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The influence of tree ferns on the composition and structure of New Zealand native forests

James Michael Robert Brock

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Biological Sciences, The University of Auckland, 2017
Abstract

Tree ferns are an abundant, ubiquitous and conspicuous feature of New Zealand’s indigenous forests, creating shady understories and substantially contributing to litterfall, amongst other effects. Previous research has hypothesized that tree ferns influence forests by suppressing the establishment of conifers in particular, and stalling successions. However, these hypotheses have not been examined, the importance of tree ferns to forest structure and dynamics in general is poorly understood, and variation in the ecological roles of different tree fern species has not been elucidated.

The aim of this thesis was to determine the importance of tree ferns to New Zealand forests, and explore the mechanisms underpinning the different distributions and roles of the different species. First, the way in which tree ferns enter ecosystems was considered through a laboratory experiment on gametophytes of three New Zealand species. Second, using field data and manipulative experiments, I compared possible mechanisms by which tree ferns might influence community composition. Finally, the effects of different tree fern abundances on forest structure over 2,500 year periods were assessed using simulation modelling.

Using an experimental approach I quantified gametophyte growth rates in varying orthophosphate concentrations and irradiance levels. These experiments suggested that gametophyte tree ferns of pioneering (*Cyathea medullaris*) and understorey (*Cyathea dealbata* and *Cyathea smithii*) species have different ecological strategies. Different gametophyte development rates suggest niche differentiation between understorey species.

Though common in the landscape in northern New Zealand, I recognised and described a successional pathway based on *C. medullaris* as a pioneer canopy with abundant *C. dealbata* in the understorey. I present correlative associations, between tree fern basal area and dissimilarities across seedling communities, indicative of tree fern biotic influence on community assembly. This tree fern successional pathway leads to forests dominated by shade-tolerant broadleaf trees, and differs significantly from successional trajectories predicted under angiosperm pioneers such as *Kunzea* or *Leptospermum*.

Observations on the effects of understorey tree ferns showed that they suppressed seedling densities by up to 50% suggesting long-term suppression of canopy species establishment. Also, conifers were present at significantly lower densities within the canopy drip-lines of tree ferns,
consistent with previous observations. Experimental manipulations removing tree fern fronds led to a consistent increase in the establishment of shade-intolerant conifers.

Using *in-silico* experiments, I showed that increasing tree fern densities was associated with increased height and age of angiosperms and conifers. Notably, increased tree fern density was associated with increased conifer persistence, contradicting assertions in the literature. Seedling suppression underneath tree ferns appeared to affect tree fern regeneration more than woody vascular plants, ultimately promoting canopy dominants over long time periods.

Overall, I conclude that tree ferns are a fundamental component of the indigenous temperate rainforests of New Zealand playing a significant role in their structure and composition. Further research on the sporophyte niche, mortality and inter-specific gametophyte competition is recommended.
Acknowledgements

I am extremely fortunate to have fantastic friends and colleagues who contributed in so many ways to my PhD through intellectual, emotional, and occasionally financial (beer/coffee/cuts of meat) support. I have crossed paths with many wonderful people and would like to acknowledge them here; to name is potentially and unintentionally to exclude, but I will do my best:

Starting with my supervisors, Bruce Burns, George Perry and Bill Lee…

Bruce, your faith in me, and excellent sense of humour got us through this process! The breadth of your ecological knowledge has always and will continue to inspire me to be a more thoughtful and questioning scientist. Your patience (in getting me up to speed on the New Zealand flora), tolerance (of me wandering into your office at all times asking ill-formed questions), and availability (for long polemic debate/rants on road-trips) has been sincerely appreciated. As to being a hands-off supervisor (remember that chat we had one year in?), you always came through, would always make yourself available, and never failed in providing support and guidance (even when the answer was right in front of me). If it’s not too sad to admit, I still recall the excitement on receiving your first email saying that you were keen to develop a research project… look where it brought us! It’s been an amazing journey, I can never thank you enough.

George, well, it’s been a wild ride. My eternal thanks to you for your empathy, introspection and multi-faceted support, not least your excellent and entirely sick sense of humour. Your mind is an amazing thing and I have near-continuous existential angst derived from the thought of trying to live up to your standards and be as capable a scientist as you are. Thank you (in no particular order) for Mount Misery, beer, discussions on ecological theory, absurdity, song, winding up Ando, coherent explanation of complexity in statistics, silliness, and the opportunity to be a lecturer. You continue to inspire me and make me want to be a better scientist.

I don’t think I can articulate here what you (Bruce & George) have given me, but at a bare minimum: Much love to you both for teaching me what it means to be a scientist, how to be a more objective thinker, and for opening up a wonderful world of plant community ecology to me. I sincerely hope that I have the privilege of working with you again.

Bill, I’d like to thank you for being so engaged from far away! Your insight and your assistance in framing my research questions in particular was invaluable. I particularly appreciate your
offer to take on half-formed ideas and manuscripts that were barely more than lists! Many thanks for your input and support.

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To Louise McMillan and Luitgard Schwendenmann who persisted in their attempts to install some semblance of an understanding of Markov chain models and soil nutrient chemistry respectively into my brain. I appreciate your time and multiple explanations a great deal; it was a pleasure to work with you both!

I had never considered being a teacher before it became a necessity. Having no stipend or research funds I needed to work to fund this PhD; the most obvious option was to take on demonstrating, then tutoring roles in the University. I started with stage 1 lab demonstrating in plant sciences and ended up teaching on courses ranging from foundation science to post-graduate landscape ecology. Many thanks to Dave Seldon for employing me first and to recommending me for other roles (and the food parcels, and gin); also thanks to Mandy Harper and Caroline Aspden for keeping the faith when I missed prep meetings and employing me for the better part of four years! Thanks also to Joe Fagan, George, Anne Gaskett, and Bruce for offering me roles that had me giving lecture series and running sections of field trips. Some of my favourite teaching moments have been in the field and I will always hold the Kauaeranga Valley and Great Barrier field trips dear. Those weeks in the bush teaching plant ecology have been a ridiculous pleasure and I will always be grateful for the opportunity to be involved. Working with students in a teaching role is a privilege, and has been an amazing experience. To the course co-ordinators, teachers and mentors who employed me to look after their charges the last four years, you have my deepest gratitude. It has been an absolute pleasure…

Outside University, my most constructive distraction was sailing with the National Maritime Museum. To Wayne MacDonald, Stuart Birnie, Simon Carryer, Peter Entwhistle, Oliver Jevons,
Jacob Corcoran, James Ashwell, Dita Donaldson, Dan Brown, Alex Newman, Mike Hannah: thank you for sharing your skills, your time, personal space on long sailing trips, and tolerating me when I made bad calls on deck. Most of all thank you for making it possible that, in the midst of a summer break from PhD work, I, navigating by the stars, could be in command of a brigantine under full sail, reaching out into the Pacific.

To Mark Gasquoine who provided food parcels; Zoe Lyle for wine; and Kate and Casey Lee who fed me and put a roof over my head for my first 3 months in New Zealand while waiting for the University of Auckland to acknowledge that I was in the country.

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Finally, to my family in the UK, with apologies for visiting only twice in five years!

I dedicate this thesis to all the people mentioned here, the people who made this PhD possible…
Publications

Chapters 2 & 4 of this thesis were prepared as papers, as allowed under the 2011 PhD Statute and Guidelines. The papers that these chapters are based on are as follows:

Chapter 2

Chapter 4
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Chapter Two: Tree fern ecology in New Zealand

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Chapter Three: Decoupling the gametophyte and sporophyte niche in Cyathea

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- Chapter Four: Pioneer tree ferns influence community assembly in northern New Zealand forests

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Chapter Five: Seedling community response to tree fern micro-site filtering

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**Chapter Six: Tree fern facilitation of gymnosperm persistence and angiosperm growth in simulated forests**

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Chapter 1

General Introduction

1.1 Of understories and tree ferns

Plants in forest understories contribute to resource heterogeneity across the forest floor through shading effects (Canham et al. 1994; Valladares et al. 2016) and litter accumulation (Molofsky & Augspurger 1992; Dar et al. 2017), driving responses in the regeneration niche (Grubb 1977; Ahlgren & Ahlgren 1981; Farris-Lopez et al. 2004). Where present in the understorey, species, such as palms and tree ferns, with strong shading and macro-litter production traits can have significant effects on the seedling community (Denslow & Guzman G. 2000; Zucaratto & dos Santos Pires 2014). Sub-canopy palms reduce seedling densities and select for seedlings of shade-tolerant species with larger seeds under their canopies (Farris-Lopez et al. 2004). Furthermore, in ecosystems where the disturbance regime has become disrupted, competitive release of opportunistic understorey species can drive recalcitrant understorey entirely suppressing canopy regeneration (De La Cretaz & Kelty 2002; Royo & Carson 2006).

The indigenous forests of New Zealand are characterised by their mixed broadleaved and conifer communities, and abundant tree ferns (Wardle 1991; Wiser et al. 2011). Tree ferns are widespread and often abundant in the forest ecosystems of New Zealand (Brock et al. 2016); however, unlike the physiognomically dominant angiosperm and conifer species in the canopy, study of the ecology of this distinctive life-form has been neglected (Wardle 1991; Wiser et al. 2011; Brock et al. 2016). This neglect is surprising as tree fern abundance alone suggests they will substantially influence forest processes. As well, being disregarded for study may have arisen because common things are often overlooked (Ogden 1991). Ogden (1991) argues that ecologists often focus on rare species because of threats to their existence, and that such a focus is often justified. However, he makes a plea for researchers to consider common species, as understanding their ecology is probably more important for wider management issues.

The tree fern life-form is an ancient structure, representative of the earliest known pteridophytes, and a common component of vegetation communities from the Carboniferous (Calder et al. 1996). The earliest example of a fern with a trunk that supports a structurally comparable stele and caudex to that expressed in present-day tree ferns is that of members of the genus Psaronius, common during the Westphalian stage (318-303 MYA), which grew to 10 m tall (Morgan 1959). Forest systems dominated by Psaronius tree ferns (89.7% of stems, > 3,850 individuals ha⁻¹;
Falcon-Lang 2006) were evident during the Mid-Pennsylvanian at densities higher than tree fern dominated communities present in the landscape today (3,200 ha⁻¹; Brock et al. 2018). The most recent iteration of a trunked fern evolved with the Cyatheales approximately 190 MYA (Korall & Pryer 2014).

Palynological and fossil records provide evidence that tree ferns were a prominent component of New Zealand’s landscape prior to separation from Gondwana 85 MYA (Cieraad & Lee 2006). The extant species of Dicksonia and Cyathea (clade Alsophila) arose during the Oligocene, with a single species (Cyathea dealbata) arising as recently as the Pleistocene (Korall & Pryer 2014). Tree ferns, of varying taxa, have therefore been a prominent functional component of New Zealand’s forest communities for the greater part of the known evolutionary history of all extant New Zealand forest-associated gymnosperm and angiosperm species. It seems reasonable, therefore, to assume some level of co-evolutionary dependencies or associations have developed among tree species co-occurring with tree ferns. This thesis aims to address the neglect around the ecology of this ancient life-form, and to contribute to filling the knowledge gap on tree ferns.

A full discussion of the ecology of contemporary tree fern species in New Zealand, accompanied by a review of their influence at different spatial and temporal scales is presented in Chapter 2, which comprises a more complete introduction to this thesis, and as a published paper is presented as a stand-alone chapter. The key questions produced by this review provided structure and focus for the research presented in this thesis:

1. Ten species of tree fern occur naturally in New Zealand; seven species of Cyatheaceae and three (two spp, two sub-spp) species of Dicksoniaceae. Species of Cyathea differentiate spatially along gradients of irradiance and temperature, whereas Dicksonia species differentiate on frost tolerance (Brock et al. 2016). The drivers of landscape-level spatial partitioning of some species, in particular C. dealbata and C. smithii, remain unclear and it has been hypothesised that gametophyte ecology may be influential (Bystriakova, Bader & Coomes 2011a). Q: How does gametophyte ecology influence sporophyte distribution?

2. Tree ferns such as Dicksonia squarrosa and C. smithii will establish on mounds produced by wind-throw of canopy trees (Adams & Norton 1991) or on soils disturbed by agriculture or landslides (Pope 1924; Blaschke 1988). Cyathea medullaris is described as having a pioneering habit, establishing in high irradiance conditions (this species is shade-intolerant; Bystriakova et al. 2011a) after large disturbance events in the North Island (Pope 1924). These
tree fern dominated pioneer vegetation communities have been rarely studied. Q: Do tree ferns function as pioneers and do they influence the assembly of specific communities?

3. Most tree ferns in New Zealand establish relatively early in succession and many persist into the understorey of mature forests (Wardle 1991; Wiser et al. 2011). Tree ferns have a number of traits that are considered likely to be influential on forest community: dense, shade-producing canopies, macro-litterfall production, allelopathic compounds in tissues, and slow decomposing, nutrient-rich litter (Froude 1980; Burton & Mueller-Dombois 1984; Enright & Ogden 1987; Gillman et al. 2004). Q: What response do seedlings have to understorey tree ferns and what influence do tree ferns have on seedling community assembly?

4. A dense understorey of tree ferns will decrease solar irradiance reaching the forest floor (Burton & Mueller-Dombois 1984; Forbes, Norton & Carswell 2016). Increased shading may either decrease the establishment rate or increase the mortality rate of seedlings of conifer species leading to a suppression of conifers underneath tree ferns (Coomes et al. 2005). Coomes et al. (2005) suggest an extension of the Bond (1989) analogy, angiosperm – conifer competition based on Aesop’s hare and tortoise fable, to include a third type – the crocodile – that represents the suppressive action of tall ferns in forests. Q: Do tree ferns function as ‘crocodiles’ in forests and do they reduce conifer persistence in mixed angiosperm-conifer forests?

5. Epiphytism on tree fern caudices by canopy dominant angiosperms is an important pathway in forest successions in New Zealand (Bellingham & Richardson 2006; Gaxiola, Burrows & Coomes 2008). Studies in the South Island have shown that up to 60% of individuals of Weinmannia racemosa in the canopy showed evidence of establishing on tree ferns (Gaxiola et al. 2008). The importance of hemi-epiphytism of canopy trees on tree ferns in the drier, upper North Island remains unclear (Richardson, Holdaway & Carswell 2014). However, processes of community assembly around epiphytism on tree ferns were not considered further in this research.

1.2 Thesis aim, objectives and outline

The aim of this thesis is to quantify whether tree ferns in understoreys significantly influence the composition and structure of New Zealand’s forest ecosystems. Building on the research questions raised in the review of tree fern ecology presented in Chapter 2, this thesis aims to:
1. Determine how environmental filters influence tree fern gametophyte establishment and possibly lead to niche partitioning among tree fern species (Chapter 3).

2. Identify how pioneering tree ferns influence community development by determining the biotic and abiotic characteristics of ecosystems that develop under pioneering stands of *C. medullaris*, and determine whether these tree ferns play a significant role in structuring plant communities beneath their canopies (Chapter 4).

3. Determine the effect of understorey tree ferns on forest structure and composition by identifying how *C. dealbata* influence angiosperm and conifer seedling regeneration, and through which mechanisms (Chapters 5 and 6).

4. Resolve the long-term effects of tree fern presence in the understorey by developing an individual-based model of forest dynamics that represents the presence and abundance of tree ferns (parameterised for *C. dealbata*), and analysing the long-term effects on forest communities from varying densities of tree ferns (Chapter 6).

The research presented in this thesis provides a body of evidence on the importance to temperate rainforest vegetation dynamics of tree ferns in understoreys. The research contains evidence from laboratory and field experiments, and a modelling approach. This research is relevant to the possible use of early successional tree fern species in forest restoration projects, and the possible manipulation of tree ferns in forest management. This work will contribute to the global literature on the ecology of this often abundant, widespread and ancient plant group on vegetation dynamics of forest communities, and more generally to understanding how understorey species may influence canopy composition and structure.

This research comprises five main components (Chapters 2 – 6):

**Chapter 2** is a literature review into the current state of knowledge of tree ferns in New Zealand incorporating, where necessary to support an argument, data from other countries. I consider the ecology of tree ferns, the significance of the ecologically separate alternate life-stages, and the influence of tree ferns both in space and in successional time in an ecosystem. Key mechanisms of influence are described and discussed; finally, potentially fruitful future research directions are highlighted and suggestions made as to key gaps in our knowledge of tree fern ecology.

**Chapter 3** examines the relative influences of varying concentrations of plant available orthophosphate and varying irradiance levels on the developmental rate of gametophytes of three common New Zealand Cyatheaceae: *C. medullaris*, *C. dealbata*, and *C. smithii*. In a
growth chamber-based experiment, I investigated whether environmental filters differentially influence gametophyte distribution and growth among species by comparing differential rates of gametophyte development across orthophosphate and irradiance gradients. I also sought evidence of inter-specific niche differentiation at the gametophyte stage (in the relative development rates across experimental treatments) to explain the environmental filtering and spatial separation of sporophytes of *C. dealbata* and *C. smithii*.

**Chapter 4** identifies vegetation patterns in the successional communities associated with either *C. medullaris* or *Kunzea robusta* (Myrtaceae; a common New Zealand pioneer), and whether the vegetation communities associated with these different pioneers are initiated by different abiotic conditions or disturbance types. I investigated compositional data from vegetation plots across the Auckland region, both existing data obtained from Auckland Council and from my own survey work. I measured slope, soil characteristics, canopy cover and a range of other biophysical properties including publicly available modelled data from Landcare Research to determine whether these abiotic factors are associated with the composition of early successional plant communities. Environmental factors and metrics of tree fern abundance were then evaluated through correlation as drivers of seedling community assembly. Finally, I considered whether spatial separation of the plots in the landscape explained differences in successional communities.

**Chapter 5** entails both field study and experimental manipulation. I studied patterns of seedling community structure and composition in relation to key abiotic and biotic variables (including adjacency of tree ferns) in the Waitākere and Coromandel Ranges. The key environmental differences present within and away from tree fern micro-sites was identified, and the influence of these micro-sites considered on angiosperm and gymnosperm seedlings. I used an experimental manipulation, set up at the University of Auckland’s forest reserves at Huapai and Oratia (Waitākere Ranges) to test the relative contributions of macro-litter accumulation and frond shading to seedling community composition and temporal turnover.

**Chapter 6** models the long-term effects of the presence and relative abundance of tree ferns in the understorey of New Zealand northern temperate rainforest. I parameterised a new growth form to add to an existing spatially explicit individual-based model (Morales & Perry, 2017) to represent a tree fern growth pattern. Three virtual experiments were undertaken to identify patterns in simulated forest structure and composition in response to: i) tree fern presence, ii)
the absence of external propagule rain (the importance of spore rain on tree fern persistence in forests), and iii) the long-term effects of macro-litterfall damage to saplings.

Finally, **Chapter 7** provides a synthesis of the research highlighting the important processes identified in the preceding chapters. Management implications of the findings, as well as suggestions for future research are provided.

Chapters 2 – 6 of this thesis were written as a series of independent papers, which have been published or are to be submitted for publication (see list of publications on page xi). The overlap in the introductions of the various chapters is a reflection of this.
Chapter 2

Tree fern ecology in New Zealand

2.1 Abstract

Tree ferns are a ubiquitous and often locally dominant element of wet southern temperate rainforests across Australasia, southern Africa and in regions adjacent to the tropics in South America. Published data on the ecology of tree ferns throughout these forest ecosystems is piecemeal, with the most comprehensive literature describing the ecology of tree ferns coming from New Zealand. Therefore using New Zealand forests as a model system, I review the ecology and importance of tree ferns for forest structure and composition. Most studies of the ecology and function of forest species in New Zealand have focussed on spermatophytes. Even though tree ferns (Cyatheaceae, Dicksoniaceae) can represent more than 50% of basal area and more than 20% of forest biomass they have been largely overlooked and quantitative information on their contribution to forest structure and function is relatively scarce. Here for the first time I synthesise information on NZ’s indigenous tree ferns published over the last 100 years and present new data on their ecology and potential ecosystem influences. Irradiance and nutrient (N, P) levels constrain development of tree fern gametophytes, with P limitation potentially influencing sporophyte production. Tree ferns establish during temporary removal of forest canopies across various spatio-temporal scales including after local disturbances, wind-throw openings of the canopy, and landslides. Members of the Cyatheaceae exhibit spatial differentiation along temperature and solar radiation gradients; the Dicksoniaceae species differentiate most strongly on their frost tolerance. Frequency / abundance of all nine understorey tree fern species indigenous to New Zealand increases with total soil phosphorus, with some niche differentiation among species along a broader nutrient gradient. Tree ferns are prominent in early and mid-successional forest communities where they may persist for >250 years. Individually, and as a group, tree-ferns impact nutrient cycling, organic matter accumulation and ground-level irradiance, often shading out tree seedlings. Tree ferns also have long-term physical impacts on the regeneration niche of associated species, with epiphytism on tree fern trunks providing alternative establishment surfaces for many species. Domination of nutrient resources by tree ferns early in succession is likely a key factor influencing community establishment. I conclude with key recommendations for future research on fundamental unknown elements of the ecology and synecology of tree ferns including greater determination of their ecophysiology and influence on forest community assemblages.
2.2 Introduction

Tree ferns are a well-established clade within the leptosporangiate ferns dominating the order Cyatheales (Korall et al. 2006; Christenhusz, Zhang & Schneider 2011). Many of these ferns have escaped the confines of the forest understorey (see Section 2.3) by evolving trunk-like structures (caudex) comprising a columnar base of adventitious roots, a root mantle, and an upper trunk of dead stipes (Roberts, Dalton & Jordan 2005; McGhee 2011). Originating from different organs, the trunks of tree ferns are also distinguished from the woody trunks of angiosperms and conifers by having a pith core surrounded by a starch-filled cortex, with the axial strength of the trunk derived from crescent-shaped vascular bundles surrounded by lignin impregnated sclerenchyma (Large & Braggins 2004). This successful life-form, which arose in the early Carboniferous (DiMichele & Phillips 2002) has enabled tree ferns to diversify across the tropics, sub-tropics and both the northern and southern temperate zones, with the greatest species richness of the (approximately) 650 taxa in the Cyatheaceae and Dicksoniaceae (Conant et al. 1995; Churchill, Tryon & Barrington 1998) in the tropical region (Large & Braggins 2004; Arcand et al. 2008; Korall & Pryer 2014). The Cyatheaceae is the family with the greatest latitudinal extent (23° N to 50° S latitude).

The forest ecosystems of New Zealand are relatively well understood (Enright & Hill 1995; Veblen, Hill & Read 1996; Wiser et al. 2011; Allen et al. 2013), and tree ferns are a dominant component of many vegetation communities (Wardle 1991) across the latitudinal range of the three main islands of this country (McGlone, Richardson & Jordan 2010), more so than in most other regions. I therefore examine tree ferns in New Zealand as a model system to understand the influence of tree ferns on forest assemblages; with literature from outside New Zealand and the southern temperate biome incorporated, where relevant, to generalise my arguments. The historic lack of natural fire in New Zealand’s ecosystems (Perry, Wilmshurst & McGlone 2014) potentially confounds comparisons with Australia and South Africa; I provide a comparison of the response of tree ferns in New Zealand’s contemporary ecosystems (where anthropic fire is now common) to that of tree ferns in other regions with higher natural fire activity.

The indigenous temperate evergreen rainforests of New Zealand (see Fig. 2.1 for illustration of main islands and sites referred to herein) include a range of mixed angiosperm (Cunoniaceae, Lauraceae, Myrtaceae, Nothofagaceae)-conifer (Podocarpaceae, Araucariaceae, Cupressaceae) communities (Ogden 1985; Wiser et al. 2011) that have a high proportion (c. 82%) of endemic vascular plant species (McGlone, Duncan & Heenan 2001). This level of endemism is mirrored
in the tree ferns, with 80% (8 of 10) of the taxa endemic (Allan 1961; Large & Braggins 2004). Tree ferns are present throughout modern New Zealand forest ecosystems, from sea level to 1500 m above sea level and from 34°S to 50°S. Only one introduced species, *Cyathea cooperi*, an Australian species first recorded growing outside of cultivation in New Zealand in 1993 (Gardner 1994), occurs, and it is currently limited to the Auckland region (Heenan *et al.* 1998).

New Zealand's modern tree fern assemblage has at least a 35 - 30 million year spore and macrofossil record (Brownsey 2001; Perrie & Brownsey 2007; Homes *et al.* 2015), and probably dates back to the Cretaceous at the generic level (Cieraad & Lee 2006). Fossils of Dicksoniaceae and Cyatheaceae are recorded from the Triassic and early Cretaceous, respectively, with the genera *Dicksonia* and *Cyathea* first appearing in New Zealand’s spore record during the Cretaceous period, around 85 – 66 mya (Cieraad & Lee 2006). The earliest records of spore-types of modern species from New Zealand are from the Paleocene (56-66 mya) for *C. dealbata* and *D. squarrosa*, Eocene (33.9 – 56 mya) for *C. smithii* and the Miocene (5.5 – 23 mya) for *C. colensoi*, *C. medullaris*, *D. lanata*, and *D. fibrosa*. These tree fern species have consequently been continually present in New Zealand forest assemblages since the Paleocene (Lee *et al.* 2012) and are, therefore, an ancient Gondwanan component of New Zealand's indigenous forest ecosystems.

Since human settlement of New Zealand, around 1280 AD (Wilmshurst *et al.* 2008), forest clearance disturbances through burning and logging have reduced the forest cover from 85% to c. 23% and significantly transformed the landscape (McGlone 1989; Perry *et al.* 2014). In addition, the introduction of invasive mammalian species has influenced the composition and structure of New Zealand forests (Atkinson 2006). Tree fern species effectively colonise recently disturbed sites such as those arising from land clearance. This pioneer role was demonstrated early in New Zealand’s European history when Captain Cook cleared an area of land at Ships Cove, Marlborough, in 1770 attempting to establish a wheat crop. The trial failed and a grove of tree ferns (species unrecorded) established displacing the wheat (Pope 1924).

Tree ferns do not play a significant role in modern forestry and silviculture in New Zealand or elsewhere; they are, however, collected for horticultural use in New Zealand (Veale 1986), and are harvested in vast numbers for export from Tasmania and Victoria to service an international ornamental market. More than 140,000 plants were imported into the United Kingdom between 1995 and 2000, and recently attempts have been made to cultivate *Dicksonia* in Australia to
provide a sustainable source of these desirable plants (Unwin & Hunt 1997; Lawson 2002; Vulcz et al. 2002).

Figure 2.1. The main islands of New Zealand including the place names of locations mentioned in the text.

Few (13) publications specifically focus on tree ferns in New Zealand forest communities, although numerous studies exist that contain other insightful information. This review provides an overview of tree fern ecology in New Zealand, with a focus on their role in forest community dynamics, as a model for southern temperate rainforests. I identify the key specific gaps in our current knowledge of tree fern ecology, highlight the significant general gap in the knowledge of tree fern ecology across the biome, and suggest how future research might fill these.
2.3 What is a tree fern?

The term ‘tree fern’ includes, but is not limited to, ferns with trunk-like structures in the order Cyatheales (Large & Braggins 2004; Korall et al. 2006; Smith et al. 2006). Taxa of the eight families that comprise this order are highly varied in habit including the inconsistent presence of a distinctive trunked form (Kubitzki 1990; Korall et al. 2006) characteristic of the Cyatheaceae and Dicksoniaceae. Confusingly, the expression of a trunk is not limited to the Cyatheales, being rarely found in other fern families (e.g. Blechnaceae) (Korall et al. 2006). Two main morphological synapomorphies have been identified for tree fern taxa: the presence of pneumathodes (pneumatophores or aerophores) and radial shoot symmetry, the latter is considered the predominant character although it is homoplastic in the Loxomataceae and Metaxyaceae (Pryer, Smith & Skog 1995; Wolf et al. 1999; Korall et al. 2006).

