bioreactors.
- Planting of late-successional trees into exotic, herbaceous, weed-infested forests for enrichment purposes is best achieved by using tree seedlings ≥ 1 m tall and planting into forest understoreys with appropriate light levels and microclimatic conditions. This requires identification of the right temporal and spatial windows of opportunity during forest development.

5.3 RECOMMENDATIONS FOR FURTHER RESEARCH

This research has identified the following areas for future research:

- The approach described in Chapter 2 should be replicated in more cities at different latitudes to determine whether the structural equation model identifying main ecosystem properties driving plant regeneration in Hamilton and New Plymouth holds true elsewhere.
- Aside from establishment limitations, the main barriers to seed arrival in urban forest fragments need to be identified. Restoring urban forests so that environmental conditions are appropriate for late successional plant regeneration is pointless if propagules do not arrive. By identifying any barriers, they can then be reduced or supplemental enrichment planting can

be planned for. Barriers could include shortage of fruiting adult trees, poor pollination, low patch connectivity or lack of dispersal agents.

- Additional ecological functions should be studied in relation to forest structural restoration. This information will help set specific restoration goals to achieve desired functions.
- The late successional tree seedling experiment (Chapter 4) should be monitored longer than the two years reported here as it can take tree seedlings many more years to establish and grow.
- It should be determined if below-ground dynamics are influencing establishment of planted late successional tree seedlings. Late successional trees sometimes invest substantial resources into root growth for years without much apparent above-ground growth. It would be helpful to know if this is occurring, perhaps by measuring root biomass. Research should also be done to determine if the late-successional trees are limited by lack of mycorrhizal associations.
- Analysis should be done on the optimal light availability for growth of *Beilschmiedia tawa* planted into patches of the exotic weed *Tradescantia fluminensis*. As determined in Chapter 4, *B. tawa* seedlings grow faster with higher light availability, however there is likely an upper limit where the seedling has reached maximum photosynthetic capacity. At this point *T. fluminensis* may outcompete the tree seedling with a higher photosynthetic capacity. If an optimal canopy gap size or percent light availability for *B. tawa* was identified, managers could create appropriately sized canopy light wells that minimize weed growth while encouraging *B. tawa* growth. A breakpoint analysis could answer this question.
- The late successional experiment in Chapter 4 should be expanded to include other species besides *B. tawa* to determine if all late successional trees are similar in their responses to environmental conditions and weed management techniques in restored urban forests.

5.4 LITERATURE CITED

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