The trunk growth forms in tree ferns are highly variable and include creeping, ascendant and erect habits (Ward & Cranwell March 5; Large & Braggins 2004; Korall et al. 2006); tree ferns with erect forms, i.e. producing a stem or trunk-like structure are described as arborescent, and are the subject of this review. In New Zealand there are 10 native species of arborescent tree ferns (Table 2.1); this excludes one sub-species of the Dicksoniaceae, the entirely stemless Dicksonia lanata subsp. lanata (Brownsey & Perrie 2014).

Phylogenetic analysis (Korall & Pryer 2014) suggests that the Cyatheaceae could be split into four lineages at the genus level: Cyathea, Sphaeropteris, Alsophila, Gymnosphaeris. In this revised classification the New Zealand species would be placed in Alsophila with the exception of Cyathea medullaris, which would be the sole New Zealand representative of Sphaeropteris. However, this revision has not been adopted and so the nomenclature in this review follows the Ngā Tipu Aotearoa – New Zealand Plants database (Landcare Research 2014a), which places all of the New Zealand members of the Cyatheaceae in the genus Cyathea.
Table 2.1 Native arborescent tree fern species of New Zealand with recorded trunk heights and frond lengths (Allan 1961; Large & Braggins 2004; NZPCN 2013); all Māori and pākehā (European) names encountered during the review are listed for each species with nomenclature following the Ngā Tipu Aotearoa – New Zealand Plants database (Landcare Research 2014a). New Zealand tree ferns, *C. medullaris* and *C. cunninghamii* are among the tallest tree ferns globally (Large & Braggins 2004); the former has been reliably measured at 19.6 ± 0.6 m in the Kauaeranga Valley, Coromandel (Brock Unpublished).

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Max Recorded Height (m)</th>
<th>Max Frond Length (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cyathea colensoi</em></td>
<td>Grove-fern, stemless, rough, mountain or creeping tree fern</td>
<td>≤1</td>
<td>1.5</td>
</tr>
<tr>
<td><em>C. cunninghamii</em></td>
<td>Ponga, pūnui, guily or slender tree fern</td>
<td>20</td>
<td>3</td>
</tr>
<tr>
<td><em>C. dealbata</em></td>
<td>Ponga, puna, kāponga or silver fern</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td><em>C. kermadecensis</em></td>
<td>Kermadec tree fern</td>
<td>20</td>
<td>4</td>
</tr>
<tr>
<td><em>C. medullaris</em></td>
<td>Mamaku, kōrāu, katātā, pītāu, black mamaku or black tree fern</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td><em>C. milnei</em></td>
<td>Milne’s tree fern</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td><em>C. smithii</em></td>
<td>Kātote, whē, neineikura, ponga, soft or Smith’s tree fern</td>
<td>8</td>
<td>2.5</td>
</tr>
<tr>
<td><em>Dicksonia fibrosa</em></td>
<td>Kuranui-pākā, kurfākā, pūnui, tūkirunga, wekī, wheki, wheki-ponga, wheki-kōhunga, wheki-kōhoonga, wheki-ponga or golden tree fern</td>
<td>10</td>
<td>3.6</td>
</tr>
<tr>
<td><em>D. lanata</em> subsp. <em>hispida</em></td>
<td>Tūōkura, tūākura, woolly or stumpy tree fern</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><em>D. squarrosa</em></td>
<td>Atewheki, pakue, pēhiakura, tio, tirawa, tūākura, tūōkura, urururuhenua, wekī, wheki, rough, hard or harsh tree fern</td>
<td>8</td>
<td>3</td>
</tr>
</tbody>
</table>

### 2.4 Autecology of New Zealand’s Tree Ferns

#### 2.4.1 Spore dispersal and viability

Tree fern sporophytes produce abundant small spores that are readily wind dispersed, with spore sizes for the New Zealand *Cyathea* species range from 39 - 49 μm (Braggins & Large 1990). Conant (1978) estimated that a mature *Cyathea arborea* could produce 492,800 spores annually.
Tree ferns are therefore capable of colonising most habitats and are unlikely to be dispersal limited; McGlone et al. (2010) showed that tree ferns have the largest ranges of all the New Zealand forest species. Spores are either dispersed by sporangial dehiscence or are retained in sporangia, which themselves detach from the fronds, and the spores undergo intrasporangial development adjacent to the parent plant providing for persistence in suitable habitat (Gaston 1974; Conant 1978).

Conant (1978) describes the volume of sporangia-captured spores of a single 8 m tall Caribbean tree fern *Cyathea arborea* as being densest (per unit volume of air) up to 7.5 m from the sporophyte. Released free spores, in contrast, had a uniform density between 7.5 and 30 m (the most distant measurement) from the source plant (Conant 1978). A study of hand-released Osmundaceae and Dryopteridaceae spores (54 and 45 μm respectively) in a forest habitat (Raynor, Ogden & Hayes 1976), recorded dispersal distances up to 100 m in regularly spaced spore traps. Peck et al. (1990) caution that estimates of dispersal ability in pteridophytes cannot be translated between taxa solely on the basis of size or mass of spores as such extrapolation overlooks potentially important dissimilarities in fecundity, habitat requirements, mating systems and gametophyte ecology. As New Zealand tree fern spores are similar in size (see above), and are released from similar heights (Table 2.1) it is suggested that they may be dispersed over comparable distances in a mature forest, and significantly greater distances in open vegetation.

The ability of tree ferns to successfully establish at long distance, however, has not been quantified. Korall and Pryer (2014) suggest that there is evidence for a causal relationship between breeding system and ploidy level (the requirement for outcrossing in diploids versus the ability to self in polyploids) with the success of long distance dispersal (distance not quantified) in Cyatheaceae. Successful dispersal over long distances is shown by a recent range expansion in *Gymnosphaera* (a group including tetraploid species) from South America into south-east Asia, compared to the dispersal of the proposed genus *Sphaeropteris* from Australasia into south-east Asia which, by their timings (43-36 MYA), are most likely a product of vicariance (Korall & Pryer 2014).

Spore viability ranges from two months (*Cyathea delgadii*) to 13 months (*C. caracasana, Dicksonia sellowiana*), from species native to tropical regions of the Americas, compared to up to 22 years for the Australasian *Dicksonia antarctica* (Lloyd & Klekowski 1970; Goller &
2.4.2 Conditions Required for Colonisation – Establishment Events

Little is known about either the establishment requirements of tree fern gametophytes or the conditions required for sporophyte development. Reis Moura et al. (2012) suggest that phosphorus is important for gametophyte development and sporophyte production. Small-scale (<25 cm²) disturbance, such as removal of leaf litter and soil exposure / scarification, is important for the gametophytic establishment of terrestrial tropical fern species (Watkins Jr, Mack & Mulkey 2007), and is also necessary for the successful establishment of temperate species (Cousens 1981). Therefore, physical disturbance of soil surface may create a competition-free habitat, exposing extant spores in the soil, facilitating germination and tree fern dominance for decades if not centuries.

Cyclonic and tectonic disturbances are major drivers of regeneration in New Zealand forests, frequently inducing landslides and areas of wind-throw (Blaschke 1988). Blaschke et al. (1992) described vegetation colonisation following landslides in Taranaki over a 25 to 40 year period during which the vegetation community was initially dominated by Dicksonia squarrosa and Cyathea smithii. Wassilieff (1986) and Smale et al. (1997) examined post-landslide successions in the drier East Cape region (half the annual rainfall of inland Taranaki; 1100 vs 2250 mm yr⁻¹ respectively) dominated initially by Kunzea robusta alongside Cyathea dealbata and Cyathea medullaris; these latter two species are more drought tolerant than those recorded colonising the wetter Taranaki disturbance sites.

Studies into wind throw of forest trees describe D. squarrosa and C. smithii dominating canopy gaps for up to 30 years after initial ground fern cover, which lasts approximately two years (Adams & Norton 1991). Studies of sites around fallen podocarps in Pureora Forest, west of Lake Taupo, have shown that these areas are rapidly colonised and dominated by D. squarrosa (Beveridge 1973), which commonly establishes rhizomatously (Dingley 1940). C. medullaris will gradually colonise Paesia scaberula and Pteridium esculentum fernland, weakening the fern canopy and permitting the establishment of seedlings of shrub and canopy species (Silvester 1964; Wardle 1991). Similarly, D. squarrosa establishes in level, fallow P. scaberula dominated pastureland, and forest succession initiates from ‘islands’ of the tree ferns (Silvester 1964). This pattern contrasts with those that result in communities dominated by tree ferns (basal area in
excess of 21.1 m² ha⁻¹), which are thought to have an inhibitory effect on succession (Walker et al. 2010; Richardson et al. 2014).

Figure 2.2. Dense *Cyathea medullaris* stand in the Hūnua Ranges south-east of Auckland established after plantation forest removal

The disturbance created after logging of forestry plantations in New Zealand (generally *Pinus radiata*) may also result in the development of stands of *C. medullaris* (Fig. 2.2) with an associated shrub community of *Melicytus ramiflorus*, *Hedycarya arborea*, *Geniostoma ligustrifolium* and *Knightia excelsa* (Clarkson 1986). Although *C. medullaris*, *M. ramiflorus*, and *G. ligustrifolium* have been recorded in *P. radiata* plantation understoreys (Ogden et al. 1997; Forbes et al. 2016), Australian studies indicate that tree ferns struggle to survive clear-felling events, and that regeneration of tree ferns is lower in these conditions than after natural disturbances (Ough & Murphy 2004), indicating that *C. medullaris* would likely re-colonise after each rotation in plantation forests. Nevertheless, these observations still emphasise the role of tree ferns in pioneering communities.
Low intensity fires can lead to localised tree fern dominance because their apical growing stem are protected by a tight cluster of leaf primordia, allowing resprouting after burning (Ough 2001) (Fig. 2.3). Pope (1924) and Wardle (1991) both record tree ferns re-shooting after fire in New Zealand, with similar recovery recorded in Australian tree ferns (Ough 2001). Ough (2001) also reports a greater abundance of Cyathea australis and Dicksonia antarctica in in forests regenerating after wildlife than after clear-felling in southeast Australia. In contrast Watson and Cameron (2002) recorded Cyathea capensis in South Africa as experiencing high levels of mortality in response to fire, with juveniles (< 150 cm height) as most susceptible. Tree ferns are fire-prone and are categorised as moderate-high flammability by the New Zealand Fire Service, indicating they will burn readily during moderate to high forest fire danger conditions and partially ignite during moderate conditions (Fogarty 2001). This flammability is due to heavy accumulations of litter, elevated dead material and flammable green foliage on tree ferns (Fogarty 2001). A physical assessment of frond material by Wyse et al. (2016) comparing plant
Trait flammability ranked *C. medullaris* as moderate, *C. dealbata* as moderate-high and *D. squarrosa* as having high flammability.

### 2.4.3 Gametophyte ecology

Little is known about the gametophyte ecology of tree ferns. The germination period for tree fern spores varies among species from a few days to several months whereupon they rapidly produce rhizoids, prothalli and become sexually mature within four months (Goller & Rybczyński 1995; Kuriyama, Kobayashi & Maeda 2004; Reis Moura *et al.* 2012); *in vitro* studies have shown that the length of time before a sporophyte is produced varies significantly (from 4 to 14 months) among species (Goller & Rybczyński 2007).

Stokey (1930) found that under lower light levels (specific irradiance levels not described), the structure of the gametophytes of *Cyathea dealbata*, *C. medullaris* and *C. smithii* are ameristic (i.e. become elongated and produce antheridia and archegonia at separate times, rarely progressing beyond the antheridial stage; the sex organs will be located terminally or laterally on the prothallia, rather than at the normal ventral location) reducing the chance of sporophyte production. Macro-nutrient availability also appears to affect the growth rate and pattern of tree fern gametophytes (Stephenson 1907; Stokey 1930; Kuriyama *et al.* 2004; Goller & Rybczyński 2007; Reis Moura *et al.* 2012), however the response to specific nutrients remains unknown. Evidence of possible nutrient requirements of gametophytes is suggested by the distribution of the sporophytes on young, alluvial or volcanic soils (Aston 1916; Wardle 1991; Walker & Aplet 1994; Coomes *et al.* 2005). However, extrapolating from the conditions supporting a mature sporophyte to those relevant for gametophyte ecology could be misleading as different biotic and abiotic filters may be involved.

### 2.4.4 Sporophyte ecology

Tree fern species are typically associated with fertile or semi-fertile soils over a range of hydrological conditions, slope, soil stability, forest-type or successional stages. However, a quantitative assessment of the environmental and biotic factors controlling tree fern distribution has not been undertaken. Correlative species distribution models suggest that the macro-scale distribution of tree ferns across New Zealand is largely determined by temperature (mean annual temperatures of 1.5 – 15.9 °C) and solar radiation (11.7 – 15.3 MJ m⁻² day⁻¹) (Brownsey 2001; Lehmann, Leathwick & Overton 2002). The growth and reproduction of Australian tree ferns *C. australis* and *D. antarctica* have been consistently associated with temperature and
precipitation (Forest Practices Authority 2012; Syfert, Smith & Coomes 2013; Fedrigo et al. 2014).

Some New Zealand tree ferns are exceptionally cold-tolerant compared to most other tree fern taxa (Bystriakova, Schneider & Coomes 2011b). For example, at Port Ross in the sub-Antarctic Auckland Islands (50°32'42"S 166°13'38"E) the southernmost populations of *C. smithii*, the tree fern with the highest latitudinal extent, experience a mean daily temperature of 2.9 °C during winter (de Lisle 1965). New Zealand’s tree ferns also show interspecific elevational habitat preferences (as a function of climate; Figs. 2.4a – d), with the species distribution along latitudinal and elevational gradients suggesting that temperature is a major niche discriminator. This pattern is most clearly seen in *Cyathea*, (Fig. 2.4a) with the upper elevational limits set by a minimum mean temperature of -4.9°C.

While *Dicksonia* taxa do not appear to be differentiated by temperature preference, niche differences appear more strongly in relation to solar radiation, and it is likely that localised environmental factors, such as frost, also influence the location of *Dicksonia* both in the wider landscape and in relation to vegetation structures. Frost tolerance has been recorded for juvenile *Dicksonia fibrosa* (-8°C), which is considered one of the more hardy New Zealand species, and can tolerate temperatures lower than *Cyathea smithii* (-4.2°C) (Warrington & Stanley 1987; Wardle 1991; Bannister 2003). *Dicksonia fibrosa* will survive temperatures as low as -8 °C but not below -11 °C (Warrington & Stanley 1987) and the species establishes and grows in edge habitat in elevated areas. The foliar frost resistance temperature for *D. squarrosa* is -6.5 °C (Bannister 2003).

Lehmann et al. (2002) noted maximum tree fern diversity on steep slopes or on landslides; whether this is a product of soil conditions, light availability or simply site turnover is uncertain. Aston (1916) described *C. dealbata* as being prominent in developing scrub in steep volcanic ash ravines around Mount Tarawera. *C. colensoi*, *C. smithii* and *D. squarrosa* have also been associated with slopes supporting fertile soils (Wardle 1991).

Community structure on chronosequences at Waitutu (291 000 y), Haast (6 500 y) and Franz Josef (120 000 y), in South Island, New Zealand suggested a negative correlation between substrate age (and P availability) and the presence of tree ferns (Coomes et al. 2005; Richardson et al. 2005; Turner et al. 2012; Jangid et al. 2013). The youngest sand dune at the Haast chronosequence supported a community with *D. squarrosa* and *C. smithii* contributing 17-31% of the basal area.
Figures 2.4a-d. Presence-only distribution data (from GBIF.org, 3rd August 2015) of the New Zealand tree fern species: (a) Cyathea spp., (b) Dicksonia spp.; with mean annual temperature (c) and solar radiation maps (d) as key drivers of fern diversity in New Zealand (Lehmann et al., 2002). The grey histograms adjacent to (c) and (d) represent the mean of each column and row in the diagrams to emphasis overall trends. Figures (a) and (b) have been derived using presence-only data therefore any apparent distinctions between the distribution of the tree fern species should be treated with caution as no corrections have been made for sampling bias (Syfert et al. 2013).
However, these species were almost entirely absent from older dunes (Turner et al. 2012; Turner, Wells & Condron 2014), with tree ferns occurring only in those areas with relatively higher total phosphorus (181 year old dunes with 885 mg P kg$^{-1}$ vs. 4,422 year old dunes with 492 mg P kg$^{-1}$). Coomes et al. (2005) recorded a strong positive relationship ($r^2 = 0.78$ and 0.58, respectively) between basal area (m$^2$ ha$^{-1}$) of $C. \text{smithii}$ and $D. \text{squarrosa}$ and total soil phosphorus. Furthermore, Coomes et al. (2013) suggest that $C. \text{smithii}$ is a nutrient-demanding species, whereas $D. \text{squarrosa}$ is a relatively low-nutrient tolerating tree fern species. This inference is supported by the forest community pattern along the Franz Josef chronosequence (Doblas-Miranda et al. 2008) where $D. \text{squarrosa}$ was on older soils (60,000 years with soil C:P of 567.1) than $C. \text{smithii}$ (250 years with soil C:P of 186.2), with both species absent from older successional communities (120,000 years with soil C:P of 743.3). Jangid et al. (2013) confirmed that tree fern basal area and total P were correlated along the Haast chronosequence. Combined, these studies support the conclusion that tree ferns are generally nutrient demanding, particularly in relation to phosphorus, with considerable inter-specific variation in nutrient niche breadth.

Both $D. \text{squarrosa}$ and $C. \text{medullaris}$ have been associated with boggy conditions (Dingley 1940; Wardle 1991). $D. \text{squarrosa}$ is found in transitional communities between oligotrophic lowland mires and forest in Fiordland (Wardle 1991). By comparison, $C. \text{dealbata}$ is generally associated with free-draining soils (Pope 1924; Wardle 1991). Areas with poor drainage in Dacrycarpus dacrydioides – Weinmannia racemosa forest remnants in Westland (South Island, NZ) support $D. \text{squarrosa}$ and $C. \text{smithii}$ in greater abundance than drier patches of similar forest types (Miller, Norton & Miller 2004). A similar trend was observed around the Typha orientalis swamps in the Waitotara and Wellington districts for $D. \text{squarrosa}$ (Pope 1924); however, specimens were showing signs of deterioration, e.g. short, wasted fronds, and appeared unable to survive with waterlogged roots. $C. \text{medullaris}$ has been recorded both in bogs (Dingley 1940) and dry forests (Pope 1924) suggesting a tolerance for a range of moisture conditions. The Australian Dicksonia antarctica has a broad ecological niche and is capable of surviving in environments with a range of water supply conditions and evapotranspirational demands (Hunt et al. 2002). Hunt et al. (2002) identified extremely conservative water use, and the potential for the fronds of $D. \text{squarrosa}$ to intercept rainfall and guide this water supply to adventitious roots at the stem apex as traits supporting this broad moisture tolerance.

Sporophyte distributions in NZ tree ferns also appear to be associated with irradiance gradients in forest and scrub communities (Table 2.2); this light response is also observed in Australia for
*C. australis* and *D. antarctica* (Forest Practices Authority 2012). Bystriakova *et al.* (2011a) reported that *C. dealbata* and *C. smithii* have near identical sporophytic demographics and leaf physiology, yet analysis of relative densities of the two species, in 30 × 30 m survey plots, indicates that they are spatially distinct in the landscape. Niche differentiation for these species may occur at the gametophytic stage (Bystriakova *et al.* 2011a). Experimental testing of growth and responses of gametophytes to controlled light conditions would address this hypothesis.

**Table 2.2** Forest type and structural position in which sporophytes of the New Zealand tree ferns have been recorded, along with maximum estimated age of sporophytes (ages reported by Bystriakova *et al.* (2011a) estimated by monitoring growth of tagged individuals over a 28 year period).

<table>
<thead>
<tr>
<th>Species</th>
<th>Position in forest</th>
<th>Vegetation Association</th>
<th>Max. Age</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cyathea colensoi</em></td>
<td>Sub-canopy / edge</td>
<td>Forest / alpine scrub</td>
<td>-</td>
<td>1, 7</td>
</tr>
<tr>
<td><em>C. cunninghamii</em></td>
<td>Sub-canopy</td>
<td>Gully forest</td>
<td>155</td>
<td>1, 2, 7</td>
</tr>
<tr>
<td><em>C. dealbata</em></td>
<td>Sub-canopy / edge</td>
<td>Forest / lowland scrub</td>
<td>250</td>
<td>1, 3, 4, 7</td>
</tr>
<tr>
<td><em>C. kermadecensis</em></td>
<td>Sub-canopy</td>
<td><em>Metrosideros kermadecensis</em> forest</td>
<td>-</td>
<td>1, 7</td>
</tr>
<tr>
<td><em>C. medullaris</em></td>
<td>Canopy / edge</td>
<td>Disturbed ground / lowland scrub / tree-fall gaps / early succession remnant</td>
<td>100</td>
<td>1, 3, 5, 7</td>
</tr>
<tr>
<td><em>C. milnei</em></td>
<td>Sub-canopy</td>
<td><em>Metrosideros kermadecensis</em> forest</td>
<td>-</td>
<td>1, 7</td>
</tr>
<tr>
<td><em>C. smithii</em></td>
<td>Sub-canopy / edge / canopy</td>
<td>Forest / scrub</td>
<td>250</td>
<td>1, 3, 4, 7</td>
</tr>
<tr>
<td><em>Dicksonia fibrosa</em></td>
<td>Canopy / edge</td>
<td>Scrub / forest</td>
<td>-</td>
<td>1, 3, 6, 7</td>
</tr>
<tr>
<td><em>D. lanata</em> subsp. <em>hispida</em></td>
<td>Sub-canopy</td>
<td>Kauri Forest</td>
<td>-</td>
<td>1, 7</td>
</tr>
<tr>
<td><em>D. squarrosa</em></td>
<td>Canopy / edge / sub-canopy</td>
<td>Disturbed ground / open scrub / forest</td>
<td>155</td>
<td>1, 3, 4, 6, 7</td>
</tr>
</tbody>
</table>


Extrapolation of ecological requirements based on current distribution in the landscape may also be confounded by actions of non-native pest species in New Zealand modifying tree fern distributions. Evidence of tree fern browsing by native New Zealand fauna is limited to coprolites of extinct upland moa (*Megalapteryx didinus*) that contain spores of *Cyathea colensoi* (Wood *et al.* 2012). However, tree ferns are browsed by several introduced vertebrate herbivore
species that affect their abundance locally (Mark, Baylis & Dickinson 1991; Nugent et al. 2002; Smale et al. 2008). *C. medullaris*, and to a lesser extent *C. smithii* and *D. squarrosa* are palatable and susceptible to brushtail possum (*Trichosurus vulpecula*) feeding (Ogden & Buddenhagen 1994; Nugent et al. 2002). Direct browsing is less important that the indirect effect of competitive release of *C. dealbata* and *C. smithii* in the Orongorongo Valley (Fig. 2.1), the frequency of these species increased after brushtail possum browse removed dominance of more palatable species in the canopy (Campbell 1990). Continued presence of brushtail possums in the area would transition the forest assemblage into a tree fern-shrub community (Campbell 1990; Richardson et al. 2014). *C. colensoi* and *D. squarrosa* are susceptible to browsing by ungulates, and where these herbivores are abundant, tree ferns may die off (Veblen & Stewart 1980; Mark et al. 1991; Wardle 1991). However, *D. squarrosa* can resprout after disturbance (Martin & Ogden 2006; Smale et al. 2008), which provides it with an advantage over the other tree fern species.

2.4.5 Influence in Space – Abundance of Tree Ferns in Forest Associations

Tree ferns are abundant in New Zealand’s forest systems and can represent a significant proportion of the forest community in number of individuals (28-62%), basal area (2.3-41.7%) and biomass (3.8-21.0%) (Table 2.3). These data confirm that tree ferns are prominent in early successional communities in all of New Zealand’s forest types and the understorey of forest plantations (a list of vegetation communities with which tree ferns are associated can be found in Appendix 1). Similar levels of total biomass have been recorded from the tropical montane forest systems of Puerto Rico where *Cyathea bryophila* and *C. arborea* represented 33% of the biomass of a site of post-disturbance regeneration (Weaver 2008).

2.4.6 Influence in Time – Tree fern growth rates and survival

Tree fern growth rates vary between species and also with changes in light environments/successional stage, elevation and latitude (Table 2.4). The fastest growing tree fern species in New Zealand is *C. medullaris* (height increase of 18 cm yr⁻¹ on the central highlands of the North Island); the growth rates of all species increase with decreasing latitude and increasing mean annual temperature.

Unpublished tree fern height data collected over a 34 year period from repeat-measure vegetation plots in the Kauaeranga Valley near Thames, provides long-term height growth rates for *C. dealbata, C. smithii* and *D. squarrosa* (Table 2.4). There is considerable intra- and inter-
specific variability in growth rates at one site; changing light environments in response to shifts in canopy density is likely to explain some of this variation. Bystriakova et al. (2011a) identified a trade-off between growth-rate and shade tolerance in the New Zealand Cyathea with a faster-growing species C. medullaris restricted to higher light environments and having a low survivorship in shade (3.22% yr\(^{-1}\) mortality) compared to 0.69 to 1.85% yr\(^{-1}\) mortality for the slower-growing, more shade-tolerant C. dealbata, C. smithii and C. cunninghamii.

**Table 2.3** Percent of total abundance, basal area and biomass of tree ferns in native New Zealand forests

<table>
<thead>
<tr>
<th>Source</th>
<th>Forest Community</th>
<th>% Total Abundance*</th>
<th>% Total Basal Area</th>
<th>% Total Biomass¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Enright and Ogden (1987)</td>
<td>Secondary kauri Agathis australis forest</td>
<td>-</td>
<td>21.7</td>
<td>-</td>
</tr>
<tr>
<td>Burns and Smale (1990)</td>
<td>Secondary kauri Agathis australis forest</td>
<td>33.6 ± 1.9</td>
<td>20.5 ± 2.1</td>
<td>-</td>
</tr>
<tr>
<td>Kendall (Unpub. Data)</td>
<td>Secondary kauri Agathis australis forest</td>
<td>32.1 ± 7.9</td>
<td>20.0 ± 11.9</td>
<td>3.8 ± 5.0</td>
</tr>
<tr>
<td>Smale et al. 1997</td>
<td>Upland broadleaf/podocarp forest</td>
<td>34.2 ± 11.0</td>
<td>55.5 ± 34.0</td>
<td>-</td>
</tr>
<tr>
<td>McKelvey (1963)</td>
<td>Upland broadleaf/podocarp forest</td>
<td>36.9 ± 14.3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Daniel (1975)</td>
<td>Lowland broadleaf/podocarp forest</td>
<td>10.5</td>
<td>2.3</td>
<td>-</td>
</tr>
<tr>
<td>Ogden (Unpub. Data)</td>
<td>Lowland broadleaf/podocarp forest</td>
<td>46.3 ± 26.4</td>
<td>27.7 ± 4.0</td>
<td>-</td>
</tr>
<tr>
<td>Kendall (Unpub. Data)</td>
<td>Lowland broadleaf forest</td>
<td>28.3 ± 18.4</td>
<td>29 ± 16.6</td>
<td>8.1 ± 10.2</td>
</tr>
<tr>
<td>Kendall (Unpub. Data)</td>
<td>Early successional lowland forest</td>
<td>34.0 ± 20.7</td>
<td>41.7 ± 22.2</td>
<td>21.0 ± 11.9</td>
</tr>
<tr>
<td>Ogden et al. (1997)</td>
<td><em>Pinus radiata</em> stands</td>
<td>62.8 ± 31.2</td>
<td>12.7 ± 12.1</td>
<td>-</td>
</tr>
</tbody>
</table>

*Stems ha\(^{-1}\), mean ± 1 SD; ¹Biomass estimated from volume of a cone calculated from DBH and height, canopy tree and tree fern height recorded in height classes and stem tissue densities obtained from Beets et al. (2012) and Richardson et al. (2014).

Ash (1987) found that Cyathea tree ferns surviving selective logging activities (in Fiji) may exhibit accelerated growth under the newly opened canopy. The ability of tree ferns to acclimate to significant changes in microclimatic condition following disturbance events has also been highlighted in the Australian tree fern Dicksonia antarctica, which is capable of producing fronds with ecophysiological characteristics that reflect the local conditions (Hunt et al. 2002).
Table 2.4 Growth rates (cm yr⁻¹) of tree fern species from demographic studies, North Island of New Zealand.

<table>
<thead>
<tr>
<th>Latitude / Elevation</th>
<th>-41.33 S / 130 m</th>
<th>-38.40 S / 340 m</th>
<th>-37.09 S / 100 m</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean Ann. Temperature (°C)</strong></td>
<td>12.6</td>
<td>12.2</td>
<td>15.0</td>
</tr>
<tr>
<td><strong>Mean Ann. Precipitation (mm yr⁻¹)</strong></td>
<td>2505</td>
<td>1600</td>
<td>1600 – 2000</td>
</tr>
</tbody>
</table>

Cyathea cunninghamii 8.0 (7.0–9.0) - -
C. dealbata 3.2 (2.9–3.4) 5.0 11.0 ± 1.5
C. medullaris 11.5 (9.4–13.7) 18.0 -
C. smithii 3.4 (3.2–3.6) - 11.2 ± 7.8
Dicksonia squarrosa 4.8 (4.3–5.4) - 18.5 ± 2.9

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Podocarp-broadleaved forest</th>
<th>Pinus plantation</th>
<th>Podocarp-broadleaved-forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reference</td>
<td>Bystriakova et al. (2011)²</td>
<td>Ogden et al. (1997)³</td>
<td>Ogden /Burns (Unpublished data)⁴</td>
</tr>
</tbody>
</table>

¹ Data from CliFlo website [accessed 14.05.2016], ² 95% confidence intervals, ³ no CI/SD values provided,⁴ ± 1 SD; location: Kauaeranga Valley, Coromandel.

Bystriakova et al. (2011a) attempted to age New Zealand tree ferns by monitoring tagged individuals over 28 years (Table 2.2) and estimated age ranges of up to 100 (C. medullaris) to 250 years (C. dealbata). Efforts to age individuals from various Australian tree fern species using radio-carbon (¹⁴C) dating suggest that individual Dicksonia antarctica and Cyathea australis may exceed 500 years in age (Mueck, Ough & Banks 1996). It is possible that some species of New Zealand tree ferns might be similarly long-lived.

### 2.5 The Influence of Tree Ferns in Forest Communities

#### 2.5.1 Evidence of effect

The ecosystem-level influences of tree ferns, such as their effects on species richness and diversity, composition and the surrounding structure of the forest, remain poorly understood in New Zealand. In Puerto Rico, tree ferns suppress forest regeneration on landslides by inhibiting the establishment and growth of woody species through competition for nutrients or light (Walker et al. 2010) and similar suppression effects in New Zealand are described below. As
Tree ferns mature, frond shedding (Gillman & Ogden 2001; Gillman, Wright & Ogden 2002; Gillman et al. 2004) alongside the deep layer of decaying fronds that accumulate in a mature stand will influence regeneration dynamics of woody species. Through their distinctive biochemistry, e.g. low Ca concentrations which slow decomposition and therefore mineralisation rates (Amatangelo & Vitousek 2008), dead tree fern fronds are also likely to have a distinct influence on nutrient cycling processes (Richardson & Walker 2010) (Fig. 4).

There is evidence for tree fern suppression of conifer and angiosperm woody species in New Zealand, as well as overseas (Drake & Pratt 2001; Walker et al. 2010); Duncan (1991) and (1993) cites Wardle (1974) who describes an absence of juvenile Dacrycarpus dacrydioides in a wind-throw gap in South Westland due to localised D. squarrosa and C. smithii dominance. The suppression of podocarp regeneration by D. squarrosa was also observed post-logging in podocarp-Beilschmieda tawa forests (Smale et al. 1987). McKelvey (1952) recorded restricted podocarp regeneration in forests where tree ferns (and hardwood scrub) were prevalent and concluded that tree ferns were responsible. Norton (1991) evaluated podocarp seedling and sapling distribution patterns beneath podocarp, broadleaved and tree fern canopies, and showed that although tree ferns represented 25% of the basal area of the plot, less than 0.4% of all seedlings recorded in the plot were within the drip-line of tree ferns. Although suppression has most commonly been reported as influencing podocarp species, Burns and Smale (1990) observed that the establishment of woody species (e.g. Weinmannia silvicola, Dysoxylum spectabile, Knightia excelsa) was inhibited beneath a dense C. dealbata canopy on the lower valley slopes of a secondary Agathis australis – Phyllocladus trichomanoides forest stand on the Coromandel Peninsula.

2.5.2 Mechanism – macro-litterfall and shading

Tree ferns in New Zealand exhibit several modes of frond excision:

i. Retention: those that retain senescent fronds intact and entire at the base of the crown forming a dense persistent skirt; represented by *D. fibrosa*.

ii. Partial-retention: those that retain the stipe (rachis) of the senescent frond only, the pinnae decaying and falling from the fronds; represented by *C. smithii*.

iii. Shedders: those that excise and drop the entire senescent frond from the base of the stipe. All eight of the other arborescent tree fern species in New Zealand are shedders.

It is not known why frond excision behaviour varies between tree fern species. Page and Brownsey (1986) theorised that frond retention protects the growing crown from epiphytes and
climbers. In comparison, Pope (1926) suggested a mechanism for epiphyte reduction that was the product of frond shedding in the relatively long (>30 cm) sections of stipe that are retained by *D. squarrosa*. The effects of the different excision behaviours do, however, influence the seedling communities beneath tree ferns.

Tree fern fronds of shedders comprise macro-litterfall (Gillman & Ogden 2001) and create local disturbance beneath adults when they fall, restricting seedling establishment (Gillman et al. 2004). Litter damage to woody seedlings varies with seedling size, community composition and structure (Clark & Clark 1989; Gillman et al. 2004); increasing tree fern macro-litterfall strongly correlates with an increase in vascular plant seedling mortality (Gillman et al. 2004). The regular frond shedders *C. dealbata*, *C. medullaris* and *D. squarrosa* (along with the palm *Rhopalostylis sapida*) have been recorded as being responsible for up to 14% of seedling mortality along 100 m forest transects (Gillman et al. 2004). The sheer depth of frond litter around tree fern stands, which can be up to 90 cm deep (Brock Unpublished raw data), will suppress seedlings under tree fern canopies (Beveridge 1973; Gillman et al. 2004); an absence of seedlings is particularly notable beneath *D. squarrosa* and *C. medullaris*, both of which can form dense stands or thickets (Fig. 2.2).

Forbes et al. (2016) experimentally removed tree ferns from forestry plantations to assess their influence, via shading, on the woody seedling community. This modification of the understorey resulted in a significant increase in growth rates of the seedlings of the two canopy species present: *Podocarpus totara* and *Pittosporum eugenoides* (2.6-fold and 1.5-fold respectively). Burton and Mueller-Dombois (1984) undertook a tree fern frond removal experiment in Hawai‘i and recorded an increase from 10.1 to 42.8% of incident radiation on the forest floor immediately below the de-fronded tree ferns. The increase in light levels and implied competitive release following the removal of the tree ferns provides support for the suggestion made by Coomes et al. (2005) that shade cast by tall ferns contributes to the restriction of regeneration opportunities.

### 2.5.3 Mechanism - influences on nutrient cycling

Richardson et al. (2005) and Vitousek et al. (1995) have shown that *D. squarrosa*, *C. smithii* and *Cibotium* spp. (the latter studied in Hawai‘i) inhabit a wide soil fertility gradient (from 1 to 5 mg P kg\(^{-1}\) and 15 to 110 mg N kg\(^{-1}\)) and can deposit relatively high levels of nutrients in their litter; studies of Hawai‘i’ian tree ferns show that they capture and retain relatively high proportions of nitrogen (twice that of canopy trees) and phosphorus (up to three times canopy
trees) in early successional communities (Balakrishnan & Mueller-Dombois 1983; Walker & Sharpe 2010). Tree fern frond litter has a mean nitrogen content of 0.83% dry mass, compared to that of associated angiosperms (0.54%) and conifers (0.57%), but there appears to be relatively little difference in litter P across these plant groups (Enright & Ogden 1987; Richardson et al. 2005). While increased foliar nitrogen will enhance litter decomposition, the availability of calcium can limit decomposition rates and interactions with invertebrates (McLaughlin & Wimmer 1999; Silver & Miya 2001; Hobbie et al. 2006); non-polypod ferns in Hawai’i (Amatangelo & Vitousek 2008) have higher N:Ca ratios than angiosperms. Enright and Ogden (1987) recorded a N:Ca ratio in *Cyathea dealbata* 3.5-times greater than that in associated angiosperm species (14.8 vs 3.7 for *Vitex lucens*) indicating the potential for slowing litter decomposition and delaying the release of nutrients. Thus, communities supporting relatively high abundances of tree ferns might experience delayed release of nutrients from decomposing organic matter, but this dynamic requires further empirical investigation.

The decomposition rates of fern litter vary widely (Richardson & Walker 2010). Amatangelo and Vitousek (2009) found that leptosporangiate fern fronds in nutrient-poor environments decomposed more slowly than angiosperms leaves. Shiels (2006), working in Puerto Rico, compared the decomposition rates of a pioneer tree (*Cecropia schreberiana*) with those of a pioneer tree fern species (*Cyathea arborea*) and found the latter decomposed significantly more quickly (*Cyathea: k = 0.93 ± 0.06; Cecropia: k = 0.68 ± 0.06, where k=decomposition factor*). Enright and Ogden (1987), in their study of the decomposition dynamics of *Agathis australis* forest associates, compared the rate of decay (loss of mass over time) of the stipe of *C. medullaris* to the leaf blades of a number of common woody species, and found that the stipe decayed significantly more slowly, reflecting its sclerophyllous nature.

### 2.5.4 Mechanism - allelopathic effects

Cambie et al. (1961) tested for the presence of phytochemicals in New Zealand tree fern species (stem material and frond samples) focussing on compounds that affect herbivores, for example leucanthocyanins, which were recorded in *D. squarrosa* (frond and trunk), *D. fibrosa* (frond and trunk), *C medullaris* (trunk, but not the frond) and *C. smithii* (frond and trunk). The trunks of *C. milneii* and *C. kermadecensis* were found to contain saponins, while samples of *D. lanata* (treated as a single species) and *C. colensoi* tested negative for alkaloids. Other phytochemicals that may have allelopathic effects, include secondary metabolites such as terpenoids and phenolics (Inderjit 1996), but these were not considered by Cambie in his assays.
Froude (1980) showed that aqueous extracts from green frond material of tree ferns (C. medullaris, C. smithii, D. squarrosa) stunted the radicle development of salad cress (Lepidium sativum); and C. medullaris extract caused stunting in kakabeak (Clianthis puniceus) radicle growth. Froude observed similar inhibitory effects of the leachates of the three tree fern species on the seedling germination and growth of W. racemosa. Although not conclusive, Froude’s studies suggested that tree ferns may influence species establishment through the presence of alkaloid phytochemicals in their fronds and trunks. In general little is known about allelopathy in New Zealand forests (but see Michel et al. (2011), Morales (2015)) and therefore any comment on the relative importance of any possible allelopathic effects of tree ferns on the forest community remains speculative at this point.

2.5.5 Mechanism - establishment surfaces for epiphytes

Tree fern trunks increase the available establishment surface area of a forest, with the root mantle of the trunk suitable for seed and spore adherence and germination (Beever 1984; Leitch 1997; Moran, Klimas & Carlsen 2003; Mehltreter, Flores-Palacios & Garcia-Franco 2005). Tree ferns often provide advantages above the forest floor for seedlings where they may be protected from herbivory, low light levels, low soil fertility, macro-litterfall and deep leaf litter (Veblen & Stewart 1980; Wright & Cameron 1985; Smale & Kimberley 1993; George & Bazzaz 1999; Coomes et al. 2005; Wardle et al. 2006; Gaxiola et al. 2008). Species that establish on tree fern trunks are those species with small, wind-dispersed seeds that on the forest floor preferentially establish on exposed subsoil but are unable to establish in deep litter, e.g. Weinmannia spp. (Beveridge 1973; Bellingham & Richardson 2006).

Epiphytism on tree fern trunks by regenerating canopy tree species has been recorded worldwide including in the Mascarenes (Derroire et al. 2007), the Caribbean (Newton & Healey 1989), Australia (Ashton 2000; Bowkett 2011), North America (Mehltreter et al. 2005) and New Zealand (Gaxiola et al. 2008). However, epiphytes on tree ferns are constrained by regional climactic limitations (Roberts et al. 2005); for example, epiphytic establishment appears to be more successful (24% of tree fern stems had seedlings ≥ 15 cm high) and a more important pathway for canopy species regeneration on the wet, west coast of New Zealand, than it does on the relatively drier east coast (up to 1.5% of stems supported seedlings ≥ 15 cm high) (Gaxiola et al. 2008; Richardson et al. 2014).

The most common successional pathway through epiphytic establishment on tree ferns in New Zealand involves the widespread angiosperm canopy trees Weinmannia racemosa and W.
silvicola Cunoniaceae (Beveridge 1973; Blaschke et al. 1992; Burrows 2006). Hemi-epiphytism is apparent in up to 60% of Weinmannia canopy trees at some sites in Waitutu (Gaxiola et al. 2008). In dense forest communities, tree ferns, in particular D. squarrosa (Pope 1926; Wardle & MacRae 1966) and C. smithii (Lusk & Ogden 1992; Smale & Kimberley 1993), form an important establishment surface for regenerating Weinmannia spp. in conditions where Weinmannia would not be able to establish successfully on the forest floor. Oliver (1930) and Pope (1926) provide observational data from the Wellington region that Pseudopanax arboreus, Raukaua edgerleyi, W. racemosa, Ackama rosifolia and C. grandifolia survive to maturity as epiphytes on tree ferns. Regeneration of many canopy species (e.g. Myrsine chathamica) on the Chatham Islands depends on epiphytic establishment on tree ferns (Wardle 1991).

2.6 Use and management of tree ferns

Historically tree ferns have been used in a variety of ways by indigenous communities throughout the southern temperate biome. Food storage pits would be lined with hard plates of Cyathea medullaris by Māori in New Zealand (Anderson 2000) to protect against rodent ingress; Dicksonia sellowiana was used by Guarani communities in northern Argentina to treat disease and sclerenchyma tissue used to make arrowheads (Keller, Torres & Prance 2011). Tree ferns were also used medicinally and as a regular component of diet: indigenous communities of south-eastern Australia would cook the pith of Cyathea australis and Dicksonia antarctica (Nash 2004); similarly in New Zealand the consumption of Cyathea medullaris was a common source of carbohydrate (Leach 2003).

The first record of trade in tree ferns is their apparent use as ballast in sailing ships carrying cargo from Australia to Great Britain (Page 2004); because their stem density would not lend them to functioning effectively as ballast it is suggested they were used to line the hold to protect the cargo. Tree ferns (D. squarrosa, D. fibrosa and C. medullaris) were regularly harvested from the old growth Pinus plantations of the central North Island of New Zealand during the 1980s, supporting an industry worth some $2.75M year\(^1\) (Veale 1986). Similar salvage operations were being undertaken from forests in south-eastern Australia where Dicksonia antarctica was collected and exported (Vulcz et al. 2002). Extraction of tree ferns from native and plantation forests in New Zealand and Australia has not been deemed sustainable either ecologically (Lawson 2002) or economically, and in tree fern nurseries have been established in Tasmania and Victoria in Australia (Ogle, La Cock & Halsey 2000; Hunt et al. 2002; Vulcz et al. 2002; Forest Practices Authority 2012). While tree ferns are frequently harvested in Australia for the
ornamental plant market (Vulcz et al. 2002), tree ferns are commonly used in New Zealand for fencing, stakes and garden pots (Veale 1986). No information is available on modern use or extraction of tree ferns in Southern Africa or South America.

While active management of tree ferns has not been reported from productive forests, native or plantation, in the southern temperate region, the suppressive influence of tree ferns on seedlings, particularly of shade-intolerant species, could inhibit crop tree regrowth in forests where native hardwoods are selectively cropped (Carswell et al. 2007; Forbes et al. 2016). Where tree ferns dominate early successional communities this effect could diminish establishment potential of tall tree species and may leave systems vulnerable to exotic invasion (Walker et al. 2010; Richardson et al. 2014), suggesting potential benefits with regard to controlled local management of common tree fern species. The only published example of the active management of tree ferns in forest systems comes from tropical Hawai‘i where non-native invasive tree ferns have had profound effects on soils and growth of native plants and have been the subject of selective management (uprooting, herbicide application) (Chau, Walker & Mehltreter 2013; Loh et al. 2014).

2.7. Conclusions

2.7.1 Do tree ferns influence forest composition and structure?

Tree ferns are an ancient, widespread and significant component of the indigenous forests of New Zealand and many other countries across southern temperate forest biomes, and play an important part in forest dynamics and ecosystem function. Characteristically they dominate early and mid-successional stages of the forest community after disturbance on more fertile soils, and may suppress regeneration of several associated canopy angiosperms and conifers.

Tree ferns may alter angiosperm community structure by influencing seedling composition within their drip-line, and therefore, where they are abundant, the successional trajectory of the forest community as a whole. It is evident that tree ferns provide a different successional pathway compared to other trajectories involving early successional woody forest species such as Kunzea robusta – Leptospermum scoparium or Metrosideros excelsa scrub (Pope 1924; Wardle 1991; Sullivan, Williams & Timmins 2007). Understorey tree ferns C. dealbata and C. smithii have a considerable influence on the forest community through their effects on nutrient cycling, formation of deep organic layers and by their physical impacts of their macro-litterfall
on the regeneration niche. The regeneration of canopy tree species via epiphytism on tree fern trunks provides a successional pathway for some species, e.g. *Weinmannia* spp., but is mediated by local climatic conditions.

### 2.7.2 Future research priorities

Long-term data following the fate of tree fern individuals is lacking, with the majority of studies based on snapshot measurements of mature tree fern individuals. This approach is limited and does not provide information on key ecological events such as the point of entry of tree ferns into succession, and the length of time a cohort is present in a particular community. This narrow view is problematic given the longevity of individual tree ferns (potentially > 350 years), the difficulty in ageing individual tree ferns, and the uncertainty around the events and conditions that trigger their establishment. Dynamic forest models may provide a means of understanding the long-term effects of tree ferns in communities, and scaling issues (Perry & Millington 2008).

![Figure 2.5](image)

**Figure 2.5.** A summary of the published information on the ecology and synecology of the New Zealand tree ferns highlighting research recommendations that will advance our understanding of tree fern influence on forest composition and structure.
The uncertainties around establishment conditions are particularly pertinent when considering the likely influences of these species on successional processes in forest; data obtained from a narrow temporal sample represents a particular section of the life-history and role of a species and will not define a regeneration mechanism (Smale et al. 1997). A comprehensive picture of the ecology of tree ferns requires an understanding of how life-history traits of the various species respond to particular sets of biophysical conditions over time (Nakashizuka 2001), and this requires long-term monitoring of individuals along environmental gradients.

My synthesis of the ecology and function of New Zealand’s tree ferns highlights important gaps in our knowledge of these important components of New Zealand’s forests and of those across the southern temperate biome (Fig. 2.5). Future research of tree-fern ecology should consider both the autecology and synecology of these taxa, for example: i) laboratory experiments manipulating environmental conditions for developing gametophytes; ii) field surveys to obtain data on the selective effect on seedling recruitment by tree fern canopies; and, iii) modelling forest systems to compare regeneration in the presence and absence of tree ferns in the community. Resolving these knowledge gaps will clarify our fundamental understanding of tree fern ecology, particularly with regard to their role in forest regeneration dynamics in southern broadleaf-podocarp forests, and with regard to their influence on forest systems under silviculture.
Chapter 3

Decoupling the gametophyte and sporophyte niche in *Cyathea*

3.1 Abstract

Fern gametophytes are independent organisms, usually haploid, that represent the establishment phase for all fern sporophytes. Despite being small (< 1 cm diameter) and cryptic, their distribution, development and ecology determine the recruitment and maintenance of fern populations, and hence their role in community structure. The niche of gametophyte tree ferns may constrain the niche of sporophyte tree ferns and could in part explain inter-specific niche differences across tree fern species and their landscape-level responses to environmental filtering. I compared the development of fern gametophytes of three New Zealand *Cyathea* (tree ferns) along nutrient and irradiance gradients under controlled conditions to compare niche characteristics between taxa and with those described for the corresponding sporophytes. I used a categorical method for comparing and modelling developmental rates of gametophytes across a multi-factorial, multi-level (3×4) experiment. Spores of *C. dealbata*, *C. smithii* and *C. medullaris* were collected, sterilised and inoculated onto agar plates of varying plant-available phosphorus (orthophosphate) concentrations (5, 10, 20, 40 mg kg⁻¹). The plates were kept in three different lighting treatments mimicking field light levels experienced under dense canopy ($\bar{\mu} \pm SD, n = 4; 2.8 \pm 1.0$ mmol m⁻² s⁻¹), sparse canopy ($20.8 \pm 22.9$ mmol m⁻² s⁻¹) and in open environments ($165.7 \pm 244.5$ mmol m⁻² s⁻¹). Spore germination and gametophyte development were assessed every 12 days over a period of 168 days; development was quantified by assigning gametophytes to six growth stages. Transition matrices representing gametophyte development per species per treatment for five phases *en route* to maturity. Similar development rates of shade-intolerant pioneer (*C. medullaris*) across experimental treatments showed greater tolerance of low irradiance and substrate P than did those of the shade-tolerant understorey *C. dealbata*, *C. smithii*. The treatments in which development rates differed most across taxa broadly reflect sporophyte niches of the three species ranked along irradiance and soil P levels. Sporophyte *C. dealbata* is ecologically similar, sympatric to and yet spatially separated at a landscape-level from sporophyte *C. smithii*; however, gametophytes of *C. dealbata* developed more quickly under treatments of low P concentrations (10 mg kg⁻¹) and high to medium light levels. In comparison, gametophytes of *C. smithii* developed more rapidly than *C. dealbata* in three treatments (5 mg kg⁻¹, low and medium light; 20 mg kg⁻¹ low light) indicating niche differentiation of these understorey species gametophytes. The different rates of gametophyte
development across experimental treatments, when compared to field data on soil orthophosphate and sporophyte occurrence, suggest that *C. dealbata* and *C. medullaris* have similar ecological optima, but these are not the same as *C. smithii*, suggesting potentially decoupled life-stages in this species. Future studies of gametophyte development rate should be undertaken to determine success in inter-specific competition to establish niche-partitioning.

### 3.2 Introduction

Forest community dynamics are nearly always described in terms of spermatophytes where the gametophyte is much reduced, nutritionally dependent on the sporophyte, and therefore of relatively little consequence in species distribution and development. Many ferns and fern allies (monilophytes and lycophytes), however, complete a two-phase life-cycle where an independent gametophyte determines the location of the subsequent sporophyte generation (Farrar et al. 2008; Pinson et al. 2017). The separation of intra-specific niche-space across the two life-stages, coupled with the near impossibility of identifying gametophytes to species-level in the field is a challenge for ecologists trying to understand recruitment and community structure in ecosystems where ferns or fern allies represent a significant component of the community (e.g., tree ferns in forests).

Five distinct morphological and functional types of fern gametophytes have been described: cordiform, strap (gemmiferous and non-) and ribbon (gemmiferous and non-; Farrar et al. 2008). Pittermann, Broderson & Watkins (2013) suggest that most (non-cordiform) gametophytes are more stress tolerant than their sporophytes and can establish and grow in micro-sites and persist (up to 12 years in cultivation; Walp 1951) until local conditions different to those conducive for sexual reproduction and sporophyte development. Cordiform gametophytes appear the least stress-tolerant (essentially in equilibrium with environmental moisture conditions) and establish after disturbance events, grow rapidly and rarely persist more than one year (Watkins Jr et al. 2007; Pittermann et al. 2013). Surface moisture is the key driver of gametophyte development and survival in all types; the sporophyte life-stage is further constrained by other environmental filters, in particular temperature and light (Watson & Vazquez 1981; Sato & Sakai 1981; Watkins & Cardelús 2009; Pittermann et al. 2013).

Fern gametophytes can occupy a broader range (varying significantly across taxa) of a single environmental gradient (elevation) than their sporophyte generation (Nitta et al. 2017).
Although gametophyte distribution is less environmentally limited, gametophyte fecundity (gametangia production) is greatest in conditions similar to those of the sporophytes (Greer & McCarthy 1999), suggesting a strategy for sporophyte production. However, gametophytes exhibit a range of morphologies and sexual expression driven by gametophyte density and, in some taxa, antheridiogen production and inter-gametophyte chemical interactions (Stephenson 1907; Stokey 1930; Gureyeva 2003; Ranker 2008; Nitta et al. 2017). Furthermore, the ability of a gametophyte to develop to maturity depends not only upon the availability of suitable microsites for spore germination, but also intra and interspecific gametophyte competition (Greer & McCarthy 1999; Gureyeva 2003; Testo, Grasso & Barrington 2014). Priority effects may influence intra-specific gametophyte development, drive inter-specific competition among gametophytes, and will likely be a strong predictor of sporophyte distribution (Greer 1993; Greer & McCarthy 1999).

In this study, I compared the development of fern gametophytes of three New Zealand *Cyathea* species along nutrient (phosphorus) and irradiance gradients to determine whether gametophyte niches were similar to or decoupled from those of sporophytes and were different across taxa. The three species I considered were *Cyathea dealbata*, *Cyathea smithii* and *Cyathea medullaris*; these represent two key functional groups of tree ferns in New Zealand: abundant understorey and forest pioneers (Brock et al. 2016, 2018). *C. dealbata* and *C. smithii* are both shade-tolerant species that commonly occur in the understorey of native broadleaved podocarp forests and frequently co-occur in northern New Zealand forests. *C. dealbata* and *C. smithii* have similar demographies (slow-growing, shade-tolerant, continuous regeneration; as Bystriakova et al. 2011a) and are frequently sympatric in their natural ranges in New Zealand (Brock et al. 2016). However, these species are spatially segregated where they co-occur, and Bystriakova et al. (2011a) suggest that this is evidence of niche-differentiation at the gametophyte life-stage. *C. medullaris* occurs frequently as a shade-intolerant fast-growing pioneer species in continuous stands covering large areas, and has a sporophyte ecology that is distinct to *C. dealbata* and *C. smithii*, both of which are shade-tolerant, slow-growing species that establish under a *C. medullaris* canopy (Brock et al. 2018). The niches of the sporophyte tree ferns of the three study species differ; the pioneer is closely associated with disturbance (at both landscape and forest canopy gap scale) and the understorey species are associated with established canopy. I predict that to maximise the potential to capture space after disturbance events, pioneer tree fern sporophytes establish from rapidly growing gametophytes that can establish in a wide range of conditions. I hypothesise that: (i) gametophyte developmental response in *C. medullaris* will
have wider environmental tolerances and be faster than the gametophytes of the two understorey species; and (ii) the gametophyte niche of the understorey species will more closely correspond to the environmental filters of the sporophyte life stage.

Information on the ecology of the gametophyte life stage of tree ferns in New Zealand is limited to a single study describing ‘extreme-low light’ limitations on gametophyte growth (Stokey 1930). More generally, aside from moisture availability, spore germination is probably influenced by light gradients, with gametophyte growth driven by available phosphorus (Greer 1993; Moura et al. 2012; Pittermann et al. 2013). As fern gametophyte morphology is relatively conservative across gametophyte type in varying environmental conditions, laboratory grown gametophytes provide an opportunity to observe the relative development rates and patterns in a range of environmental conditions (Farrar et al. 2008).

To compare gametophyte development rates of the three *Cyathea* species, (Greer 1993) I undertook a multi-factorial experiment using varying concentrations of plant-available phosphorus (four levels) and the amount of photosynthetically active solar radiation (three levels) under controlled conditions. I quantified developmental progression of gametophytes using a series of readily identifiable morphological features/stages. This approach enabled me to identify comparable stages of development across variable growth forms within and between taxa. As the production of a sporophyte is dependent upon the development of mature female/bisexual gametophytes, achieving female gametangia was the final threshold recorded during monitoring. I modelled this developmental data (per treatment) using a simple Markov process; this allowed me to derive patterns of individual growth from population-level sampling. Using these matrices I could ascertain the similarities in the relative rates of development to production of mature female/bisexual gametophytes for each species across treatments.

By comparing published data on the niche requirements of sporophytes of three species of *Cyathea* to the findings of my *in vitro* study into gametophyte ecology, I consider the following questions:

1. *Do environmental filters differentially influence sporophyte and gametophyte distribution and growth?* This question was answered by compiling data from a literature review on sporophyte occurrence and available orthophosphate in soils, and comparing the distribution of these presence-by-phosphorus data to the differential rates of gametophyte development across the four phosphorus levels (across all light levels).
2. Is there evidence for greater environmental tolerance in C. medullaris compared to the two, understorey tree fern spp., suggesting a strategy at the gametophyte life-stage relative to sporophyte habit? A comparison, as above, of the range of treatments in which C. medullaris gametophytes developed to maturity compared to the distribution of sporophytes in known phosphorus and irradiance conditions.

3. Is there evidence for inter-specific niche differentiation at the gametophyte stage that could explain the environmental filtering and spatial separation of sporophytes? A comparison of differential gametophyte development rates of two species of sympatric but spatially separated species C. dealbata and C. smithii to establish whether these otherwise ecologically similar species have different niches in the gametophyte stage.

3.3 Methods

3.3.1 Niche of sporophyte tree ferns

I obtained data on the range of plant available phosphorus (orthophosphate) and light (PAR) conditions in which the sporophytic generation of the three tree fern species have been recorded via a literature review. As no data were available on individual survival, or reproduction in these studies (necessary data to infer habitat requirements; Van Horne 1983), these data describe the environmental filter (available phosphorus conditions) at the sites where the three species were recorded. I included studies where the vegetation at a site included one of the three study species, as well as soil analysis reporting the Olsen’s P test – the standard method in New Zealand to quantify phosphorus available to plants (Landcare Research 2017). The sporophyte-soil phosphorus association data were presented graphically (abundance vs soil P conditions) to allow visual comparison to the gametophyte development data.

3.3.2 Gametophyte – in vitro experiment

To determine appropriate experimental irradiance levels, photosynthetic active radiation (PAR) was recorded at ground level in four different forest types between 10 AM and 3 PM during September and October 2015 on clear sky days using a LI-COR Quantum and Campbell CR10X logger. The forest types were: seral (canopy height c. 5 m) with dense understorey ($\bar{x} \pm SD, n = 4; 2.8 \pm 1.0 \text{ mmol} \text{ m}^{-2} \text{ s}^{-1}$); seral with sparse understorey (19.1 ± 20.7 mmol m$^{-2}$ s$^{-1}$); mature forest (canopy c. 20 m) with sparse understorey (22.1 ± 24.4 mmol m$^{-2}$ s$^{-1}$); and, in a canopy
gap in mature forest (165.7 ± 244.5 mmol m⁻² s⁻¹). These values informed the levels for the light treatment in the growth cabinet experiment.

I collected spore material for *C. dealbata*, *C. smithii* and *C. medullaris* from the University of Auckland campus grounds and forest reserves at Huapai and Oratia in West Auckland (Fig. 3.1). Fertile pinnules were obtained from four separate plants per species and were subsequently stored at room temperature for one week in an A4 manila envelope. The spores from different sampling locations were then combined into a single sample per species. Spores were then sterilised using domestic bleach (sodium hypochlorite solution <5%) and, after rinsing, suspended in solution.

![Figure 3.1. Spore-collection locations around the Auckland region indicated by a star.](image)

The growth cabinet was lit for 14 hours per 24 hour cycle with a maximum temperature of 21 °C (14 hours) and a minimum of 14 °C (10 hours) to approximate summer conditions in northern New Zealand (Auckland (Henderson north climate station)) climate data obtained from NIWA’s CliFlo website [accessed 27.07.17]). Irradiance levels were set to a maximum of 180 mmol m⁻² s⁻¹; three distinct light environments were achieved by wrapping shelves in the cabinet with two grades of shade cloth (advertised shading effect between 50/60 and 20/30%). This method enabled me to create light environments of 5.4 ± 4.4 mmol m⁻² s⁻¹ (‘low’), 59.1 ± 44.3 mmol
m\(^{-2}\) (‘medium’), and 107 ± 74.1 mmol m\(^{-2}\) s\(^{-1}\) (‘high’ – no shade cloth). PAR levels were measured using the same equipment as described above; light treatment levels in the chamber were designed to be as close to the levels observed in forest conditions, with the strength of PAR produced in the growth cabinet the main limitation.

Agar nutrient solutions were prepared as per Chuter et al. (2008), with concentrations (5, 10, 20, 40 mg kg\(^{-1}\)) of plant available phosphorus / orthophosphate (KH\(_2\)PO\(_4\)), representing the range of naturally occurring values in New Zealand forest soils (Blakemore, Searle & Daly 1987), and within the range of values identified by the literature review described above. I inoculated 60 plates per P concentration per species (240 plates total per species) with 0.1 ml of spore solution (varying concentrations) and transferred these to a growth cabinet, 20 plates per P concentration per species per light treatment. This method yielded twenty replicates per combination of P concentration and light level per species (720 plates in total).

I sampled spore germination and gametophyte development in a randomly selected subset of 10 of the 20 plates every 12 days over 168 days. It was impractical to standardise the number of spores deposited on each plate. However, areas of relatively high spore density (> 100 ± spores cm\(^{-2}\)) were marked and avoided. For each observation per plate, I selected the first one hundred spores and/or developing gametophytes and recorded their developmental stage (description below; Table 3.1; Fig. 3.2). Working in boustrophedon progression across the plates in areas of low spore density, that I did not measure the same individuals at each time-step.

**Table 3.1.** Spore germination and developmental growth stages recorded for tree fern gametophytes (adapted from Srivastava & Uniyal 2014)

<table>
<thead>
<tr>
<th>Stage</th>
<th>Appearance of developing gametophyte</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Un-germinated spore</td>
</tr>
<tr>
<td>2</td>
<td>Germinated spore – emergence of first rhizoid</td>
</tr>
<tr>
<td>3</td>
<td>Prothallus – initial emergence from spore</td>
</tr>
<tr>
<td>4</td>
<td>Prothallus achieving &gt;20 cells</td>
</tr>
<tr>
<td>5</td>
<td>Appearance of the notch</td>
</tr>
<tr>
<td>6</td>
<td>Sexually mature cordiform gametophyte</td>
</tr>
</tbody>
</table>

To provide a uniform and consistent method of categorising gametophytes into developmental stages a series of five thresholds were established on the basis of gametophyte ontogeny, following Srivastava & Uniyal (2014) and Stokey (1930). The thresholds were based on development stages that would be readily identifiable across all possible cordiform gametophyte development patterns, as under low light levels it is possible that gametophytes would develop
ameristically (Stokey, 1930). The thresholds between stages were: 1) spore germination – evidence of first rhizoid penetrating the spore coat; stage 2) evidence of the prothallus – first photosynthetic cells developing; 3) prothallus developing more than 20 cells (spatulate stage; sensu Srivastava & Uniyal, 2014); 4) appearance of the notch in the developing prothallus; 5) development of a mature prothallus with gametangia (Table 3.1). No observations were recorded of gametophyte mortality, and therefore mortality was not a threshold considered further in analysis.

Figure 3.2. Stages of tree fern gametophyte development: a) stage 3 (initial emergence of prothallus; ~50 μm across); b) stage 4 (prothallus achieving > 20 cells; ~150 μm); c) stage 5 (appearance of the notch; ~450 μm); and d) stage 6 (mature gametophyte; 6 mm)
3.3.3 Analysis

For Markov modelling of the development process (Jones 2005; Pasanisi, Fu & Bousquet 2012), I derived a transition matrix, representing germination and gametophyte development per species per treatment \( n = 36 \) with germination as a time-variable step, using the following assumptions:

i. All petri-dishes (replicated conditions) were independent of each other within a particular set of treatments;

ii. Gametophytes developed through a series of readily recognisable morphological features/stages, which corresponded to the discrete states of a Markov model (i.e., developmental change is represented as a discrete-stage model);

iii. Gametophytes on one dish were both independent and subject to the same treatments of light and phosphorus;

iv. Gametophytes could not and did not retrogress. Probabilities of transitioning to a previous developmental stage were always zero; and,

v. Gametophytes could not progress through more than two stages during a single time-step (12 day monitoring period), and could not progress beyond germination in a single time-step.

The iterative fitting process described by MacRae (1977) was used to parameterise transition matrices and fit them to aggregate data comprising imperfect state observations (i.e. at each observation the developmental stage of a different subset of gametophytes was sampled; a complete census was not undertaken). This estimation approach was necessary because it was not feasible to follow the growth of single individual gametophytes across multiple experimental treatments over time. Instead, I sampled a random subset of gametophytes from the population at each timestep; every gametophyte sampled per timestep was, therefore, independent of gametophyte samples on other occasions.

Thirty-six different transition matrices had to be estimated (three species \( \times \) 12 treatments). First, a candidate transition matrix was parametrised using a set of initial proportions. The predictions of gametophyte development (simulated gametophytes) were then tested from one timestep to the next against the observed proportions for each timestep, the transition matrix corrected and the process repeated. For each of the 36 species-experimental treatments the transition matrix was fitted based on 60% of the development data (six replicate counts selected randomly from each treatment per timestep, the ‘training’ set). The matrix as estimated from the training set
was then tested against the remaining 40% of the count data (the ‘test’ set) by simulating the developmental process as above, and sampling simulated gametophytes using the same sampling and counting process as in the experiment (100 gametophytes selected at random and their developmental stage recorded). This iterative process was ended when the simulated count data were within an order of magnitude of the test data.

The matrices describe the probability that a spore of known species in a given treatment would develop into a fully mature gametophyte over a set period of time (so the probabilities are analogous to rate). Gametophyte mortality was not considered in the model (the sampling methodology prevented mortality from being sampled). As an indication of differential growth across the experimental treatments, I compared the modelled intra-specific probabilities of development between all stages across the twelve experimental treatments ($\Sigma_{dfs}$; the squared differences between probabilities of transitioning to the next developmental stage between treatments, per time-step, and summed per experimental treatment). The $\Sigma_{dfs}$ along with final count data on mature stage (6) gametophytes, were used to identify:

i. whether the gametophyte life-stage differs in ecological requirement from the sporophyte; and,

ii. the treatments most conducive to rapid gametophyte development (gametophyte strategy).

Final counts of mature gametophytes of *C. dealbata* and *C. smithii* per experimental treatment were compared using the Kruskall-Wallis test with multiple $p$-value corrections to ascertain which species developed most rapidly in each treatment (niche differentiation). The threshold for differentiation between the relative development rates (final counts were all conducted at day 168) after correction was deliberately conservative ($\alpha = 0.005$) to ensure robustness of any conclusions drawn on intra-specific competition, given that gametophytes were in monoculture. All analyses were conducted using R-3.2.3. (R Core Team 2015).

### 3.4 Results

Three previous studies across 37 sites in New Zealand included the presence (as sporophytes) of at least one of the three *Cyathea* species with associated soil P values. These data were used to generate a frequency distribution of site P conditions occupied by each species (*C. dealbata* $n = 16$; *C. medullaris* $n = 12$; *C. smithii* $n = 29$) (Fig. 3.3); Smith & Lee 1984; Richardson *et al.*
2004; Brock et al. 2018). These data suggest that the sporophytes of *C. medullaris*, *C. dealbata* and *C. smithii* separate out along a soil phosphorus gradient, with *C. smithii* present where soils support relatively lower available phosphorus (9.7 ± 5.2 mg kg$^{-1}$) than sporophytes of the other two species (Fig. 3.3). Both *C. medullaris* and *C. dealbata* sporophytes are associated with higher available phosphorus levels (19.8 ± 12.0 and 16.4 ± 12.0 mg kg$^{-1}$, respectively).

![Figure 3.3. Comparison of sporophyte-soil P occurrence data and gametophyte development success (in 168 days) of the tree ferns *C. dealbata*, *C. smithii* and *C. medullaris*. Percentage of mature gametophytes developed in varying orthophosphate concentrations (with loess smoothing) vs. probability density of numbers of published records on soil available orthophosphate where sporophytes have been recorded (*n* = *C. dealbata* (12), *C. smithii* (16), *C. medullaris* (29) records).](image)

*C. medullaris* is a pioneer species associated with relatively high light levels; *C. medullaris* also occurs in forest in response to canopy gaps (Ogden et al. 1997; Brock et al. 2016). *C. dealbata* and *C. smithii* are forest understorey species and can occur sympatrically (occurring in the same vegetation plots; Bystriakova et al. 2011a (30 × 30 m); Brock et al. 2018 (20 × 20 m)), although the former has a more northerly distribution (Brock et al. 2016). Although specific light
requirements are not reported in the literature, a coarse ranking of preferred light treatments for each species can be derived: C. medullaris >> C. dealbata > C. smithii (Brock Unpublished; S. Richardson, pers. comm.).

Spore germination for all species occurred in a pulse approximately 12 days after inoculation and first exposure to PAR in the growth cabinet (Fig. 3.2). Once germination had occurred, I did not observe any evidence of gametophyte senescence or mortality on the plates, although gametophyte development varied between the experimental treatments. Gametophytes developing in the lowest light (5.4 ± 4.4 mmol m⁻² s⁻¹) treatments frequently formed ameristic structures (elongated, linear gametophytes producing antheridia only and laterally, i.e. not abaxially), where the thallus was elongated, linear and did not develop a notch or archegonia.

The summed squared differences in probabilities of gametophyte development to the next stage across the twelve different treatments (Σₐₙₙ) varied across the three tree fern species. The Σₐₙₙ for C. dealbata were lower than other species (5% - median – 95%; 0.17 – 0.51 – 1.23; Fig. 3.4b) indicating low differences in probabilities of development (relative to the other species) across most treatments, with a few treatments in which the probability of development is distinctly different to other treatments. The gametophytes of C. dealbata attain stage 6 most rapidly (i.e. largest proportion of gametophytes reaching stage 6 over the trial period of 168 days) in treatments where phosphorus is between 10 and 20 mg kg⁻¹ and in the medium light treatment. The most successful experimental treatment (most gametophytes reaching stage 6 per 168 day treatment period) for establishing gametophytes of C. dealbata was 10 mg kg⁻¹ of available phosphorus and the medium light (59.1 ± 44.3 mmol m⁻² s⁻¹) treatment (Fig. 3.4a).

In comparison, the Σₐₙₙ for C. smithii were relatively high (0.31 – 1.10 – 1.43; Fig. 3.4b) indicating large differences in probabilities of development across treatments (Figs 3.4a, b). The differences across development rates in the treatments were less distinct for C. smithii than for C. dealbata; rather than showing distinctly different growth rates under a few treatments, the response of C. smithii gametophytes falls along a gradient from high to low development rates. Probabilities of C. smithii gametophyte development were highest where phosphorus was between 10 and 20 mg kg⁻¹ in both medium (59.1 ± 44.3 mmol m⁻² s⁻¹) and high (107 ± 74.1 mmol m⁻² s⁻¹) light treatments. The treatments with the highest probability of gametophytes developing to a mature stage (6) in C. smithii was 20 mg kg⁻¹ of available P and the medium (59.1 ± 44.3 mmol m⁻² s⁻¹) light treatment (Fig. 3.4a).
Figure 3.4. (a) Percentages ($\bar{x} \pm SD$) of tree fern gametophytes that had reached maturity (stage 6) across all 36 experimental treatments per species; (b) Intra-specific differences in summed squared probabilities of gametophytes developing to the next stage ($\Sigma df$) per experimental treatment per species, with median, 25% and 75% quantiles represented, among all experimental treatments.
**Cyathea medullaris** gametophytes achieved stage 6 relatively quickly and successfully across a wide range of treatments. The low median and narrow distribution of Σdfs (0.28 – 0.75 – 1.58; Fig. 3.4b) suggest that the probability of development of gametophytes of *C. medullaris* is similar in many of the treatments; the few high Σdfs relate, therefore, to the few treatments in which the gametophytes developed least (Figs. 3.4a, b). The greater proportion of relatively low Σdfs and overall similarity in probability of development to the next stage relates to the large number of treatments in which *C. medullaris* gametophytes developed successfully (Figs. 3.4a, b).

Table 3.2. Pairwise comparisons of percentages of mature (stage 6) gametophytes of *C. dealbata* and *C. smithii* per experimental treatment after 168 days. Where distinctions between developmental numbers are clear (< 0.005 with multiple *p*-value corrections), this provides an indication of which species might out-compete the other in the gametophyte niche.

<table>
<thead>
<tr>
<th>Experimental treatments</th>
<th>Mean % mature gametophytes (x ± sd)</th>
<th>p-value</th>
<th>Predicted more competitive spp. / treatment (= species equivalent)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Phosphorus (mg kg⁻¹)</strong></td>
<td><strong>C. dealbata</strong></td>
<td><strong>C. smithii</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Light (mmol m⁻² s⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low (5.4 ± 4.4)</td>
<td>0.4 ± 0.7</td>
<td>6.4 ± 2.6</td>
<td>&lt;0.001  <em>C. smithii</em></td>
</tr>
<tr>
<td>5</td>
<td>Medium (59.1 ± 44.3)</td>
<td>0.9 ± 1.4</td>
<td>7.5 ± 3.0</td>
</tr>
<tr>
<td></td>
<td>High (107 ± 74.1)</td>
<td>0.6 ± 0.8</td>
<td>2.1 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>10.6 ± 3.0</td>
<td>16.4 ± 3.7</td>
</tr>
<tr>
<td>10</td>
<td>Medium</td>
<td>40.8 ± 4.1</td>
<td>18.6 ± 4.2</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>22.0 ± 6.2</td>
<td>7.2 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>10.2 ± 2.9</td>
<td>22.8 ± 6.4</td>
</tr>
<tr>
<td>20</td>
<td>Medium</td>
<td>23.1 ± 7.2</td>
<td>30.0 ± 4.5</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>9.4 ± 4.4</td>
<td>9.9 ± 3.7</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>7.7 ± 2.9</td>
<td>8.5 ± 2.4</td>
</tr>
<tr>
<td>40</td>
<td>Medium</td>
<td>13.2 ± 3.6</td>
<td>9.2 ± 2.7</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>1.9 ± 1.7</td>
<td>4.4 ± 2.4</td>
</tr>
</tbody>
</table>

Comparisons of the rates of development (number gametophytes developed to a mature stage (6) per 168 day period) of *C. dealbata* and *C. smithii* (Table 3.2) shows seven experimental treatments with statistically significantly different rates of development. In two treatments (10 mg kg⁻¹ P, high and medium light levels), *C. dealbata* developed more rapidly than *C. smithii* (high light: *C. dealbata* 22.0 ± 6.2 vs *C. smithii* 7.2 ± 1.7; medium light: *C. dealbata* 40.8 ± 4.1 vs *C. smithii* 18.6 ± 4.2). Gametophytes of *Cyathea smithii* developed more rapidly than *C. dealbata* in three treatments: low light levels at 5 and 20 mg kg⁻¹ phosphorus (*C. dealbata* 0.4 ±
0.7 vs C. smithii 6.4 ± 2.6; C. dealbata 10.2 ± 2.9 vs C. smithii 22.8 ± 6.4 respectively), and in medium light levels at 5 mg kg\(^{-1}\) phosphorus (C. dealbata 0.9 ± 1.4 vs C. smithii 7.5 ± 3.0).

### 3.5 Discussion

#### 3.5.1 Do gametophytes respond to the same environmental filters that determine the distribution of the sporophyte stage?

In the sporophytic stage the three tree fern species are ranked C. medullaris > C. dealbata > C. smithii in relation to both their preferences for available phosphorus and irradiance, highlighting the co-dependency of early successional species on above and below ground resources. Under laboratory conditions, gametophytes of C. medullaris respond positively to a range of phosphorus concentrations, paralleling the wide range of soil conditions in which the sporophyte has been recorded. Therefore, C. medullaris appears relatively tolerant of low P conditions in both life-stages making it well adapted to early successional communities (Brock et al. 2016, 2018). The highest light levels (107 ± 74.1 mmol m\(^{-2}\) s\(^{-1}\)), however, appear to inhibit the development of the gametophytes of this species. C. medullaris gametophytes develop more rapidly to a mature stage under medium light levels (59.1 ± 44.3 mmol m\(^{-2}\) s\(^{-1}\)) associated with early-successional vegetation indicating that the gametophytes of this species are generalists, not solely associated with pioneer conditions as the sporophyte.

The light treatments under which gametophyte transitions were most rapid were broader than those experienced by sporophyte life-stages. In contrast, Cyathea dealbata and C. smithii gametophytes both develop most rapidly in light conditions associated with the sporophyte life-stage.

The distribution of the development rates of the gametophytes of C. dealbata along a phosphorus gradient (with data from treatments of all light levels) shows a peak of development rates to maturity (stage 6) across the 10 to 20 mg kg\(^{-1}\) treatments (19.3 ± 12.1 gametophytes per 168 day period), which corresponds to soil orthophosphate levels derived from distributions (16.4 ± 12.0 mg kg\(^{-1}\)) of the sporophytes. In contrast, C. smithii sporophytes are associated with low available P soil concentrations (9.7 ± 5.2 mg kg\(^{-1}\)). However, C. smithii gametophytes develop successfully across the treatment concentrations with a maximum gametophyte growth rate in the 20 mg kg\(^{-1}\) P concentration treatment suggesting potential separation of niches between the two life-stages. My data suggest that soil phosphorus is influential in gametophyte...
development, but not a limitation on the establishment and growth of the sporophyte of \( C. \text{smithii} \).

3.5.2 **Is there evidence for greater environmental tolerance in \( C. \text{medullaris} \) compared to the two, understorey tree fern species, suggesting a strategy at the gametophyte life-stage relative to sporophyte habit?**

Gametophyte development rates differed between a pioneer (disturbance associated) and later successional (stable, lower-light environment) species (Fig. 3.4a), with the former a generalist (\( C. \text{medullaris} \)) and the latter more specialist (\( C. \text{dealbata}, \ C. \text{smithii} \)) in their response to irradiance and soil nutrient gradients. This interpretation depends on the assumption that gametophyte development, which was entirely ameristic in the low light level treatments, are unlikely to develop archegonia (without a change in conditions) and hence not produce sporophytes.

Sporophytes of \( C. \text{medullaris} \) establish stands in areas of soil disturbance and where forest canopy has been removed (Brock *et al.* 2018). As a forest gap pioneer species, the gametophyte stage is likely to develop in highly disturbed, light environments, and rapid development is therefore advantageous in terms of survival to sporophyte stage, similar to the rapid gametophyte growth described in Watkins *et al.* (2007). \( C. \text{medullaris} \) must also compete for space with other pioneer plant taxa such as the angiosperm *Kunzea robusta*. For a fern to be in a position to compete with an angiosperm (at a similar, or later stage of development), the arriving or newly exposed spore must germinate, a gametophyte develop, and sexual reproduction occur in the time that a seed can arrive and establish at a site (if not in the seed bank). However, to have gametophytes pre-established in a wide range of conditions that, should a disturbance event occur, could produce juvenile sporophytes to establish dominance suggests opportunism via a generalist gametophyte life-stage. Further experimental work is required to establish whether pioneer gametophytes can persist in understories in a pre-reproductive state, and to identify any specific environmental triggers for sporophyte production in gametophytes such that \( C. \text{medullaris} \) can quickly capture space after disturbance and form the mass-stands of this species evident in northern New Zealand (Brock *et al.* 2018).

Sporophytes of \( C. \text{dealbata} \) and \( C. \text{smithii} \) usually establish in lower irradiance (< 165.7 ± 244.5 mmol m\(^{-2}\) s\(^{-1}\)) environments beneath existing canopies of forest evergreen angiosperm or \( C. \text{medullaris} \). The range of treatments that these gametophytes established in was constrained compared to \( C. \text{medullaris} \), yet extended beyond the envelope of conditions in which the
sporophytes are known to occur (Fig 2), complementing field evidence of decoupling of the distributions of the life-stages of ferns (Watson & Vazquez 1981; Farrar 1990; Watkins Jr et al. 2007; Nitta et al. 2017). My experiment indicated that the distributions of *C. dealbata* and *C. smithii* sporophytes and gametophytes might be decoupled; however, this can only be confirmed by further field studies.

3.5.3 Is there evidence of niche differentiation at the gametophyte stage among species with similar sporophyte ecology?

While it is difficult to infer the outcome of inter-gametophyte competition without growing gametophytes of different species together in controlled conditions, evidence suggests that priority effects may be an important driver of gametophyte communities (Greer 1993; Greer & McCarthy 1999). If maximum gametophyte development rate is used as a competitive index, variation in the rate of gametophyte development in the different treatments provides insight into the conditions in which each species might be most interspecifically competitive in the gametophyte life stage (Greer 1993). However, this interpretation is limited to the two environmental variables manipulated in the treatments and does not include antheridiogens and inter-gametophyte chemical competition, along with other abiotic factors that might influence development patterns.

The summed squared differences in probabilities of gametophyte development to the next stage between the intra-specific experimental conditions (Σdfs) and developmental data showed that *C. dealbata* and *C. smithii* developed at different rates along gradients of phosphorus and light, indicating that priority effects (based on rate) will vary with resource availability. The experimental data suggest that *C. smithii* gametophytes develop faster and might therefore outcompete *C. dealbata* in lower light (32.2 ± 41.4 mmol m⁻² s⁻¹) and phosphorus environments (5 mg kg⁻¹). *Cyathea dealbata* gametophytes might therefore outcompete *C. smithii* where light levels are similar to those in early successional vegetation and more open environments, and where plant available phosphorus is around 10 mg kg⁻¹ (Table 3.2). Relative similarities of gametophyte development rates are based on a Kruskal-Wallis test and a conservative significance threshold (α = 0.005) (Table 3.2). To ascertain the significance of differential development rates in inter-specific competition between gametophytes of different species, further experimental work into gametophyte communities is required.
3.6 Conclusion

Differing ecological requirements of the alternate life-stages results in a potential decoupling of the distribution of sporophytes and gametophytes in the landscape; however, shade-tolerant understorey species (continuously regenerating underneath the canopy) have a narrower range of tolerances than species with pioneer sporophytes. Gametophytes show different responses to varying phosphorus and light levels in terms of their rates of development, and it is suggested, therefore, competitive ability with other fern species in New Zealand forests. I suggest that spatial differentiation of sporophytes with similar habit/demography in the landscape is a response to differential gametophyte development rates and competition based on priority effects.

This study is the first attempt to present gametophyte development as a Markov process. Further work on gametophytes should include efforts to identify intra-specific competitive effects on development rate of gametophytes, the persistence potential of pioneer gametophytes, and identifying triggers of sporophyte production.
Chapter 4

Pioneer tree ferns influence community assembly in northern New Zealand forests

4.1 Abstract

*Cyathea medullaris* (Cyatheaceae) is a frequent pioneer of disturbed areas (e.g., landslides) or edge environments, sometimes forming near continuous canopies. I test the hypothesis that colonisation by this species as a pioneer alters the seedling assemblage to favour more shade-tolerant broadleaved trees than that beneath another common native pioneer (*Kunzea robusta*, Myrtaceae) in the same landscapes. I compared vegetation and abiotic characteristics of 166 sites across the Auckland region where *Cyathea medullaris* or *Kunzea robusta* were abundant (≥ 20% basal area) along successional gradients. Using hierarchical classification and ordination, I identified distinct communities associated with the different pioneers. In the forests I consider, *Cyathea dealbata* is another common understorey tree fern, which sometimes, but not always, co-occurs with *Cyathea medullaris*. *Cyathea medullaris*/*Cyathea dealbata* successions occurred on steep sites with lower annual water deficit whereas *Kunzea robusta*/*Cyathea dealbata* successions were located on flatter, drier sites. The prevalence of macro-charcoal in *Kunzea robusta*/*Cyathea dealbata* forest suggests the prominence of that community is in part an outcome of the increased importance of fire disturbance in New Zealand. Dominance of *C. medullaris*, with *C. dealbata* understoreys, influences community assembly of tree species towards dominance by shade-tolerant species, whereas seedlings of less shade-tolerant small-leaved species are more prevalent in *Kunzea robusta*/*Cyathea dealbata* forests. I provide evidence to suggest that, where present in early forest communities, high tree fern abundance influences the assembly of seedling communities, supporting my hypothesis. Contrary to previous suggestions, a high abundance or basal area of tree ferns on sites not historically affected by fire, did not limit the establishment and growth of canopy trees including fleshy-fruited broadleaf species.

4.2 Introduction

The distinctive traits of different pioneer species can influence community assembly and natural succession processes after disturbance (Hille Ris Lambers et al. 2012; Paterno, Siqueira Filho...
& Ganade 2016). For example, the biotic influence of pioneers is evident in the different forest successions occurring beneath Kunzea spp.\(^1\) (Myrtaceae), a group of New Zealand native pioneers, compared with those beneath Ulex europaeus (Fabaceae), a non-native invasive nitrogen-fixing shrub in the same landscapes in New Zealand (Sullivan et al. 2007). However, abiotic filters (e.g., topography, soil conditions) initially underpin heterogeneous spatial patterns of pioneer taxa across the landscape, based on the tolerances of different pioneer species to disturbance type, abiotic characteristics and competition (Poff 1997; Ejrnæs, Bruun & Graae 2006; Perry et al. 2014). Community assembly will thus reflect historic disturbances, the abiotic conditions influencing pioneer establishment, and the subsequent biotic influence of the dominant pioneer (Connell & Slatyer 1977; Weiher & Keddy 1995; Sullivan et al. 2007; Burton et al. 2011).

The prevailing view of secondary successions initiated by fire and/or other stand destroying disturbances in New Zealand’s temperate forest ecosystems is one where pioneer communities are commonly dominated by Myrtaceae, in particular Kunzea spp.\(^2\) (de Lange 2014) and Leptospermum scoparium (Cameron 1960; Esler & Astridge 1974; Wardle 1991; Smale et al. 1997; Richardson et al. 2014). These species arrived in New Zealand from Australia between 2-3 Ma, moving from a landscape where fire is a major determinant of plant traits and communities to New Zealand where natural fire pre-human was relatively infrequent (Thompson 1989; Battersby et al. 2017). However, since human arrival in New Zealand c. 1280 AD (Wilmshurst et al. 2008), fire frequency has dramatically increased in New Zealand’s terrestrial ecosystems (Perry et al. 2012a), likely favouring Kunzea spp. and L. scoparium as pioneer species. The increased likelihood of occurrence of these Myrtaceae pioneers may influence the potential for other pioneers to establish (Esler 1967; Esler & Astridge 1974; Smale 1994; Atkinson 2004; Perry et al. 2010).

In Agathis australis (kauri) and conifer-broadleaved forest in the North Island, early successional communities dominated by tree ferns can often be a prominent feature of

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\(^1\) Following revision of Kunzea de Lange (2014), K. ericoides is likely to be at the Nelson sites, and K. robusta around Wellington in the sites studied in Sullivan et al. (2007).

\(^2\) Previously recognised as Kunzea ericoides (A.Rich) Joy Thomps., Kunzea has recently been revised to recognise 10 species within New Zealand (de Lange 2014) with three commonly occurring in the study area: K. robusta, K. linearis and K. amathicola. The data used in this study, other than that which was collected by the authors, was obtained prior to this taxonomic revision and therefore all records refer to Kunzea ericoides. Of the three species of Kunzea now present in the Auckland region, the most common forest associated species is K. robusta. K. amathicola is strongly coastal and K. linearis is also restricted to coastal habitat around Auckland’s Waitematā harbour. I therefore assign all Kunzea records to K. robusta in the historic non-coastal forest plots compiled for this study.
lakes (Pope 1924; Silvester 1964; Beveridge 1973; Richardson et al. 2014) (Fig. 4.1). Near-continuous canopies of pioneering *Cyathea medullaris* with dense understories including *Cyathea dealbata* have been described (Pope 1924; Ritchie, Easton & Lambert 2003; Brock et al. 2016), but rarely studied. Early successional vegetation communities dominated by tree ferns are rare globally; however, *Cyathea* tree ferns acting as pioneers have been described in tropical ecosystems from Colombia (*C. caracasana* Arens and Sánchez Baracaldo (2000)), Puerto Rico (*C. bryophila* and *C. arborea* Weaver (2008), Shiels (2006), Walker et al. (2010)), and on Trinidad Island off the coast of Brazil (*C. copelandii*, Alves, R. & Silva, N. (pers comm)).

Other early successional communities, developing on retired pasture and agricultural land and after fire, roadworks and landslides, may feature tree ferns as a prominent component, even if not as the dominant pioneers (Wardlaw 1931; Arens & Sánchez Baracaldo 1998; Restrepo & Vitousek 2001; Chacón-Labella et al. 2014). In New Zealand, succession through tree fern dominated stages has been described for *Dicksonia squarrosa* (Dicksoniaceae) and *Cyathea smithii* (Silvester 1964; Blaschke 1988; Walker & Sharpe 2010) where these establish approximately 25 years after the commencement of natural regeneration on landslides and in retired pastures; although none of these reported tree fern dominated stages are pioneering. I am unaware of any published studies of secondary succession involving tree fern pioneer dominated phases for any temperate forest ecosystem.

The two North Island pioneer species I focus on, *K. robusta* and *C. medullaris*, have many similar traits, including rapid height growth (c. 30 cm yr\(^{-1}\)), prolific production of wind-dispersed propagules, and relatively short life-spans (approx. 150 years; 120 years respectively) (Burrows 1973; Esler & Astridge 1974; Esler 1976; Allen, Partridge & Efford 1992; Smale 1994; Brock et al. 2016). Unlike New Zealand’s other native tree ferns, *C. medullaris* will regenerate immediately after both gap-phase and landscape-level disturbances and is associated with high light environments (Wardle 1991; Large & Braggins 2004). *Cyathea medullaris* is shade-intolerant (Bystriakova et al. 2011a), and often occupies habitats such as edges and canopy gaps (Pope 1924; Cockayne 1958; Large & Braggins 2004). *Kunzea robusta* is similarly shade-intolerant and associated with open habitats (Burrows 1973; Wardle 1991).

In association with both of these pioneers, *Cyathea dealbata* is a common component of the understory. In contrast to *C. medullaris* however, *C. dealbata* is a relatively drought and shade-tolerant tree fern species (Bystriakova et al. 2011a; Brock et al. 2016). Also, *Cyathea dealbata* is a relatively long-lived, slow-growing tree fern, persisting in forests for up to 250 years (Wardle 1991; Bystriakova et al. 2011a; Brock et al. 2016).
Tree ferns are likely to have an important influence on the regeneration niche of potentially dominant tree species in forests through macro-litterfall, shading, influences on nutrient cycling and provision of substrates for epiphytic woody seedlings (Gillman et al. 2004; Gaxiola et al. 2008; Brock et al. 2016). Tree ferns have been described as ‘inhibiting’ and ‘slowing’ forest succession (Connell & Slatyer 1977; Walker et al. 2010). For example, Walker et al. (2010) describe the inhibitory influence of tree ferns on the establishment of woody forest canopy species in Puerto Rico, when compared to an area artificially cleared of tree ferns, over a seven year period. On the other hand, Walker and Aplet (1994) suggest that, over the long-term, tree ferns act as a biotic filter on canopy species composition through their influence on nutrient cycling and soil moisture retention. In regenerating *Agathis australis* forest in New Zealand, Burns and Smale (1990) observed a lack of woody plant regeneration beneath *Cyathea dealbata* (Cytetheaceae); and Norton (1991) recorded an absence of podocarp seedlings around tree ferns. More specifically, Richardson et al. (2014) suggested a causal link between high tree fern basal area (BA), concomitant with the browsing effect of invasive ungulates, and a significant
reduction in the establishment success of fleshy-fruited canopy tree species in the Te Urewera area.

I hypothesise that *C. medullaris* will influence the communities developing beneath it in a way different to other pioneer species such that they show distinct assemblages indicative of subsequent forest types. Furthermore, I hypothesise that these differences in species composition are not related to differences in geographic distance from seed sources, which is an alternative possible explanation for variation in early successional vegetation communities at landscape scales.

This study aims to identify whether:

1. successional communities dominated by either *C. medullaris* or *K. robusta* are associated with different abiotic conditions or disturbance types;
2. tree ferns influence community assembly and resultant forest composition; and,
3. any differences in successional communities are determined by spatial separation of the plots in the landscape (i.e. dispersal failure) and not by abiotic conditions.

### 4.3 Methods

#### 4.3.1 Data Collection

*Vegetation community data*

To characterise early successional communities, I obtained a dataset from Auckland Council (AC) comprising 154 20 m × 20 m permanent vegetation plots (data collected between 2009 and 2013) (Fig. 4.2). These plots were a subset from a total of approximately 400 permanent plots established systematically across Auckland (Auckland Council 2014; Ruffell *et al.* 2015), with this subset targeting forest plots that support either *C. medullaris* and/or *K. robusta* with relative BAs of at least 20% of total BA. To improve representation of plots with a high abundance of *C. medullaris*, I supplemented the database with a further 12 plots across the Auckland Region. These supplemental survey sites with dense tree fern canopies were identified using aerial photography accessed through the AC GIS map viewer (http://maps.aucklandcouncil.govt.nz/aucklandcouncilviewer/). The survey methodology for the Auckland Council and supplemental plots followed permanent plot protocols established by Hurst and Allen (2007). Vegetation plots (20 m × 20 m) were installed in areas of homogenous vegetation.
For vascular plants, I recorded species and diameter at breast height of all trees (and tree ferns) > 2.5 cm DBH; counted saplings (< 2.5 cm DBH but > 1.35 m tall) over the entire plot; and subsampled seedlings (0 - 1.35 m tall) in 24 0.49 m radius circular plots (= 0.75 m² area each) in the plot (Hurst & Allen 2007). For each of the additional C. medullaris plots (12) and a comparable number of K. robusta plots (12) from the AC database, I collected data on a subset of biophysical conditions (described below).

**Abiotic factors**

To obtain general abiotic data for each of the 166 plots, I downloaded spatial data comprising modelled abiotic values and geological data for the Auckland region from the LRIS portal (see https://lris.scinfo.org.nz/ and Table 4.1). I derived a topographic position index (TPI) layer from elevation data using the `raster` package (Hijmans 2015) in R version 3.2.3 (R Core Team 2015). These data were loaded into a GIS (ArcMap™ 10.3.1) with the physical locations of the vegetation plots used to extract site specific values for these variables. Aspect data for each plot was converted from a bearing (0-360°) into partitioned values of ‘northness’ and ‘eastness’ (Zar 1999).

**Figure 4.2.** Survey sites were situated throughout the Auckland Region, the extent of the sites is delineated by the black outline (latitudinal range of polygon: 36°02.85’S to 37°14.80’S). Approximate location of Fig. 4.1 indicated by star.
Table 4.1. LENZ modelled environmental variables used to analyse vegetation community data. All layers are at a spatial resolution of 25 × 25 m.

<table>
<thead>
<tr>
<th>Data Layer</th>
<th>Units</th>
<th>Range (5% - Median - 95%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acid soluble phosphorus</td>
<td>Index</td>
<td>1 – 1 – 4</td>
</tr>
<tr>
<td>Annual water deficit</td>
<td>mm</td>
<td>0 – 38 – 119</td>
</tr>
<tr>
<td>Exchangeable calcium</td>
<td>Index</td>
<td>1 – 1 – 2</td>
</tr>
<tr>
<td>Induration soil hardness</td>
<td>Index</td>
<td>1 – 4 – 4</td>
</tr>
<tr>
<td>Mean annual solar radiation</td>
<td>MJ m² day⁻¹</td>
<td>149 – 152 – 155</td>
</tr>
<tr>
<td>Mean annual temperature</td>
<td>°C</td>
<td>11.3 – 14.4 – 15.8</td>
</tr>
<tr>
<td>Mean minimum temperature of the coldest month</td>
<td>°C</td>
<td>3.9 – 6.2 – 8.9</td>
</tr>
<tr>
<td>Monthly water balance ratio</td>
<td>Index</td>
<td>20 – 27 – 45</td>
</tr>
<tr>
<td>October vapour pressure deficit</td>
<td>kPa</td>
<td>25 – 36 – 41</td>
</tr>
<tr>
<td>Slope</td>
<td>° (degrees inclination)</td>
<td>0 – 11 – 33</td>
</tr>
<tr>
<td>Soil age</td>
<td>Index</td>
<td>1 – 2 – 2</td>
</tr>
<tr>
<td>Soil drainage</td>
<td>Index</td>
<td>2 – 4 – 5</td>
</tr>
<tr>
<td>Soil particle size</td>
<td>Index</td>
<td>1 – 2 – 5</td>
</tr>
<tr>
<td>Winter solar radiation</td>
<td>MJ m² day⁻¹</td>
<td>5.8 – 6.0 – 6.5</td>
</tr>
<tr>
<td>Fundamental soil layer (North Island)</td>
<td>Various</td>
<td>Various</td>
</tr>
<tr>
<td>Topographic Position Index</td>
<td>Index</td>
<td>71 – 471 – 34,970</td>
</tr>
</tbody>
</table>

Biophysical conditions

I used sub-canopy photography using a hemispheric fish-eye lens (Canon 450D, Sigma 4.5mm f/2.8 EX DC HSM) to quantify the understorey light environment in a subset of 24 plots, with photos taken at the north-east and south-west corners and the centre of the plot. Topography around the location of each photo was mapped using a compass and clinometer, and accounted for in the subsequent digital analysis. These photos were processed using Gap Light Analyzer 2.0 (Frazer, Canham & Lertzman 1999) to estimate canopy openness as a proxy for understorey light environment.

Soil samples were collected from three random locations in each of the 24 plots using a coring ring of 10 cm diameter. Loose litter was removed, then a 5 cm deep sample was extracted from the organic soil layer. Soil samples were returned to the lab and dried at 35 °C for 24 hours, root tissue removed, and the soil passed through a 2 mm sieve; samples for each plot were then combined. Samples were ground and analysed for total C and N concentration using an elemental analyser (TruSpec, LECO Corporation, St. Joseph, Michigan, USA). Soil standards (LECO Lot 1016, 1007) were used for calibration. Ten percent of samples were replicated and results were within the range of variation given for the standards. Analysis of pH was undertaken using the water method (# 106i). The remaining material was sent to the Landcare Research...
Environmental Chemistry Laboratory (Palmerston North) for analysis of available nitrogen (nitrate and ammonium by 2 M KCl extraction, method # 118) and phosphorus (Olsen-available Phosphorus, method # 124), respectively (Blakemore et al. 1987). Descriptions of methods 106i, 118 and 124 are available from http://www.landcareresearch.co.nz/resources/laboratories/environmental-chemistry-laboratory. A second 5 cm deep sample (using a cylindrical ring 10 cm in diameter) was taken at each location to derive bulk density; the samples were dried at 105 °C for 24 hours and then weighed (Gradwell & Birrell 1979).

Separate small samples (approx. 1 cm³) of soils from the organic soil layer were collected to estimate charcoal abundance as a proxy for recent fire history. These samples were prepared as described by Whitlock and Larsen (2001) and macro-charcoal fragments (> 2 mm) counted under a dissecting microscope.

4.3.2 Analysis

Vegetation community data

I analysed my data in four stages:

1. discrete vegetation assemblages were identified and their distinctiveness tested;
2. correlative relationships between these vegetation assemblages and environment were identified;
3. the potential influence of tree fern abundance on community assemblage was examined; and
4. the relative contributions of location and environment to variation in species composition were estimated.

Identification of discrete vegetation assemblages

For each plot, the BA of each species (combining trees and saplings) were calculated. The BA contribution of saplings (individuals < 2.5 cm DBH) was calculated using 1 cm DBH as a standard for each sapling. I used BA values as an index of relative abundance of each of the species per plot to calculate dissimilarities among plots using the Bray-Curtis dissimilarity measure (Faith, Minchin & Belbin 1987). This dissimilarity matrix was used to classify the plots using hierarchical agglomerative clustering with the complete linkage method (Quinn & Keough)
Non-metric multidimensional scaling (nMDS) was used to ordinate and graphically represent the data (Clarke 1993; Quinn & Keough 2002).

I used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to assess whether the groups identified by hierarchical classification were compositionally distinct. As *K. robusta* is more prevalent in the landscape than *C. medullaris*, the number of plots representing these pioneers is potentially unequal. PERMANOVA is sensitive to the relative dispersion of groups in unbalanced designs (Anderson & Walsh 2013); therefore, to assess whether any groups differed in their dispersion I used multivariate homogeneity of variance tests (PERMDISP2; Anderson 2006). To ensure the robustness of the analysis of any unbalanced groups, multiple permutations of PERMANOVA were undertaken using all plots (*n*) from the smaller group against the same number of plots (*n*) randomly sampled, without replacement, from the larger group, as suggested by Alekseyenko (2016). Previously only weak relationships have been derived between tree fern BA and height / crown size (although allometric equations have been produced; Beets *et al.* 2012), casting doubt on the use of BA as an index of tree fern biomass. Therefore, multiple PERMANOVA analyses were undertaken on the groupings using density (species stems plot$^{-1}$) and presence/absence data, and finally with the *C. medullaris* and *K. robusta* species data values entirely removed. The latter analysis was designed to avoid potential circularity in my arguments, i.e. are the statistical assemblages produced by hierarchical classification defined by more than simply the presence of the dominant pioneer species? Non-metric multidimensional scaling (nMDS) was used to ordinate and graphically represent the data and the groupings produced by the presence/absence and density data. I used similarity percentage (SIMPER) analysis on the complete vegetation dataset to identify the species that contributed most to dissimilarities between groups. The groups were then named using the approach established by Atkinson (1985) based on the structural and compositional features characterising the vegetation communities in each group. To assess whether there was any consistency in the community composition of the groups, indicator value analysis for species combinations (De Caceres & Legendre 2009) was applied to the forest stand and seedling data to identify any species that were faithful to the groups identified by the classification, irrespective of abundance.

**Abiotic factors**

Data were extracted from the GIS using the Spatial Analyst package (in ARcGIS) to produce a matrix of abiotic and topographic conditions present at each of the 166 vegetation plots (Table
Collinear variables were identified using multiple pair-wise correlations using a standard threshold of $r = |0.7|$, and removed from further analysis (Dormann et al. 2013). The data were standardised with a covariance matrix, and a principal components analysis (PCA) of the abiotic data then undertaken. Vectors representing the components explaining greater than 5% of variance were then fitted to the nMDS ordination of the floristic data; those components that had a statistically significant ($p < 0.05$) association with the distribution of plots in ordination space were plotted.

Regeneration niche

An index of seedling height-abundances for each species per plot was derived by multiplying their density by their height class (height class 1: 0–15 cm; 2: 16–45 cm; 3: 46–75 cm; 4: 76–105 cm; 5: 106–135 cm; Hurst & Allen 2007), then summing across the plot. Index values per species per plot were ordinated (nMDS with Bray–Curtis dissimilarity). PERMANOVA was used to assess separation in ordination space of plots on the basis of the previous groupings from the tree and sapling data. The abiotic data matrix had a new parameter ‘tree fern BA’ added, and another PCA and the analysis workflow described above repeated.

I used linear regressions between the total BA of tree ferns per plot and the numbers of woody species with BAs of $>0.5$ m$^2$ ha$^{-1}$ per plot to provide a comparison with the woody species richness vs tree fern BA data presented by Richardson et al. (2014).

Influence of space versus environment on composition

Geographic (Euclidean) distances between all plots were calculated as was the Euclidean distances between sites based on the abiotic data matrix used in the PCA analysis. These abiotic and geographic dissimilarity matrices were, along with the original vegetation dissimilarity matrix, subjected to simple and partial permutational Mantel tests (Mantel & Valand 1970).

All analyses were conducted using R-3.2.3 (R Core Team 2015) and the vegan 2.3-2 and indicspecies 1.7.5 libraries (De Cáceres et al. 2012; Oksanen et al. 2015).

### 4.4 Results

#### 4.4.1 Community analysis

Hierarchical classification and ordination suggest that the 166 plots fell into two groups (Fig. 4.3). SIMPER analyses show that the dissimilarities between these two groups are based on the
relative contributions of three species: *K. robusta* (17.1% contribution) in one group, and the tree ferns, *C. medullaris* (11.6%) and *C. dealbata* (13.4%) in the other. Resampled PERMANOVA analyses showed that these groups were distinct in ordination space ($F_{1,116} = 27.06 – 35.86; P < 0.001$), and PERMDISP2 analysis indicated that the two groups differ in their dispersion ($F_{1,116} = 0.04 – 5.95; P < 0.05$), with the *C. medullaris* pioneer-associated group more compact than the *K. robusta* pioneer-associated group in ordination space. Analysis of the tree and sapling density data produced two groups largely consistent with the BA analysis: 93% of plots remained in the *C. medullaris* group, and 71% of the *K. robusta* plots remained in the same group. Multiple PERMANOVA analyses on these density data also showed that the distinction between the groups remained ($F_{1,116} = 16.60 – 24.14; P < 0.001$). The hierarchical classification of the presence/absence data suggested three groups; 75% of the plots previously associated with the *C. medullaris* pioneer-associated communities remained distinct, while the *K. robusta* pioneer-associated plots were now represented by two groups. PERMANOVA of the groupings of the presence/absence data confirmed that they were compositionally distinct ($F_{1,116} = 16.66 – 22.48; P < 0.001$). In the final tree and sapling vegetation analysis, in which the BA values of the pioneer species *C. medullaris* and *K. robusta* were removed, the *K. robusta* group fragmented further into six separate groups (ordinations of these datasets in Appendix 2). The communities were named, following Atkinson (1985), on the basis of their composition and structure as *Cyathea medullaris / Cyathea dealbata* forest, and *Kunzea robusta / Cyathea dealbata* forest. *Cyathea dealbata* was common to both groups; however it had significantly greater basal area in the *C. medullaris* pioneer-associated communities ($13.4 ± 9.2 \text{ m}^2 \text{ ha}^{-1}$) than the *K. robusta* pioneer-associated communities ($4.9 ± 7.5 \text{ m}^2 \text{ ha}^{-1}$).

Indicator value analysis (using the complete BA dataset) recognised 14 species as ‘faithful’ (where $p < 0.001$ after Bonferonni correction) to *Cyathea medullaris / Cyathea dealbata* forest and 10 species to *Kunzea robusta / Cyathea dealbata* forest (Table 4.2, Appendix 2). Shade-tolerant forest canopy species with large fleshy fruits such as *Beilschmiedia tawa* (Lauraceae) were faithful to *Cyathea medullaris / Cyathea dealbata* forest in the tree and sapling data, with broadleaved canopy species such as *Hedycarya arborea* (Monimiaceae) faithful in both tree, sapling and seedling data. Species such as *Leucopogon fasciculatus* (Ericaceae) and *Phyllocladus trichomanoides* (Podocarpaceae) were most commonly associated with *Kunzea robusta / Cyathea dealbata* forest (Table 4.2; Appendix 2).
**4.4.2 Abiotic factors**

The first PCA component was significantly correlated with Axis 1 ($P < 0.05$) of the vegetation ordination, highlighted a gradient from steep ($13.4 \pm 6.5^\circ$ (mean $\pm$ 1 SD)), moist (annual water deficit $= 30.5 \pm 27.5$ mm) slopes towards lower elevation sites with increased annual water deficit ($53.2 \pm 25.9$ mm) and flatter topography ($10 \pm 5.6^\circ$) (Fig. 4.3).
**Table 4.2.** A summary of the canopy tree, understorey and tree fern species (tree, sapling and seedlings) that are identified as faithful to either *Cyathea medullaris / Cyathea dealbata* forest or *Kunzea robusta / Cyathea dealbata* forest; species presented here were faithful to a highly significant (*P* < 0.001) degree. The complete list of faithful species is in Appendix 2.

<table>
<thead>
<tr>
<th>Tree and Sapling Data</th>
<th>Species</th>
<th>Family</th>
<th>Species</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hedycarya arborea</em></td>
<td>Monimiaceae</td>
<td><em>Phyllocladus trichomanoides</em></td>
<td>Podocarpaceae</td>
<td></td>
</tr>
<tr>
<td><em>Olearia rani</em></td>
<td>Asteraceae</td>
<td><em>Kunzea robusta</em></td>
<td>Myrtaceae</td>
<td></td>
</tr>
<tr>
<td><em>Beilschmiedia tawa</em></td>
<td>Lauraceae</td>
<td><em>Leucopogon fasciculatus</em></td>
<td>Ericaceae</td>
<td></td>
</tr>
<tr>
<td><em>Dysoxylum spectabile</em></td>
<td>Meliaceae</td>
<td><em>Coprosma rhamnoides</em></td>
<td>Rubiaceae</td>
<td></td>
</tr>
<tr>
<td><em>Knightia excelsa</em></td>
<td>Proteaceae</td>
<td><em>Leptospermum scoparium</em></td>
<td>Myrtaceae</td>
<td></td>
</tr>
<tr>
<td><em>Melicytus ramiflorus</em></td>
<td>Violaceae</td>
<td><em>Olearia furfuracea</em></td>
<td>Asteraceae</td>
<td></td>
</tr>
<tr>
<td><em>Rhopalostylis sapida</em></td>
<td>Arecaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Coprosma grandifolia</em></td>
<td>Rubiaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Schefflera digitata</em></td>
<td>Araliaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Brachyglottis repanda</em></td>
<td>Asteraceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyathea medullaris</em></td>
<td>Cyatheaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyathea dealbata</em></td>
<td>Cyatheaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dicksonia squarrosa</em></td>
<td>Dicksoniaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyathea smithii</em></td>
<td>Cyatheaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Seedling Data</th>
<th>Species</th>
<th>Family</th>
<th>Species</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hedycarya arborea</em></td>
<td>Monimiaceae</td>
<td><em>Phyllocladus trichomanoides</em></td>
<td>Podocarpaceae</td>
<td></td>
</tr>
<tr>
<td><em>Laurelia novae-zelandiae</em></td>
<td>Atherospermataceae</td>
<td><em>Coprosma arboarea</em></td>
<td>Rubiaceae</td>
<td></td>
</tr>
<tr>
<td><em>Rhopalostylis sapida</em></td>
<td>Arecaeae</td>
<td><em>Kunzea robusta</em></td>
<td>Myrtaceae</td>
<td></td>
</tr>
<tr>
<td><em>Coprosma grandifolia</em></td>
<td>Rubiaceae</td>
<td><em>Coprosma rhamnoides</em></td>
<td>Rubiaceae</td>
<td></td>
</tr>
<tr>
<td><em>Schefflera digitata</em></td>
<td>Araliaceae</td>
<td><em>Leucopogon fasciculatus</em></td>
<td>Ericaceae</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Olearia furfuracea</em></td>
<td>Asteraceae</td>
<td></td>
</tr>
</tbody>
</table>

The organic soil layer showed significant differences in pH (*Cyathea medullaris / Cyathea dealbata* forest $\bar{x} = 5.83 \pm 0.25$, *Kunzea robusta / Cyathea dealbata* forest $\bar{x} = 4.96 \pm 0.26$) and ammonium concentrations (*Cyathea medullaris / Cyathea dealbata* forest $\bar{x} = 130.65 \pm 80.38$ mg kg$^{-1}$, *Kunzea robusta / Cyathea dealbata* forest $\bar{x} = 76.74 \pm 23.81$ mg kg$^{-1}$) between *C. medullaris* and *K. robusta* pioneer-associated communities, although the differing soil depths and densities at the sites meant little difference in ammonium pools (Table 4.3). The abundance of particulate macro-charcoal in the topsoil differed between the two communities (Table 4.3). Several *Kunzea robusta / Cyathea dealbata* forest sites had macro-charcoal amounts ($\bar{x} = 185.82 \pm 221.86$ pieces cm$^{-3}$) indicative of recent, local fire(s), whereas there was little evidence for local fire events in the *Cyathea medullaris / Cyathea dealbata* forest sites ($\bar{x} = 6.24 \pm 3.88$).
Figure 4.4. nMDS ordination of the height-weighted seedling abundance data; stress for the ordination plot is 0.25. Arrows indicate vector fits for environmental variables with significant correlations (P < 0.05); length of arrows indicates strength of correlation.

4.4.3 Regeneration niche

The seedling communities of the Cyathea medullaris / Cyathea dealbata forest and Kunzea robusta / Cyathea dealbata forest were separated in ordination space (PERMANOVA: F1-116 = 4.99 – 8.02; P < 0.001; Fig. 4.4), consistent with the separation of the tree/sapling communities. Three factors had significant correlations (P < 0.05) with the ordination axes, and indicated that nMDS Axis 1 described a gradient of decreasing elevation, increasing temperature and annual water deficit (P = 0.0001), and increasingly northerly-facing aspects on well-drained soils (P = 0.0036). The gradient most associated with Axis 2 of the ordination was increasing tree fern BA (62% of BA values represented by C. dealbata) (P = 0.036).

Woody species richness (only those with BAs > 0.5 m² ha⁻¹ counted) was not correlated with the total tree fern BA in either the entire vegetation dataset (slope ± SE = 0.05 ± 0.03, P = 0.15, adjusted R² = 0.01; total tree fern BA range: 0.00 – 42.76, \(\bar{x} = 5.54\)), or in the Cyathea medullaris
/ Cyathea dealbata forest (slope ± SE = -0.02 ± 0.04, \( P = 0.59 \), adjusted \( R^2 = 0.01 \); total tree fern BA range: 0.00 – 38.94, \( \bar{x} = 15.56 \)).

**Table 4.3.** Ranges of biophysical conditions (5% - Median – 95%) present in the organic soil layer in the Cyathea medullaris / Cyathea dealbata and Kunzea robusta / Cyathea dealbata forest communities (no multiple \( p \)-value corrections applied).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Cyathea medullaris / Cyathea dealbata</th>
<th>Kunzea robusta / Cyathea dealbata</th>
<th>ANOVA/ Wilcoxon Test ( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Carbon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conc. (%)</td>
<td>7.07 – 36.45 – 42.29</td>
<td>3.34 – 9.68 – 21.62</td>
<td>0.001 **</td>
</tr>
<tr>
<td>Pool (kg m(^{-2}))</td>
<td>0.39 – 4.97 – 9.09</td>
<td>0.31 – 2.07 – 4.77</td>
<td>0.022 *</td>
</tr>
<tr>
<td>Total Nitrogen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conc. (%)</td>
<td>0.15 – 0.24 – 0.51</td>
<td>0.01 – 0.11 – 0.16</td>
<td>0.007 **</td>
</tr>
<tr>
<td>Pool (kg m(^{-2}))</td>
<td>0.39 – 1.32 – 2.24</td>
<td>0.22 – 0.49 – 1.00</td>
<td>7.5 \times 10^{-4} ***</td>
</tr>
<tr>
<td>C:N</td>
<td>13.89 – 19.05 – 29.77</td>
<td>11.27 – 20.39 – 37.82</td>
<td>0.598 ns</td>
</tr>
<tr>
<td>Nitrate NO(_3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conc. (mg kg(^{-1}))</td>
<td>0.34 – 1.15 – 4.69</td>
<td>0.45 – 2.33 – 59.29</td>
<td>0.498 ns</td>
</tr>
<tr>
<td>Pool (g m(^{-2}))</td>
<td>0.00 – 0.02 – 0.07</td>
<td>0.00 – 0.42 – 1.27</td>
<td>0.264 ns</td>
</tr>
<tr>
<td>Ammonium NH(_4)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conc. (mg kg(^{-1}))</td>
<td>17.05 – 126.47 – 238.90</td>
<td>43.83 – 74.42 – 113.67</td>
<td>0.039 *</td>
</tr>
<tr>
<td>Pool (g m(^{-2}))</td>
<td>0.33 – 1.54 – 4.56</td>
<td>0.28 – 1.49 – 2.90</td>
<td>0.458 ns</td>
</tr>
<tr>
<td>NH(_4):NO(_3)</td>
<td>30.14 – 111.02 – 203.66</td>
<td>4.17 – 43.88 – 192.60</td>
<td>0.917 ns</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conc. (mg kg(^{-1}))</td>
<td>6.13 – 20.21 – 36.20</td>
<td>4.41 – 6.51 – 60.21</td>
<td>0.130 ns</td>
</tr>
<tr>
<td>Pool (g m(^{-2}))</td>
<td>0.03 – 0.32 – 0.53</td>
<td>0.03 – 0.14 – 1.74</td>
<td>0.682 ns</td>
</tr>
<tr>
<td>pH</td>
<td>5.52 – 5.79 – 6.17</td>
<td>4.57 – 5.01 – 5.27</td>
<td>2 \times 10^{-8} ***</td>
</tr>
<tr>
<td>Charcoal (pieces)</td>
<td>2.50 – 4.33 – 12.72</td>
<td>37.01 – 58.42 – 589.27</td>
<td>3 \times 10^{5} ***</td>
</tr>
<tr>
<td>Canopy openness (%)</td>
<td>1.07 – 2.62 – 4.05</td>
<td>1.58 – 3.79 – 11.67</td>
<td>0.104 ns</td>
</tr>
<tr>
<td>Litter depth (cm)</td>
<td>1.00 – 12.00 – 52.45</td>
<td>0.00 – 3.50 – 14.18</td>
<td>2 \times 10^{16} ***</td>
</tr>
<tr>
<td>Soil depth (cm)</td>
<td>8.14 – 13.60 – 26.11</td>
<td>1.30 – 4.20 – 10.39</td>
<td>2 \times 10^{16} ***</td>
</tr>
<tr>
<td>Tree fern BA (m(^2) ha(^{-1}))</td>
<td>3.96 – 21.28 – 57.99</td>
<td>0.00 – 2.14 – 22.39</td>
<td>2.2 \times 10^{16} ***</td>
</tr>
<tr>
<td>Bulk density g cm(^{-3})</td>
<td>0.09 – 0.21 – 0.84</td>
<td>0.34 – 0.47 – 0.82</td>
<td>0.043 *</td>
</tr>
</tbody>
</table>

4.4.4 Influence of spatial vs abiotic effects on composition

Analysis of the vegetation, abiotic and geographic dissimilarity matrices suggested a strong abiotic influence on the presence of Cyathea medullaris / Cyathea dealbata forest in the landscape (Table 4.4). There was no correlation between the abiotic variables and the distribution of Kunzea robusta / Cyathea dealbata forest in the landscape when these were considered independently of the Cyathea medullaris / Cyathea dealbata forest. Nor did I detect any dispersal limitation for successional species between the plots, with both simple and partial Mantel tests being non-significant.
Table 4.4. Partial Mantel test values for all tree and sapling data across the Auckland region, and values for separate regeneration pathways under *Cyathea medullaris / Cyathea dealbata* forest and *Kunzea robusta / Cyathea dealbata* forest.

<table>
<thead>
<tr>
<th>Vegetation Communities (n)</th>
<th>Distance</th>
<th>Mantel r</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combined pioneer communities (n = 166)</td>
<td>Geographic: environmental partialled out</td>
<td>-0.007 ns</td>
</tr>
<tr>
<td></td>
<td>Environmental: geographic partialled out</td>
<td>0.212**</td>
</tr>
<tr>
<td><em>Cyathea medullaris / Cyathea dealbata</em> forest (n = 59)</td>
<td>Geographic: environmental partialled out</td>
<td>-0.109 ns</td>
</tr>
<tr>
<td></td>
<td>Environmental: geographic partialled out</td>
<td>0.251**</td>
</tr>
<tr>
<td><em>Kunzea robusta / Cyathea dealbata</em> forest (n = 107)</td>
<td>Geographic: environmental partialled out</td>
<td>0.049 ns</td>
</tr>
<tr>
<td></td>
<td>Environmental: geographic partialled out</td>
<td>0.011 ns</td>
</tr>
</tbody>
</table>

Table 4.5. Tree fern BAs and numbers of woody species with BAs > 0.5 m² ha⁻¹ (\(\bar{x}\) ± 1.sd), in vegetation groups and in plots where tree fern BAs > 21.2 m² ha⁻¹; significance values from pairwise t-test with Bonferroni correction.

<table>
<thead>
<tr>
<th>Vegetation Groups</th>
<th>(\bar{x}) BA of tree ferns</th>
<th>(\bar{x}) no. woody species</th>
</tr>
</thead>
<tbody>
<tr>
<td>a <em>Cyathea medullaris / Cyathea dealbata forest</em> (n=59)</td>
<td>15.7 ± 9.9 b,c,***</td>
<td>9.4 ± 3.3 ns</td>
</tr>
<tr>
<td>b <em>Kunzea robusta / Cyathea dealbata forest</em> (n=107)</td>
<td>5.5 ± 8.0 a,c,***</td>
<td>6.6 ± 2.9 a,***</td>
</tr>
<tr>
<td>c Communities where tree fern BA &gt; 21.2 m² ha⁻¹ (n=21)</td>
<td>28.7 ± 5.9 a,b,***</td>
<td>7.8 ± 2.9 ns</td>
</tr>
</tbody>
</table>

4.5 Discussion

My results identified two distinct pioneer vegetation communities in northern New Zealand forests; the switch that determines which trajectory is followed is initially determined on the basis of abiotic filters (Fig. 4.3). Pioneer establishment differentiates along a gradient dominated by changes in annual water deficit and slope. I identified a distinct pioneer community associated with the pioneer species *Cyathea medullaris*, which promotes a seedling community modulated by the presence of *C. medullaris* and the presence of understorey *Cyathea dealbata*, thus supporting my first hypothesis. This pathway is different to the successional trajectory associated with sites associated with *Kunzea robusta* as a pioneer; even with *Cyathea dealbata* present in the understorey of this forest type (though at lower abundance than the *C. medullaris* associated type). Seedling community composition was associated with tree fern BA and this suggests a response in the regeneration niche to the presence of abundant tree ferns. Although it is not possible to evince independent biotic and abiotic filters (Cadotte & Tucker 2017), I suggest that, in line with the studies of Richardson *et al.*(2014), Coomes *et al.* (2005), Gillman
et al. (2004) and Walker et al. (2010), tree ferns mediate the regeneration niche beneath them when in sufficient abundance.

In considering early successional communities, one of the key questions is how different compositions are influenced by the original local site conditions or by the dominant pioneer. The influence of dominant pioneer species on the availability of seedling sites may have long-term effects on the composition of vegetation communities (Sullivan et al. 2007; Burton et al. 2011; Paterno et al. 2016). I suggest that New Zealand pioneers, both native and exotic, do influence the regeneration niche of potential forest dominants, by layering a biotic filter on the original heterogeneity in the landscape (Grubb 1977; Hille Ris Lambers et al. 2012). The relative abundance of these pioneers in the landscape is therefore likely to influence the trajectory, timeline and climax vegetation of succession.

4.5.1 Associations between C. medullaris and K. robusta pioneer communities, abiotic conditions and disturbance types

The hierarchical classification of the forest community vegetation data indicated two distinct vegetation communities associated with the pioneers C. medullaris and K. robusta. These pioneer-associated communities arose from preferential establishment under different topographic and edaphic conditions, and after fire (as inferred from soil charcoal) in the case of K. robusta. Cyathea medullaris has several specific traits that facilitate the role of a pioneer species on vegetation-free disturbed soil, often associated with edge habitats and high light environments. In particular, it can establish on exposed bare soil surfaces (after landslides and anthropic activities that disturb soils e.g. forestry harvesting) in, what are for many tree ferns, high irradiance situations (Bystriakova et al. 2011a). Cyathea medullaris pioneer-associated communities in the landscape (Fig. 4.1) lead to a (early) successional pathway supporting more notophyll (leaf length 75-125 mm) canopy species different from the well-described K. robusta succession (Wardle 1991), which supports forest communities dominated by microphyll (leaf length < 75 mm) taxa.

Kunzea robusta was more common as a pioneer species in drier, flatter, lower elevation areas (Burrows 1973); Burrell (1965) also observed an absence of Kunzea establishment on steep, wet slopes. In general, flat, relatively dry, lowland areas have been the focus of human activity over the last 750 years, particularly in terms of forest clearance of timber, intensive agriculture and susceptibility to anthropogenic fires (Ewers et al. 2006; Perry et al. 2012b). Fire destroys primary forest, maintains some fire-adapted successional communities, and causes soil and
nutrient loss from ecosystems (Perry et al. 2012a). Evidence of significant volumes of macro-charcoal in the topsoil under Kunzea robusta / Cyathea dealbata forest suggests that this community establishes in areas of the contemporary landscape that have experienced recurrent twentieth century anthropogenic fires, particularly in steeper, wetter areas where I have identified conditions that might otherwise be suitable for the establishment of Cyathea medullaris (Esler & Astridge 1974). Anthropic fire has been frequently connected to the re-establishment of K. robusta in early successional communities (Payton, Allen & Knowlton 1984; Perry et al. 2014). I suggest that the modern prevalence of K. robusta in the landscape, particularly as a pioneer species in regenerating forest, may, in part, represent reinvasion or encroachment in response to historic anthropogenic activities in the landscape, in particular fire and alteration of nutrient cycling (Perry et al. 2010). These K. robusta successions may develop where other naturally occurring successional systems would, in the absence of anthropic fire, have established.

Whilst it is almost impossible to disentangle the relative influence of fire and environment on the Kunzea robusta / Cyathea dealbata forest (Perry et al. 2010), the main abiotic drivers correlated with the establishment of the Cyathea medullaris / Cyathea dealbata forest were increased slope steepness, more neutral soil pH, lower ambient temperatures and lower annual water deficit. A more level topography (for example lowland plains) in association with drier, more acidic soils, will likely facilitate the development of a Kunzea robusta / Cyathea dealbata forest, responding to soil catena from ridge to gully, and conditions most prone to fire and historic anthropogenic activities (logging, grazing, etc.). The Cyathea medullaris and Kunzea robusta associated community establishment process is initiated by abiotic drivers and subsequently modulated and amplified in part by the traits of the pioneers, and the relative abundance of Cyathea tree ferns.

4.5.2 Influence of C. medullaris and K. robusta on the regeneration niche and compositional trajectory towards conifer-broadleaved forests vs. A. australis associated forests

Ordinations of the tree, sapling and seedling composition data suggest that pioneer communities are sorted on the basis of interactive macro-environmental gradients in temperature, elevation, topography and annual water deficit (Fig. 4.3). However, the BA of tree ferns, which appears decoupled from the abiotic drivers of pioneer species establishment, also influences the position of seedling communities in ordination space. Cyathea medullaris / Cyathea dealbata forest
supports the regeneration of broadleaved podocarp communities characterised by *Laurelia novae-zelandiae* (Atherospermataceae), *B. tawa*, *Dysoxylum spectabile* (Meliaceae) and *Prumnopitys ferruginea* (Podocarpaceae), whereas species regenerating in *Kunzea robusta / Cyathea dealbata* forest (relatively lower tree fern abundance) tend towards *A. australis* associated communities faithfully supporting species characteristic of drier, more acid and nutrient-poor soils such as *Coprosma arborea* (Rubiaceae) and *P. trichomanoides* (Burns & Smale 1990; Wyse 2014; Jager et al. 2015). This analysis does not, however, suggest conifer-dominance in post-*Kunzea robusta / Cyathea dealbata* forest; the relatively small number of faithful species in this community compared to the *Cyathea* pioneer-associated system rather suggests a less predictable community composition in *Kunzea* pioneer-associated systems.

Studies describing patterns associated with tree fern prominence in forest understories suggest a suppression of podocarp regeneration (Wardle 1974; Smale et al. 1987; Coomes et al. 2005), and Norton (1991) suggests that seedling establishment is suppressed within tree fern drip-lines. Many of New Zealand’s tall podocarp species are light demanding, hence shaded conditions are not conducive to regeneration (Ebbett & Ogden 1998; Lusk, Duncan & Bellingham 2009). My data indicate that complete suppression is not necessarily a trait of ecosystems with abundant tree ferns as a rich suite of species occur in such systems. Species associated with *Cyathea medullaris / Cyathea dealbata* forest such as *D. spectabile* and *Beilschmiedia tawa* are likely present in these communities as a result of their shade-tolerant life-history traits (Smale & Kimberley 1983; Lusk, Jorgensen & Bellingham 2015). Furthermore the shade tolerant *P. ferruginea* is, as seedlings, a faithful component of the *C. medullaris / Cyathea dealbata* forest suggesting that certain traits, in particular shade-tolerance, might be significant in determining community assembly and regeneration of the canopy in these systems. *Prumnopitys ferruginea* is also the most common species recorded in the seedling bank by Norton (1991) in a stand where tree ferns were an abundant component of the understorey.

No negative relationships were identified between total tree fern BA per plot and numbers of woody species in either the entire vegetation dataset, or the *Cyathea medullaris / Cyathea dealbata* forest in my study (Table 4.5); the BAs recorded ranged in excess (>42.8 m² ha⁻¹) of those described in Richardson et al. (2014) (21.2 m² ha⁻¹). I suggest that high tree fern BA *per se* does not suppress regenerating canopy species richness, and that other factors such as dispersal failure, herbivory and the long-term disturbance regime are a more significant driver for the recruitment failure and arrested successions observed by Richardson et al. (2014). The mechanisms underpinning the influence of tree ferns on seedling regeneration cannot be
established from my data because they lack detailed spatial resolution and the location of the tree ferns in relation to the seedling subplots was not recorded; further experimental work is necessary to determine this.

While nutrient concentrations in the organic layer of the two types of sites that were sampled were similar, they did differ in pH, and total C and N pools; all three variables were higher in the organic layer sampled underneath tree fern dominated communities. Isolating the effect of tree ferns on soil nutrient status is difficult because tree ferns are patchily abundant in the understorey of *Kunzea robusta / Cyathea dealbata* forest. Moreover, tree fern impacts may be localised as indicated by Silvester (1964) for *D. squarrosa*. The distinct differences in pH, total N and C across the two sets of communities may be a response to the presence of these distinct vegetation communities. Nevertheless, tree ferns will have a strong direct influence on the establishment of seedlings through a combination of lowering available light levels below the canopy and through macro-litterfall (Gillman *et al.* 2004) creating deep litter (Table 4.3).

Distinctive communities assembled under the canopies of *C. medullaris* and *K. robusta* were characterised by a recurring suite of high fidelity species that occurred in multiple tiers (for example, *B. tawa*, *Beilschmiedia tarairi* (Lauraceae), *D. spectabile* and *Vitex lucens* (Lamiaceae) were identified as faithful to the *Cyathea medullaris / Cyathea dealbata* forest). This outcome suggests that there is a consistent compositional assembly for the *C. medullaris* community. The *Kunzea robusta / Cyathea dealbata* forest, present in a narrower range of abiotic conditions than the *Cyathea medullaris / Cyathea dealbata* forest, was more variable in community composition, and had fewer faithful species as it fragmented into six separate groups with the removal of the pioneer species from the analysis. While it is difficult to quantify the extent of the contribution of tree fern presence, the number of species faithful to the *Cyathea medullaris / Cyathea dealbata* forest suggests that tree ferns function as a strong biotic filter. Teasing apart the influences of fire from the abiotic conditions of the *Kunzea robusta / Cyathea dealbata* forest limits interpretation, however, it is likely that the presence of *Cyathea dealbata* in varying abundance within these systems affects the regeneration niche again through shading, nutrient cycling and macro-litterfall (Gillman *et al.* 2004; Grubb 1977; Perry *et al.* 2010; Richardson *et al.* 2014). The seedling community data available to this study were limited in the full consideration of tree ferns as drivers of community assembly; tree fern trunks provide establishment surfaces for many small-seeded species (Bellingham and Richardson 2006; Gaxiola *et al.* 2008). Although the relatively smooth trunk surface of *C. medullaris* provides
relatively few attachment points for higher plants (Beever 1984), the presence of \textit{C. dealbata} is likely to influence assembly as an establishment surface.

\subsection*{4.5.3 Influence of spatial versus abiotic effects on community composition}

The lack of a strong distance effect between plots vs. community dissimilarity (low values for Mantel tests of Euclidean distance) across the entire Auckland region (including the islands of the Hauraki Gulf) suggests local abiotic conditions are a stronger filter on community assembly in these ecosystems than is species dispersal. Furthermore, it would appear that the establishment of canopy tree species in regenerating forest is occurring despite seed predation and localised herbivory of seedlings and saplings (Smale, Hall & Gardner 1995; Grant-Hoffman, Mulder & Bellingham 2010; Morales, Perry & Burns 2016). Where mammalian seed predators are present in the landscape, they preferentially use warmer, steeper topography, and prefer forest supporting \textit{Beilschmiedia} spp., \textit{D. spectabile} and \textit{V. lucens} over \textit{K. robusta} (King et al. 1996; Ogden & Gilbert 2009). This pattern suggests that if seed predation were a significant determinant of differences between the seedling communities then the \textit{Cyathea medullaris / C. dealbata} forest would be more affected, but this was not apparent in my analyses.

A common approach to the restoration of native forest systems in northern New Zealand is to plant \textit{K. robusta} as a pioneer species. This study, I suggest, should encourage promoters of such regeneration and restoration schemes in the North Island to consider using \textit{C. medullaris} where conditions are appropriate (increased slopes, more neutral soil pH, lower ambient temperatures and lower annual water deficit). Planting, and establishment of tree fern sporophytes post-translocation, may not be successful, as sporophytes are not necessarily tolerant or easily transplanted (Eleutério & Pérez-Salicrup 2009). Furthermore, little is known of the ecology of the gametophyte life-stage of the tree ferns limiting a ‘self-seeding’ approach by providing a source of spores. Herbicide spraying of \textit{Cenchrus clandestinum} (kikuyu grass) at Tāwharanui Regional Park (north of Auckland) removed a dense, deep sward of grass from a steep bank on the southern slopes of the peninsula (on which the park is located) creating an opportunity for \textit{C. medullaris} to establish (M. Maitland, pers. comm.). This outcome suggests that in some conditions it will be possible to induce a stand of \textit{C. medullaris} to establish as a precursor to tall coastal broadleaved forest.
4.6 Conclusion

Forest regeneration following stand-level vegetation removal, in northern New Zealand can commence with pioneer communities of either *Kunzea robusta* or *Cyathea medullaris*. Tree ferns as pioneers are rare globally, particularly in the temperate biome, and in this study I show that they favour steep slopes, with decreased annual water deficit. Under these conditions shade-tolerant broadleaved and podocarp forest species establish beneath the tree ferns. In contrast, *K. robusta* is more common on flat, dry sites that have often experienced fire, and is associated with less shade-tolerant sclerophyllous small-leaved forest species. The communities that establish with these distinct pioneers are different, although both comprise a *C. dealbata* understorey, and appear to support distinct vegetation associations: *C. medullaris* systems are associated with a broadleaved-podocarp forest community; *K. robusta* systems are associated with *A. australis* communities.

The presence of a high abundance or biomass of *C. medullaris* and *C. dealbata* on sites not historically affected by fire did not limit the establishment of shade-tolerant canopy trees. Furthermore, the presence of tree ferns was strongly associated with seedling communities in ordination space, which suggests biotic filtering across all communities where tree ferns are recorded, both as pioneers, and in the understorey. I found no evidence of community composition being limited by a lack of seed dispersal agents, nor evidence to suggest that high tree fern density is a limiting factor on succession.

This description of a pioneer community dominated by tree ferns is novel for the southern temperate region. Although it is not possible to clarify landscape-level feedbacks from correlative studies alone, this study serves to demonstrate the likely significant influence of tree ferns in the early development of forest ecosystems. Future studies attempting to disentangle the role of tree ferns as determinants of community assembly should focus along gradients of dominance of *K. robusta* vs. *C. dealbata*. In contrast to *K. robusta* vs. *C. medullaris*, the abiotic controls on these species’ establishment are less dichotomous, and hence the influence of tree fern presence on community assembly more detectable. Applied research into how to ‘seed’ *C. medullaris* into the landscape, coupled with research into the ecology of the gametophyte of this unusual tree fern species would usefully inform future habitat restoration projects.
Chapter 5

Seedling community response to tree fern micro-site filtering

5.1 Abstract

Large pteridophytes frequently co-occur with conifers and angiosperms in indigenous temperate evergreen forests but their interactions are poorly understood. This study investigates the impact of tree ferns on the regeneration niche of vascular woody species to determine whether the presence of tree ferns in the understorey favours seedling establishment of particular angiosperm and conifer species. The spatial pattern of vascular plant seedlings with respect to focal tree ferns (*Cyathea dealbata*) and the response of seedlings to experimental removal of fern fronds or associated ground litter were used to understand the influence of tree ferns on regeneration processes. Vascular plant seedling abundance was reduced by up to 39% in tree fern micro-sites; although apparently experiencing similar levels of suppression (up to 34%), conifer seedlings responded most consistently after a frond-removal treatment. Frond-shading and deep litter appear to reduce seedling species richness and seedling abundance. Longer-term studies coupled with simulation modelling would allow the significance of filtering of seedling establishment to be evaluated in the context of high turnover and low survival rates.

5.2 Introduction

The interaction of abiotic and biotic factors influence seedling establishment and define the regeneration niche that controls community assembly (Grubb 1977; Gillman *et al.* 2004; Cadotte & Tucker 2017). Biotic influence can constrain or facilitate the regeneration niche of many species including the presence of keystone species in the canopy, such as kauri *Agathis australis* (Rigg *et al.* 2002; Wyse, Burns & Wright 2014), seed dispersal and herbivory (Viola *et al.* 2010; Turley *et al.* 2017). Overstorey shading and litter quality and quantity are also significant filters on the success of vascular seedling establishment (Gillman & Ogden 2001; Ibáñez *et al.* 2007; Valladares *et al.* 2016). These biotic drivers are commonly considered under the dominant influence of canopy species, but understorey vegetation may also be important, yet less frequently considered, driver of the forest regeneration niche (Takahashi 1997; Weng *et al.* 2017).
Canopy structure drives understorey irradiance levels, and shade influences seedling establishment through reduced photosynthetically active radiation (PAR), modified temperature, humidity and biotic interactions (Coomes et al. 2005; Valladares et al. 2016). Shading can be increased significantly where tree ferns are present in the understorey; 10% of PAR reaches the forest floor under tree ferns in Hawai’ian forest (Burton & Mueller-Dombois 1984). However, no data is available that compares the shading effect of tree ferns to other prominent understorey species or growth forms (e.g. palms). Where ferns provide dense ground cover, e.g. Blechnum discolor, shading may be sufficient to inhibit the establishment of shade-intolerant conifer seedlings and reduce their growth rates resulting in angiosperm dominated forest communities (Coomes et al. 2005).

Tree ferns are a common component of the understorey of southern temperate and tropical podocarp-hardwood forests and can dominate the understorey (represent up to 50% of stems) and influence the spatial availability of sites suitable for seedling establishment of some canopy or understorey species (Brock et al. 2016, 2018). However, to date only the effects of tree fern macro-litterfall have been evaluated as a potential mechanism influencing vascular species establishment (Gillman & Ogden 2001; Gillman et al. 2002, 2004). It is suggested that via macro-litterfall, tree ferns appear to act as filters on the potential regeneration niche in forests, independent of canopy composition.

In New Zealand a commonly occurring species of understorey tree fern is Cyathea dealbata which has a strong presence in many shrub and forest habitats (Wiser et al. 2011). Light interception by C. dealbata is potentially significant in terms of the selective regeneration of the forest community (Brock et al. 2018). Tree ferns also develop deep (up to 90 cm) litter layers, and the conditions beneath their canopy (tree fern micro-site) is subject to macro-litterfall as fronds senesce and detach (Enright & Ogden 1987; Gillman & Ogden 2001). Experimental studies in northern NZ forests show that macro-litterfall, of tree ferns, palms and branch abscission from Agathis australis (Araucariaceae), is responsible for up to 14% of seedling mortality (along 100 m forest transects), but no information is available on the relative influence of tree fern litter on seedling establishment (Gillman et al. 2004). Litter can reduce establishment surfaces through shading, mechanical impedance, biochemically and influencing geothermal amplitude with facilitative, or suppressive effects (Facelli & Pickett 1991; McAlpine & Drake 2003). Tree fern trunks can provide an establishment surface for hemi-epiphytic canopy species, including species of Weinmannia in New Zealand (Coomes et al. 2005; Gaxiola et al. 2008); however, epiphytism on tree fern trunks will not be investigated in this study.
Table 5.1. Questions asked in this study with details of statistical analyses used and key outcomes (as described in this chapter).

<table>
<thead>
<tr>
<th>Aims and questions</th>
<th>Statistical approach</th>
<th>Key outcomes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field study: Do understory tree ferns influence vascular species seedling community composition</td>
<td>Analysis of seedling community dissimilarity by 1) ordination, 2) PERMANOVA to evaluate whether communities inside and outside tree fern micro-sites are distinct or otherwise, and 3) indicator species analysis to identify faithful species to micro-sites or otherwise</td>
<td>Figure 5.2</td>
</tr>
<tr>
<td>1. Is there any evidence of changes in seedling community in relation to tree fern micro-sites?</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Are conifer seedlings consistently less abundant in tree-fern micro-sites?</td>
<td>Kruskal-Wallis tests comparing means of conifer seedling abundance in and out of tree-fern micro-sites</td>
<td>Figure 5.3</td>
</tr>
<tr>
<td>3. How do tree fern micro-sites differ from other areas of the forest?</td>
<td>Logistic regression model with fixed and random effects (GLMM) evaluating recorded biotic and abiotic variables as predictors of TF micro-site conditions</td>
<td>Table 5.2</td>
</tr>
<tr>
<td>4. What recorded biotic and abiotic variables best predict seedling abundance in the plots?</td>
<td>Poisson regression model with random and fixed effects evaluating recorded biotic and abiotic variables as predictors of seedling abundance</td>
<td>Table 5.2</td>
</tr>
<tr>
<td>5. What recorded biotic and abiotic variables best predict conifer seedling abundance in the plots?</td>
<td>Negative binomial hurdle model with random and fixed effects evaluating recorded environmental variables as predictors of seedling abundance</td>
<td>Table 5.2</td>
</tr>
<tr>
<td>Experimental manipulation: Identify the relative influence of shade and litter accumulation on vascular plant seedling establishment beneath tree ferns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Managing experimental confounding factors: Are experiment location site effects influencing seedling communities present in study plots?</td>
<td>Analysis of seedling community dissimilarity by 1) ordination, 2) PCA of environmental data, 3) fitting of PCA vectors to ordination to identify distinctions between sites, and 4) PERMANOVA to evaluate whether communities at different sites are distinct</td>
<td>Figures 5.4a, and Table 5.3</td>
</tr>
<tr>
<td>7. Does the vascular plant seedling community reflect shade or litter treatments around tree ferns?</td>
<td>Comparisons of pre- and post-treatment communities by 1) multivariate homogeneity of dispersion analyses to evaluate how communities change in ordination space with treatment, and 2) summarise vectors (distance and angle) between pre- and post-treatment seedling plots in ordination space, 3) ordination of site-specific data, 4) compute α- and β-diversity indices for plots and compare between treatments</td>
<td>Figures 5.4b, 5.4c, 5.4d and Table 5.4</td>
</tr>
<tr>
<td>8. Are there any indicator vascular species associated with the post-treatment communities?</td>
<td>Indicator species analysis of treatment communities (pre- and post-treatment)</td>
<td>See text</td>
</tr>
</tbody>
</table>

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The aim of this study is to understand the mechanisms (frond-shading and macro-litter) by which tree ferns influence vascular plant establishment and therefore forest community assembly in New Zealand. I test the hypothesis of Coomes et al. (2005) that indigenous conifers are suppressed in tree fern micro-sites through frond-shading effects, and establish the relative influence of deep litter and shading on woody vascular species establishment. To achieve this I conducted: i) a field study to assess whether the presence of *C. dealbata* in the understorey influences vascular plant seedling establishment; and, ii) an experimental manipulation (frond and litter removal) to identify the mechanisms behind the patterns observed in seedling communities recorded in part 1.

The research was undertaken in northern New Zealand temperate broadleaved-podocarp forests where *C. dealbata* was present in varying densities. I ask two broad questions:

1. Do understorey tree ferns influence vascular species seedling community composition?
2. What are the mechanisms by which tree ferns influence vascular species seedling community composition?

These are broken down into eight questions (Table 5.1) on seedling community establishment dynamics in relation to micro-sites under tree ferns and how seedling communities respond to treatments where environmental variables, identified as influential on seedling community in the field study, are manipulated. Where appropriate throughout this chapter, italicised references [Q x.] are inserted to waypoint the reader as to what question the following paragraph relates.

### 5.3 Methods

#### 5.3.1 Field study – pattern identification [Q 1-5]

I used a combination of plots and plot-less sampling methods to sample both the seedling community and the range of potential drivers from nearest tree to topography, and the presence of understorey tree ferns: specifically *C. dealbata*. I installed plots (1 × 1 m; *n* = 164) at 10 m intervals along 17 × 100 m transects in temperate broadleaved-podocarp forest in the Waitākere Regional Park (Auckland) and Coromandel Peninsula (Waikato) through areas supporting an understorey of *C. dealbata* (Fig. 5.1). In each plot all spermatophyte seedlings (individuals with height < 1.35 m) were identified to species-level and tallied by height class (height class 1: 0–15 cm; 2: 16–45 cm; 3: 46–75 cm; 4: 76–105 cm; 5: 106–135 cm; Hurst and Allen 2007). From
the centre of each seedling plot, using a point-centred quarter (PCQ) methodology (Cottam & Curtis, 1956), the nearest four trees, where stem diameter at breast height (1.37 m; DBH) > 5 cm, and nearest four *C. dealbata* were identified. If the nearest tree fern was either *D. squarrosa* or *C. smithii*, the seedling plot was disregarded; as were plots where *Rhopalostylis sapida* was a closest tree as these palms produce macro-litter that might otherwise confound the study. I recorded the distance to each tree and tree fern, DBH for trees and tree ferns, height and maximum canopy width for tree ferns only from the location of each seedling plot, along with the declination (°) and aspect of the slope and four measurements of litter depth. To estimate canopy cover as a proxy for PAR, sub-canopy photos were taken using a hemispheric fish-eye lens (Canon 450D, Sigma 4.5mm f/2.8 EX DC HSM), and processed using Gap Light Analyzer 2.0 (Frazer *et al.* 1999). A GPS co-ordinate was recorded for each plot and was later used to extract point data from LRIS (see https://lris.scinfo.org.nz/) environmental layers using GIS (ArcMap™ 10.3.1) to provide data on soil moisture deficit and topographic index. The topographic position index (TPI) layer was derived from elevation data using the raster package (Hijmans 2015) in R version 3.2.3 (R Core Team 2015). Aspect data for each seedling plot was converted into partitioned values of ‘northness’ and ‘eastness’ (Zar 1999).

**Figure 5.1.** Locations of field study (black stars) and experimental manipulation (white stars) across the Auckland and northern Waikato regions of New Zealand
**Analysis - field study**

The vascular plant seedling data was height-weighted, by multiplying seedlings by their height class, and the seedling plot data transformed (Hellinger transformation; Legendre & Gallagher 2001), and ordinated using classical multidimensional scaling (CMDS, also known as principal co-ordinates analysis) ordination with Bray-Curtis dissimilarity (Clarke 1993). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used to assess whether the seedling communities underneath the canopy and away from tree fern canopies were compositionally distinct. Lastly, an indicator species value analysis for species combinations (De Caceres & Legendre 2009) was undertaken of communities under and away from tree ferns to identify any species that were faithful (irrespective of abundance) to either condition.

Kruskal-Wallis tests were used to compare total seedling abundance and conifer seedling abundance inside and away from tree fern influenced micro-sites. The imbalance in the sample sizes (111 plots in tree fern micro-site vs 53 away from tree fern) resulted from sampling bias: when sampling in areas where tree ferns are present, they are generally in relatively high densities such that there is a lower likelihood that plot locations selected at random will be outside a tree fern micro-site.

The following fixed and random effects models (generalized linear mixed models) were used (fixed effects: biotic and abiotic variables recorded at each plot; random effects: transect location) to determine:

1. Evaluate the recorded abiotic and biotic variables (e.g. litter depth or slope) as predictors of presence / absence of tree fern micro-sites using logistic regression.

2. Determine the recorded abiotic and biotic variables that best predict seedling abundance in a plot (e.g. canopy cover or distance to nearest tree fern) using poisson regression.

3. Determine the recorded abiotic and biotic variables (e.g. topography or distance to nearest tree) that best predict conifer seedling abundance in a plot using a negative binomial hurdle model (Bolker 2015).

**5.3.2 Experimental manipulation /Q 6-8/**

Two pairs of 100 m transects were installed, perpendicularly to access roads, at the University of Auckland’s Huapai and Oratia reserves (Fig. 5.1). At 10 m intervals along transects the four
nearest *C. dealbata* in each quarter (PCQ methodology) were identified and tagged; height and canopy width of each tree fern was recorded. A 1 m² seedling plot was installed under the north side of each tree fern with the southern point of the quadrat abutting the base of the trunk; all seedlings of woody plants were identified to species and placed into height classes (Hurst & Allen 2007). Litter depth (to firm ground) was measured at the four cardinal directions around each tree fern; and in the corner of each plot, four soil moisture recordings were taken using a Hydrosense 2 (HSII) meter. The declination (°) and aspect of the slope were recorded for each tree fern, along with trunk height and canopy width. At each site 80 tree ferns were tagged and seedling plots installed (*n* = 160); 40 tree ferns and plots per treatment.

The experimental design was multi-factorial, multi-level (2×2) where each tree fern represented one of four treatments. The two factors were light and litter, each had two levels – remove litter / fronds, or leave as found. Litter removal required the removal all tree fern macro-litter: fallen tree fern fronds, and, where partially decomposed, stipes and pinnae. Frond removal required the removal of all fronds from 270° (west) to 90° (east) above the seedling plot (i.e. on a 180° arc on the north side of the tree fern). Each marked tree fern was randomly assigned one treatment:

Treatment 1. Control (neither litter nor fronds removed; *n* = 40 plots)

Treatment 2. Litter and frond removal (*n* = 40 plots)

Treatment 3. Frond removal only (*n* = 40 plots)

Treatment 4. Litter removal only (*n* = 40 plots)

Where tree ferns had their fronds removed pre- and post-removal light levels PAR levels were recorded using a Field Scout Quantum Light Meter at ground level; fronds were removed with telescopic pruners.

Soil samples were collected for nutrient assays to factor in whether local soil conditions were driving seedling community assembly. A 60 g organic soil layer sample (from top 5 cm) was collected at a random location immediately adjacent to every seedling plot. Soil samples were dried in the lab at 35 °C for 24 hours, root tissue removed, and the soil ground and passed through a 2 mm sieve. All soil samples were sent to Brookside Laboratories Inc, Ohio (USA) for analysis of pH, organic matter, Bray I phosphorus, cation exchange capacity (and % base saturation of cation), available nitrogen (NO₃⁻, NH₄⁺), and Mehlich III Extractable P, Mn, Zn, B, Cu, Fe, Al, S, Ca Mg, K and Na.
Transects at the two sites were revisited over a 12-month period to monitor re-growth of fronds and new growth was removed as appropriate. Litter, where it had accumulated, was also removed as appropriate in the relevant treatments. Seedling plots were re-measured after one year.

Analysis – experimental manipulation

For ordination, a seedling height-abundance index per species per plot was derived by multiplying seedling density by height class (as above), then summed by species for the plot. Index values (per species per plot) of both pre- and post- treatment data were ordinated together using CMDS with Bray–Curtis dissimilarity. Biophysical and soil nutrient data were tested for collinearity using multiple pair-wise correlations; derived, or the less ecologically relevant of co-related variables that exceeded a threshold of $r = |0.7|$ were then not considered for further analysis (Dormann et al. 2013).

To ascertain whether dissimilarity in seedling community composition between sites was driven by biophysical characteristics or soil conditions (environmental), a principal components analysis (PCA) was undertaken on the standardised (covariance matrix) environmental data. Vectors representing the components explaining greater than 5% of variance were then fitted to the post-treatment points in the complete CMDS ordination of the pre- and post-treatment vegetation data to determine whether local environmental conditions are driving seedling community composition. I used PERMANOVA to assess whether the two experimental sites (Oratia and Huapai) supported distinctive seedling communities.

To define responses in seedling community to light and litter treatments I assessed whether any groups differed in their dispersion post-treatments, when compared to pre-treatment dispersion, using multivariate homogeneity of variance tests (PERMDISP2; Anderson, 2006). Differences in dispersion values were calculated for each treatment community (pre- and post-treatment) to establish whether treatment communities were becoming more or less dissimilar in their composition. I took a multi-faceted approach to interpreting and summarising the data, as single analyses are unable to adequately describe the responses in the plot-based seedling communities.

To visually represent overall change in seedling community dissimilarity between treatments (as a visual summary of multivariate homogeneity of variance tests) I calculated the change in position of plots in ordination space and summarised these per treatment. I achieved this by comparing the pre and post treatment location of each plot in ordination space. The distance
between these points and the azimuth (°) of the second (post treatment) point in relation to the first (pre-treatment) were calculated. These data were then plotted in a circular histogram.

To identify whether apparent seedling community response to treatment at either site was not a product of intra-site variation in environmental conditions, the pre and post-treatment seedling community data were ordinated per site using CMDS (Bray-Curtis dissimilarity). Site-specific environmental data were then fitted to the post-treatment points in these ordinations. PERMANOVA was undertaken to identify whether there are composition differences in the seedling communities pre- and post-treatment. Finally, all environmental data were compared between treatments using pairwise \( t \)-tests with multiple \( p \)-value corrections (Hochberg adjustment). To further describe change in the seedling communities within the treatment, pre- and post-treatment plot values I calculated metrics related to plot alpha-diversity: Shannon Wiener diversity index (SW), Simpson’s diversity index (SI), species richness (S), and community evenness (J) (Magurran 2004). Inferring patterns of change solely from abundance-based dissimilarity may overlook differences in nestedness and turnover (Baselga 2013); patterns of species loss and replacement are highly pertinent to this study. Beta-diversity values computed were: temporal seedling community turnover (\( \beta_{\text{sim}} \)) and nestedness (\( \beta_{\text{sne}} \)); these show temporal substitution of species (\( \beta_{\text{sim}} \)) and the extent to which the post-treatment community is a subset of the pre-treatment (\( \beta_{\text{sne}} \)) (Baselga 2010).

PAR levels pre- and post-frond-removal (included in treatments 1 and 2) were compared. An indicator species analysis was undertaken of pre- and post-treatment communities to identify species faithful to the pre- and post-treatment communities across both sites.

All analyses were conducted using R-3.2.3 (R Core Team 2015) and the vegan 2.3-2., indicspecies 1.7.5., betapart 1.4-1. (De Caceres & Legendre 2009; Hijmans 2015; Oksanen et al. 2015; Baselga et al. 2017; Magnusson et al. 2017) packages.

5.4 Results

5.4.1 Field study

[Q 1.] The seedling communities recorded in the plots beneath and away from tree fern canopies overlap in ordination space (height-weighted seedling data; Fig. 5.2). PERMANOVA showed that the seedling communities away from tree fern micro-sites are not distinct in ordination space (\( F_{1,162} = 1.116; P = 0.3391 \)). Indicator species analysis, with multiple \( p \)-value corrections
applied, identified only *Rhopalostylis sapida* (associative statistic 0.256, *p* = 0.001) as faithful to the seedling communities outside the tree fern micro-site.

[Q 2.] The average seedling abundance in plots underneath a tree fern canopy was significantly lower at 19.0 ± 16.0 (± 1 SD), compared with an average of 39.2 ± 34.7 seedlings in plots outside tree fern micro-sites (*H* = 17.965; *p* < 0.001). The average number of conifer seedlings in a tree fern micro-site is 0.6 ± 1.9; plots outside a tree fern micro-site supported 0.9 ± 2.2 conifer seedlings (*H* = 9.0447; *p* = 0.003). Overall, there was a reduction in total seedling abundance (up to 39%) and conifer seedling abundance (up to 34%) in a tree fern micro-site (Fig. 5.3). Across the 16 transects the *C. dealbata* average canopy width (diameter of tree fern micro-site) was 3.3 ± 2.0 m (*n* = 164).

![Figure 5.2. CMDS ordination of transformed, height-weighted field study seedling community plot data. Points are differentiated on the basis of whether the plot was within, or away from tree fern micro-sites. PERMANOVA showed that the seedling communities away from tree fern micro-sites are not distinct in ordination space (*F*_{1,162} = 1.116; *P* = 0.3391)](image)
Table 5.2. Results of generalised linear mixed models 1) predicting conditions in and outside a tree fern micro-site; 2) of recorded biotic and abiotic variables that best predict seedling abundance in each plot; and 3) of recorded biotic and abiotic variables that best model conifer seedling abundance in each plot.

<table>
<thead>
<tr>
<th>Model 1 – Logistic regression (conditions under tree ferns)</th>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Intercept</td>
<td>-0.504</td>
<td>0.708</td>
<td>-0.712</td>
<td>0.477</td>
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<tr>
<td></td>
<td>Available PAR</td>
<td>0.023</td>
<td>0.101</td>
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<td>0.816</td>
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<tr>
<td></td>
<td>Litter depth</td>
<td>0.276</td>
<td>0.081</td>
<td>3.422</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>0.005</td>
<td>0.037</td>
<td>0.125</td>
<td>0.901</td>
</tr>
<tr>
<td></td>
<td>Annual H₂O deficit</td>
<td>-0.009</td>
<td>0.032</td>
<td>-0.277</td>
<td>0.781</td>
</tr>
<tr>
<td></td>
<td>Topographic Position Index</td>
<td>0.124</td>
<td>0.126</td>
<td>0.987</td>
<td>0.323</td>
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</table>

<table>
<thead>
<tr>
<th>Model 2 – Poisson regression (seedling abundance per plot)</th>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>p-value</th>
</tr>
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<tbody>
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<td></td>
<td>Intercept</td>
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<td>0.464</td>
<td>8.481</td>
<td>&lt; 0.001</td>
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<td></td>
<td>Available PAR</td>
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<td>0.010</td>
<td>3.666</td>
<td>&lt; 0.001</td>
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<tr>
<td></td>
<td>Litter depth</td>
<td>-0.028</td>
<td>0.006</td>
<td>-4.53</td>
<td>&lt; 0.001</td>
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<tr>
<td></td>
<td>Nearest tree fern</td>
<td>0.026</td>
<td>0.012</td>
<td>18.997</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Nearest tree</td>
<td>0.028</td>
<td>0.003</td>
<td>8.593</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>-0.027</td>
<td>0.005</td>
<td>-5.201</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Annual H₂O deficit</td>
<td>-0.089</td>
<td>0.031</td>
<td>-2.825</td>
<td>0.005</td>
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<tr>
<td></td>
<td>Topographic Position Index</td>
<td>-0.062</td>
<td>0.014</td>
<td>-4.338</td>
<td>&lt; 0.001</td>
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</table>

<table>
<thead>
<tr>
<th>Model 3 – Negative binomial hurdle model (conifer seedling abundance per plot)</th>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>p-value</th>
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<tr>
<td>Truncated negative binomial</td>
<td>Intercept</td>
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<td>0.961</td>
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<td>Litter depth</td>
<td>-0.110</td>
<td>0.102</td>
<td>-1.078</td>
<td>0.281</td>
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<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Available PAR</td>
<td>0.013</td>
<td>0.122</td>
<td>0.107</td>
<td>0.915</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Nearest tree fern</td>
<td>-0.173</td>
<td>0.184</td>
<td>-0.937</td>
<td>0.349</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Nearest tree</td>
<td>-0.053</td>
<td>0.047</td>
<td>-1.127</td>
<td>0.260</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Slope</td>
<td>0.041</td>
<td>0.056</td>
<td>0.727</td>
<td>0.467</td>
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<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Annual H₂O deficit</td>
<td>0.053</td>
<td>0.052</td>
<td>1.025</td>
<td>0.305</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Topographic Position Index</td>
<td>-0.086</td>
<td>0.137</td>
<td>-0.628</td>
<td>0.530</td>
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</table>

<table>
<thead>
<tr>
<th>Logistic (binomial) model</th>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>p-value</th>
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<tbody>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Intercept</td>
<td>-3.075</td>
<td>1.005</td>
<td>-3.061</td>
<td>0.002</td>
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<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Litter depth</td>
<td>-0.055</td>
<td>0.083</td>
<td>-0.662</td>
<td>0.508</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Available PAR</td>
<td>0.133</td>
<td>0.111</td>
<td>1.199</td>
<td>0.231</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Nearest tree fern</td>
<td>0.362</td>
<td>0.170</td>
<td>2.136</td>
<td>0.033</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Nearest tree</td>
<td>0.005</td>
<td>0.049</td>
<td>0.105</td>
<td>0.917</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Slope</td>
<td>0.059</td>
<td>0.042</td>
<td>1.424</td>
<td>0.154</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Annual H₂O deficit</td>
<td>0.012</td>
<td>0.043</td>
<td>0.271</td>
<td>0.787</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------------</td>
<td>Topographic Position Index</td>
<td>-0.227</td>
<td>0.136</td>
<td>-1.666</td>
<td>0.096</td>
</tr>
</tbody>
</table>

[Q 3-5] A summary of the outcomes of the various models applied to the biotic and abiotic data in relation to tree fern adjacency, total and conifer seedling abundance is presented in Table 5.2. The key results are:

[Q 3.] Logistic regression shows that from the environmental parameters recorded during the field study, litter depth best predicts (0.276 ± 0.081, \( p < 0.001 \)) the conditions in both tree fern micro-site (5.6 ± 3.6 cm) and those elsewhere (3.6 ± 2.0 cm);
[Q 4.] Poisson regression shows that distance to a tree fern is the best predictor of vascular seedling abundance (slope = 0.026 ± 0.012, \( p < 0.001 \)) with seedling abundance increasing away from tree ferns; and,

[Q 5.] Negative binomial hurdle modelling shows that distance to tree fern best predicts conifer seedling presence (0.362 ± 0.170, \( p = 0.033 \)), with the likelihood of conifer seedling presence increasing away from tree ferns; the model for abundance, where present, did not identify a suitable predictor from the random effects.

![Figure 5.3. Differences in a) total vascular seedling and b) conifer seedling abundances in 1 × 1 m plots away from and in tree fern microsites (mean radius = 3.3 ± 2.0 m)](image)

5.4.2 Experimental manipulation

[Q 6.] The goodness of fit between distances in the dissimilarity matrix (where 61% of plots were ≥ 80% dissimilar to each other) and the distances in the ordination had an \( R^2 \) of 0.955 showing a robust representation of the dissimilarities between the seedling plots in ordination
space (Fig. 5.4a). The first five components of the PCA explained 65% of the variance; components 7-23 explained up to 5% of the variance individually and were excluded from further analysis. Only two PCA components (1 and 3) were significantly correlated ($r = 0.1052, P < 0.001; r = 0.1162, P < 0.001$ respectively) with the orientation of the post-treatment points, along Axis 1 of the ordination (Fig. 5.4a), components 2, 4 and 5 were therefore excluded from further analysis. Component 1 represented soil fertility (gradients of organic matter: 4 – 93%; ammonium $\text{NH}_4^+$: 2.1 – 74.4 ppm); Component 3 represented biophysical conditions (slope steepness (3 – 30°) and changing aspect; Table 5.3; complete data in Appendix 3). PERMANOVA analysis showed that the two seedling communities at the different experimental sites at Huapai and Oratia were distinct in ordination space ($F_{1,318} = 22.169; P < 0.001$; Fig 4a).

[Q 7.] Differential responses to treatments were observed in the dispersion (dissimilarity) of the seedling communities (Fig. 5.5). Multivariate homogeneity of dispersion analysis of the four treatment communities showed that the seedling community in treatment 2 (frond and litter removal) is becoming less dissimilar post-treatment as this group decreased in dispersion (-0.04 ± 0.08; $\bar{x} \pm SD$), as did the community in treatment 3 (frond removal only) (-0.04 ± 0.10). The communities in treatments 1 (control) and 3 (litter removal only) are becoming more dissimilar as both increased in dispersion (0.01 ± 0.09 and 0.05 ± 0.12 respectively; Fig. 5.4b).

No significant intra-site environmental variance was observed as no PCA components were significantly correlated with the orientation of the post-treatment points of the seedling community ordinations for either Huapai or Oratia (Fig. 5.4c,d). In contrast, PERMANOVA showed that for both Huapai ($F_{1-158} = 17.95, P < 0.001$) and Oratia ($F_{1-158} = 4.0299, P = 0.0011$) the pre- and post-treatment seedling communities appear to be compositionally different. Similarly, there was no significant intra-treatment environmental variance, a comparison of the environmental data (Table 5.3) shows that environmental variables are consistent across treatments.

The seedling communities in the treatment plots are distinguished by a significantly greater value for species richness in treatment 2 (frond and litter removal) than 4 (litter removal only) and 1 (control) (pairwise $t$-test with multiple $p$-value correction: $p = 0.02$; Table 5.4). Seedling density is also significantly greater in plots in treatment 2 (frond and litter removal) than in treatment 1 – the control ($p = 0.02$; Table 5.4). Beta-diversity values of turnover and nestedness show no significant differences between the treatments showing similar patterns of species substitution over time in each of the treatment communities (Table 5.4).
Table 5.3. Soil nutrients and biophysical conditions that significantly differ (pairwise t-test with Bonferroni correction) across the two experimental forest sites (Huapai and Oratia). For each treatment (spanning both experimental sites) the range (5% -Median - 95%) of these variables in the treatment plots (no significant differences in environmental variables between treatment plots with multiple p-value corrections). Complete data in Appendix 3.

<table>
<thead>
<tr>
<th>Environmental Data</th>
<th>Oratia (x ± SD)</th>
<th>Huapai (x ± SD)</th>
<th>Control (T1)</th>
<th>Frond and litter removal (T2)</th>
<th>Frond removal only (T3)</th>
<th>Litter removal only (T4)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Soil conditions</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Organic Matter (%)</td>
<td>27.5 ± 18.1</td>
<td>39.6 ± 25.6</td>
<td>11.5 – 26.0 – 88.5</td>
<td>12.7 – 25.2 – 87.7</td>
<td>11.2 – 23.4 – 80.3</td>
<td>9.7 – 26.7 – 76.5</td>
</tr>
<tr>
<td>Ammonium NH₄ (ppm)</td>
<td>11.3 ± 6.9</td>
<td>19.1 ± 11.0</td>
<td>4.9 – 15.0 – 34.8</td>
<td>4.6 – 13.5 – 26.3</td>
<td>4.0 – 11.7 – 26.9</td>
<td>3.9 – 12.2 – 30.0</td>
</tr>
<tr>
<td>Magnesium (mg kg⁻¹)</td>
<td>138.1 ± 37.3</td>
<td>187.0 ± 72.9</td>
<td>165.2 – 309.5 – 795.0</td>
<td>151.6 – 300.0 – 738.5</td>
<td>183.8 – 287.0 – 667.8</td>
<td>162.5 – 301.0 – 682.9</td>
</tr>
<tr>
<td>Potassium (mg kg⁻¹)</td>
<td>85.0 ± 32.8</td>
<td>105.3 ± 49.4</td>
<td>98.9 – 146.5 – 266.4</td>
<td>98.9 – 140.5 – 288.3</td>
<td>90.8 – 146.0 – 264.8</td>
<td>87.4 – 146.0 – 282.5</td>
</tr>
<tr>
<td>Boron (mg kg⁻¹)</td>
<td>0.6 ± 0.1</td>
<td>0.6 ± 0.2</td>
<td>0.3 – 0.6 – 0.8</td>
<td>0.3 – 0.5 – 0.8</td>
<td>0.3 – 0.6 – 0.9</td>
<td>0.4 – 0.6 – 0.8</td>
</tr>
<tr>
<td>Manganese (mg kg⁻¹)</td>
<td>31.5 ± 24.7</td>
<td>38.9 ± 32.9</td>
<td>8.9 – 28.0 – 109.2</td>
<td>6.0 – 23.0 – 86.2</td>
<td>5.9 – 21.0 – 79.2</td>
<td>7.9 – 24.5 – 87.8</td>
</tr>
<tr>
<td>Zinc (mg kg⁻¹)</td>
<td>4.1 ± 2.0</td>
<td>3.3 ± 1.7</td>
<td>1.8 – 3.6 – 8.1</td>
<td>1.7 – 3.2 – 6.8</td>
<td>1.5 – 2.8 – 5.9</td>
<td>1.5 – 3.4 – 6.6</td>
</tr>
<tr>
<td><strong>Biophysical conditions</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope (°)</td>
<td>15.0 ± 5.1</td>
<td>17.6 ± 7.0</td>
<td>9.0 – 17.0 – 27.0</td>
<td>7.0 – 16.5 – 26.2</td>
<td>6.0 – 16.0 – 24.1</td>
<td>7.0 – 16.0 – 26.1</td>
</tr>
<tr>
<td>Asp North</td>
<td>0.57 ± 0.3</td>
<td>-0.9 ± 0.1</td>
<td>-1.0 - -0.2 – 0.9</td>
<td>-1.0 - -0.4 – 0.9</td>
<td>-1.0 - -0.3 – 0.9</td>
<td>-2.0 - -0.3 – 1.0</td>
</tr>
</tbody>
</table>
Table 5.4. Alpha and beta diversity values for the various seedling treatment communities (5% - median – 95% quartiles); treatment values significantly different (pairwise \(t\)-tests with multiple \(p\)-value corrections) between treatments highlighted in bold (\(^a\) compared to treatment 1; \(^b\) compared to treatment 4 and 1).

<table>
<thead>
<tr>
<th>Diversity Analyses</th>
<th>Control (T1)</th>
<th>Frond and litter removal (T2)</th>
<th>Frond removal only (T3)</th>
<th>Litter removal only (T4)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alpha Diversity Indices (Pre-treatment)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seedling abundance</td>
<td>2.9 – 7.5 – 22.1</td>
<td>2.00 – 8.00 – 23.10</td>
<td>1.00 – 8.00 – 21.05</td>
<td>1.95 – 7.00 – 38.80</td>
</tr>
<tr>
<td>Shannon-Wiener DI (SW)</td>
<td>0.00 – 1.04 – 1.73</td>
<td>0.31 – 1.03 – 1.80</td>
<td>0.00 – 0.91 – 1.63</td>
<td>0.43 – 1.04 – 1.68</td>
</tr>
<tr>
<td>Simpson DI (SI)</td>
<td>0.00 – 0.59 – 0.79</td>
<td>0.17 – 0.61 – 0.81</td>
<td>0.00 – 0.53 – 0.78</td>
<td>0.26 – 0.61 – 0.79</td>
</tr>
<tr>
<td>Evenness (J)</td>
<td>0.67 – 0.86 – 1.00</td>
<td>0.54 – 0.88 – 0.97</td>
<td>0.55 – 0.82 – 0.99</td>
<td>0.59 – 0.88 – 1.00</td>
</tr>
<tr>
<td>Richness (S)</td>
<td>1.00 – 3.00 – 7.05</td>
<td>1.95 – 3.00 – 9.00</td>
<td>1.00 – 3.00 – 6.05</td>
<td>1.95 – 3.00 – 7.00</td>
</tr>
<tr>
<td><strong>Alpha Diversity Indices (Post-treatment)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seedling abundance</td>
<td>1.00 – 4.00 – 7.00</td>
<td><strong>2.0 – 5.5 – 11.0</strong> (^a)</td>
<td>1.95 – 5.00 – 8.05</td>
<td>1.95 – 4.00 – 7.05</td>
</tr>
<tr>
<td>Shannon-Wiener DI (SW)</td>
<td>0.00 – 1.12 – 1.67</td>
<td>0.67 – 1.45 – 2.06</td>
<td>0.54 – 1.31 – 1.80</td>
<td>0.48 – 1.22 – 1.61</td>
</tr>
<tr>
<td>Simpson DI (SI)</td>
<td>0.00 – 0.66 – 0.78</td>
<td>0.48 – 0.69 – 0.84</td>
<td>0.28 – 0.67 – 0.82</td>
<td>0.24 – 0.66 – 0.74</td>
</tr>
<tr>
<td>Evenness (J)</td>
<td>0.60 – 0.88 – 1.00</td>
<td>0.70 – 0.84 – 0.97</td>
<td>0.58 – 0.86 – 0.97</td>
<td>0.64 – 0.85 – 1.00</td>
</tr>
<tr>
<td>Richness (S)</td>
<td>1.00 – 4.00 – 7.00</td>
<td><strong>2.00 – 5.50 – 11.00</strong> (^b)</td>
<td>1.95 – 5.00 – 8.05</td>
<td>1.95 – 4.00 – 7.05</td>
</tr>
<tr>
<td><strong>Beta Diversity Indices</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turnover ((\beta_{\text{sim}}))</td>
<td>0.00 – 0.33 – 1.00</td>
<td>0.00 – 0.33 – 0.76</td>
<td>0.00 – 0.33 – 1.00</td>
<td>0.00 – 0.33 – 1.00</td>
</tr>
<tr>
<td>Nestedness ((\beta_{\text{sub}}))</td>
<td>0.00 – 0.08 – 0.33</td>
<td>0.00 – 0.10 – 0.43</td>
<td>0.00 – 0.09 – 0.46</td>
<td>0.00 – 0.07 – 0.43</td>
</tr>
</tbody>
</table>
Figure 5.4. CMDS ordinations of all pre- and post-treatment seedling data from the experimental manipulation. (a) the arrows indicate vector fits for the principal component factors associated with a gradient of biophysical and soil conditions (PCA Axis 1: soil fertility; PCA Axis 3: slope and aspect) that were significantly correlated ($P < 0.05$) with axis 1 of the ordination; (b) showing ordihulls of the treatment communities; (c) Oratia data only, showing the shift in community dissimilarity and dispersion between treatments; (d) Huapai data only. Treatment 1) control, 2) frond and litter removal, 3) frond removal only, 4) litter removal only
Figure 5.5. Circular histograms of the relative direction and distance moved by seedling plots in ordination space during treatments. Colour ramp from purple (short distance moved) to green (long distance moved in ordination space).

Indicator species analysis identified no species faithful to any seedling treatment-community before the experiment commenced. Post-treatment indicator species analysis for the two different sites combined shows that the conifers *Podocarpus totara* (0.499, $p = 0.001$ – multiple $p$-value corrections applied) and *Phyllocladus trichomanoides* (0.452, $p = 0.001$) are consistently present in treatments 2 (frond and litter removal) and 3 (frond removal only). PAR levels at ground level (above loose litter) increased by $53.8 \pm 30.4 \%$ after frond removal in treatments 2 and 3 ($n = 40$ and 40; pre: $9.6 \pm 9.9$, post: $30.4 \pm 56.7$, pairwise $t$-test (with Bonferroni correction) $p = 0.002$).
5.5 Discussion

This study shows that a widespread, common New Zealand tree fern, *Cyathea dealbata*, filters the establishment of other vascular plant species by its shading and accumulation of its macro-litter. Tree fern micro-sites are characterised by deep litter along with decreased PAR that serve to reduce seedling abundance, and filter out shade-intolerant conifer seedlings (as evinced by experimental frond-removal). I have shown that shading in *C. dealbata* micro-sites (from herein referred to as tree fern micro-sites) has a significant effect on the abundance and consistent establishment of conifer species; however, it is not possible, with my data, to qualify the seedling community response to tree fern micro-sites as distinct from that underneath other understorey species. Furthermore, whilst these filtering patterns are clear in the short-term, the eventual implications of this filtering effect on seedling establishment are unknown.

*Evidence of changes in seedling community in relation to tree fern micro-sites*

*Cyathea dealbata* tree fern micro-sites are characterised by significantly lower vascular seedling abundance than areas away from micro-sites, yet there are no significant differences in community composition with decreasing distance from tree ferns (Fig. 5.2). Furthermore, no plant species appears to be favoured by the conditions underneath tree ferns.

*Conifer seedling response to tree fern micro-sites*

Seedling abundance was reduced beneath tree fern crowns (up to 39%), and conifers (Podocarpaceae and Araucariaceae) were suppressed in similar proportion (up to 34%) suggesting that conifer seedling abundance is not suppressed significantly more than that experienced by angiosperms.

*Key environmental differences in tree fern micro-sites*

Tree fern micro-sites are characterised by significantly deeper (up to 56%) litter layers, reflecting the biomass of fronds and the slow decay rates of the relatively sclerophyllous nature of their fronds (Enright & Ogden 1987; Gillman *et al.* 2004). Light levels at ground level underneath tree ferns are difficult to quantify and using canopy cover likely does not capture the range and complexity of factors altered by the shading effect of fern frond structure. This may have severely limited the utility of this variable in the logistic model examining environmental data underneath and away from tree ferns.
Abiotic and biotic predictors of vascular seedling abundance in field study plots

In this study the environmental variable that bests predict seedling abundance in these forests is distance to *C. dealbata* tree fern (Table 5.2). However, complex biotic and abiotic interactions are likely involved based on the varying significance of six other variables (available PAR – canopy cover, litter depth, nearest canopy tree, slope, annual water deficit and topographic position). Moreover, canopy cover, litter depth and distance to nearest tree fern were not collinear (Table 5.2) highlighting both the high levels of variance in litter depth and canopy cover across the forest floor.

Abiotic and biotic predictors of conifer seedling abundance in field study plots

The relative paucity of conifer seedlings in my study ($\bar{x} = 0.7 \pm 2.2$ m$^{-2}$) reduced the sensitivity of the analysis to derive predictors of seedling abundance in the landscape. Although the negative binomial hurdle model did not identify any variables (available PAR, litter depth, distance to nearest tree fern and canopy tree, slope, annual water deficit and TPI) as a suitable model for conifer abundance, it showed that distance to *C. dealbata* tree fern was a robust predictor of conifer seedling presence/absence. This does not preclude the possibility of conifer seedlings establishing underneath tree ferns ($0.5 \pm 1.7$ m$^{-2}$), but shows that with increased *C. dealbata* abundance the probability of recording conifer seedlings is reduced (up to 34%).

Are vascular seedling communities influenced by differential conditions between experimental locations?

I identified a strong pattern of landscape-level abiotic filtering with a clear response in the height-weighted seedling abundance data to variations in soil conditions and biophysical characteristics between the sites at Huapai and Oratia. The seedling communities appeared to respond to these clear differences between the two experimental locations as the PERMANOVA analysis suggests that they are distinct in ordination space indicating strong local environmental drivers on seedling community. However, this high inter-site variance was not replicated within treatment plots, i.e. plot across the four treatments supported similar ranges in environmental conditions suggesting that although seedling establishment at Huapai and Oratia are influenced differentially by local conditions, the seedling response observed post-treatment can be attributed to the tree fern manipulation experiment.
Does vascular plant seedling community reflect shade or litter treatments around tree ferns?

Seedling communities are ephemeral by nature and susceptible to both elimination and rapid change in composition and abundance through variations in micro-climate as well as broader top-down drivers (Ogden 1985; Ibáñez et al. 2007). The complexity of these processes in the treatment-communities is evident in the trajectories the seedling plots shown in seedling ordination space. However, there is a general pattern of decreasing community dispersion within ordination space indicating that in treatments 2 (frond and litter removal) and 3 (frond removal only) the communities are becoming less dissimilar with increased light and decreasing amounts of litter; i.e. approaching conditions in forests with no ferns or other dense understorey.

Although litter was identified in the field study as the strongest predictor differentiating seedling establishment conditions between areas beyond and within a tree fern micro-site, its removal appears to have less of an effect than a reduction in tree fern frond-shading. Where litter and frond-shading were reduced beneath tree ferns, there was a positive response, over the duration of the experiment, both in seedling density and species richness. This effect was not replicated in the plots in treatment 4 (litter removal only) initially suggesting that frond-shading has a stronger local influence than litter. This apparent lesser influence of litter presence may be due to the high variance in litter levels and light environments across all plots in all treatments weakening any response. Litter appears to reduce establishment viability generally in a non-species specific way, contrary to the findings of McAlpine and Drake (2003), in comparison to frond-shading which differentially affects selected shade-intolerant conifers. The similar values for species turnover $\beta_{\text{sim}}$ and nestedness $\beta_{\text{sne}}$ across all treatments show that in terms of turnover and substitution, numerically there is no significant difference across the treatments; there is a relatively high turnover of individual seedlings, particularly those up to 45 cm tall. However, nestedness values do not specify how many different species (or of what type) are replacing a subset of the original community; consistent patterns in faithful occurrence post-treatment were identified in the indicator species analysis. Longer-term monitoring of seedling establishment in varied litter conditions may elicit a more taxa-specific response, as well as to account for differential seed production periods of species. Any similar studies should consider building up tree fern frond litter underneath canopies to maintain a constant litter depth to counter the varying litter depths occurring naturally.
Is there a consistent response by a vascular species to experimental treatment?

No vascular species were faithful to the seedling plots pre-treatment indicating high variance in community composition beneath *C. dealbata*; this mirrors the lack of faithful seedlings of any species in the tree fern micro-site seedling communities in the field study. Two species of podocarp (*Podocarpus totara* and *Phyllocladus trichomanoides*, both shade-intolerant conifers (Burns & Smale 1990; Ebbett & Ogden 1998; Forbes *et al.* 2016) were identified as faithful to the post-treatment “frond removal” communities of groups 2 (frond and litter removal) and 3 (frond removal only). The fidelity of these species establishing across the two treatment communities subject to frond removal indicates a clear response to the treatment, and that compositional sorting between the treatment-communities is a response to the treatments overlain on naturally high levels of variability in the landscape (Table 5.3; Appendix 3). Lusk, Jorgensen and Bellingham (2015) observed that at 10% mol m\(^{-2}\) day\(^{-1}\) seedlings of indigenous conifers are present, yet have significantly slower growth rates than angiosperms. The lower levels of PAR in this study (prior to frond removal) in treatments 2 (frond and litter removal) and 3 (frond removal only) was 9.6 ± 9.9 (increasing to 30.4 ± 56.7 mol. m\(^{-2}\) s\(^{-1}\)); the lower levels recorded are similar to the light conditions in the Lusk *et al.* (2015) study. However, the seedlings in the Lusk *et al.* (2015) study were sampled haphazardly using a plot-less method therefore no relative density of conifers vs. angiosperms is provided and is therefore not a useful comparison in terms of relative establishment success. Furthermore, the seedlings in Lusk *et al.* (2015) are between 500 and 1,000 mm tall and likely established at least 27-55 years prior and in different light environments to those recorded at the time of study (age range based on mean growth rate of 1.82 ± 1.6 cm yr\(^{−1}\) in 7% forest understorey light; rates obtained from Ebbett and Ogden, 1998). In this study, only 2% of conifer seedlings were > 500 mm tall, the relative success of conifers described here is in terms of development soon after germination. The response observed in the frond-removal treatments therefore shows that *C. dealbata* (and presumably other understorey species with similar shading influence) have a clear suppressive effect on conifers, and a concomitant negative response in their overall seedling abundance.

The ecological importance of light interception by *C. dealbata* is highlighted by the significant increase (53.8 ± 30.4 %) in PAR observed after frond-removal during experimental installation. It should be noted that similar increases in PAR would be expected if fronds / above-ground vegetation were to be removed from other understorey vegetation. The extent of the change in PAR levels is likely to vary, and given the specific nature of tree fern growth, I suggest that only
palms are likely to have a comparable effect on seedling establishment, however this was not tested in this experiment.

5.6 Conclusion

While this study shows that *C. dealbata* increase shading and litter depth and these factors are important in driving seedling community assembly, other understorey species and growth forms (e.g. palms) will also be influencing both shade and litter depths. Whether the response of the seedling community to shading and litter recorded here is unique to tree fern micro-sites, or whether seedling establishment would respond similarly to shading and litter accumulation from other understorey plants cannot be discerned from this data. Future research to expound upon the findings of this study should, most importantly, include other understorey species to establish whether species with similar growth patterns such as *Rhopalostylis sapida* and species not producing macro-litterfall (such as *Hedycarya arborea* and *Melicytus ramiflorus*) have varying influences on seedling establishment. This work would require a significant area of forest, due to the wholesale destruction of the understorey, yet it would identify whether the patterns I have recorded in this study, in particular the micro-site suppression of podocarp establishment, are mirrored in other understorey species. Further works would usefully include long-term monitoring of seedlings to establish whether the innate ephemerality of seedling communities influences the significance of these establishment patterns. Long-term monitoring of tagged epiphytes would also usefully provide data on whether epiphytism provides an escape route from tree fern influence (as Coomes *et al.*, 2005). The long-term effects of macro-litterfall could readily be modelled using the mortality rates established by Gillman *et al.*, (2004) to provide further context for the relative importance of these drivers of seedling mortality on forest community structure and composition.

Tree ferns influence the environmental heterogeneity of the forest floor for vascular plant seedling establishment through increased shading and macro-litter accumulation. In particular, shading influences seedling establishment and community assembly by reducing overall abundance of both angiosperm and conifer seedlings equally. However, conifer establishment appears to be facilitated when tree fern fronds are experimentally removed despite the presence of litter. This study shows that tree ferns are unlikely to impact the long-term composition of indigenous forests but may limit direct competition from vascular plants by reducing densities and regeneration opportunities immediately beneath canopies.
Chapter 6

Tree fern facilitation of gymnosperm persistence and angiosperm growth in simulated forests

6.1 Abstract

Tree ferns have long been suspected to have a significant influence on forest dynamics, but empirical evidence remains sparse, largely because of the longevity (hundreds of years) of many canopy tree species. However, simulation models provide a way to evaluate the inter-generational consequences of patterns and mechanisms observed at short time-scales, and to synthesise relevant data from multiple sources. I extended an existing spatially explicit individual-based simulation model representing the dynamics of northern New Zealand indigenous warm temperate evergreen forest by including a growth form representing tree ferns. Increased mortality of saplings resulting from tree fern macro-litterfall, and increased seedling suppression beneath tree ferns were also represented, based on observations of these effects of tree ferns on tree demographics. Further modifications to the model included the addition of a competing pioneer angiosperm (based on the ecology of *Kunzea robusta*), improvements to reproduction height-age relationships for all taxa, and refinements to the representation of external propagule rain derived from different dispersal vectors (wind or bird). I used model-based experiments to evaluate the effects of different initial relative abundance of tree ferns, the contribution of external propagule sources and the long-term effects of macro-litterfall and reduced seedling abundance on the composition and structure of northern NZ forest communities. The simulation model accurately reproduced observed tree fern growth patterns (height and age) and patterns of species replacement and dominance in forest succession. The model outcomes suggest that shade-intolerant gymnosperms persist longer and grow older and taller where tree ferns are present; this effect strengthens with increasing tree fern abundance. Although the overall abundance of angiosperm species was reduced, their longevity and height in the canopy and the understorey increased with increased tree fern abundance. I suggest that this increase is due to reduced competition from neighbours associated with reduced canopy tree density in response to tree fern presence. Spore rain from outside forest fragments is crucial for the long-term persistence of tree ferns, but the relative influence of senescing frond macro-litterfall on the long-term composition and structure of canopy trees might be over-stated in the scientific literature. Seedling suppression beneath tree ferns appears to be detrimental to tree
ferns, and suggests an emergent pattern of negative density-dependence in understorey tree ferns. Overall, this study suggests that tree ferns are important determinants of forest structure by releasing shade-intolerant gymnosperms and reducing angiosperm density and therefore competition in northern New Zealand forests.

6.2 Introduction

In New Zealand’s indigenous forests, tree ferns can comprise a significant proportion of stem density (up to 50% of stems > 5 cm diameter at breast height (DBH)), biomass (up to 20%), and by virtue of their abundance alone seem likely to play an important role in the vegetation dynamics of such forests (Bellingham et al. 1998; Brock et al. 2016, 2018). It has been hypothesised that tree ferns influence forest communities via their habit, with both macro-litterfall shading inducing seedling and sapling mortality beneath tree ferns, and significant sub-canopy shading influencing long-term composition (Chapter 4; Burton & Mueller-Dombois 1984; Clark & Clark 1989; Gillman & Ogden 2001; Peters et al. 2004; Coomes et al. 2005). These mechanisms of tree fern influence are not necessarily negative, however. For example, some species, including *Hedycarya arborea* (Monimiaceae), appear to increase their growth rates in experiments where seedlings were pinned to mimic the effects of macro-litterfall (Gillman, Wright & Ogden 2003; Gillman et al. 2004); other species, e.g. *Weinmannia* spp., use tree fern trunks as establishment surfaces (Bellingham & Richardson 2006; Gaxiola et al. 2008).

Obtaining the long-term data required to unravel the effects of biotic interactions on ecosystem composition, structure and function is challenging (Perry & Millington 2008). Some short-term (14 ± 7 months; \( n = 6 \)) studies have examined the influence of tree ferns on forest regeneration providing hypotheses as to likely long-term effects on forest ecosystems (Burton & Mueller-Dombois 1984; Clark & Clark 1989; Gillman & Ogden 2001; Coomes et al. 2005; Gaxiola et al. 2008; Forbes et al. 2016). However, designing and conducting manipulative experiments to evaluate such hypotheses is impractical because individual tree ferns can persist in forest communities for upwards of 250 years (Bystriakova et al. 2011a; Brock et al. 2016) and associated angiosperms and gymnosperms often longer. One possible solution to this challenge is to undertake experiments *in-silico* and many forest models have successfully been developed to explore vegetation dynamics over broad spatial and temporal extents (Scheller & Mladenoff 2007).
To date NZ tree ferns have been represented in three different simulation models: 1) the individual-based SORTIE/NZ model (Kunstler, Coomes & Canham 2009); 2) the LINKNZ model (adapted from a generalised temperate forest gap model; Hall & Hollinger (2000)); and 3) a forest landscape model LANDCLIM (Thrippleton et al. 2014). The SORTIE/NZ is a dynamic model representing succession in New Zealand’s kāmahi-podocarp-beech indigenous forest. However, in parametrising this model, tree ferns were not represented in a dynamic manner and were maintained at a stable population size to ensure a field-calibrated population density of this growth form. Tree ferns were included in SORTIE/NZ solely to provide a seedling substrate for hemi-epiphytic canopy tree species (i.e., as phorophytes), but the effect of their presence on other species was not considered. The LINKNZ model, adapted from a generalised temperate forest gap model, included four species of New Zealand tree fern: Cyathea medullaris, Cyathea dealbata, Cyathea smithii and Dicksonia squarrosa; these were represented in the same way as other tree species and no further comment/data is/are presented on how successfully the model captures their dynamics. The LANDCLIM model had been adapted to examine long-term (1,700 years) vegetation dynamics in Weinmannia racemosa-podocarp forest in the central North Island. Tree ferns (C. smithii) were represented in LANDCLIM as shade-tolerant, understorey species and treated by the model as other tree species. However, this approach did not successfully represent this life-form and tree ferns languished at extremely low densities (< 50 stems ha\(^{-1}\)) well below field estimates.

Using DBH-based allometric relationships to represent tree fern development is problematic for several reasons. Tree ferns do not develop structural tissues through secondary growth, are unable to significantly increase the diameter of their trunks (although a cone of dense adventitious rhizoids frequently develops at the base of the trunk), and by the time trunk height reaches 0.5 m can produce full-size fronds (Prugnolle, Rousteau & Belin-Depoux 2001; Brock et al. 2016). Tree ferns have a distinctive growth form and develop differently to the other woody vascular plant species with which they interact. Therefore, modelling tree ferns as shade-tolerant trees does not adequately represent them; modelled in this manner, tree ferns rarely persist in the understorey and occur at low densities (Thrippleton et al. 2014). Implementing and parameterising a model to evaluate tree fern influence requires accurately representing the tree fern growth form and its potential impacts on forest composition and regeneration. Thus, it is necessary to implement a life-form in which growth is not associated with an increase in DBH but with increase in height, and in which height increase is not associated with an increase in canopy dimensions (at least above heights of 0.5 m tall). Furthermore, tree ferns can persist for
long periods in the understorey and this characteristic needs to be captured (Mueck et al. 1996; Brock et al. 2016). Not representing tree ferns’ fundamental characteristics means that previous models have over-estimated tree fern growth, under-estimated their relative prevalence and failed to represent the influence of tree ferns on other forest species.

There are limited demographic data available on tree ferns at either the sporophyte or gametophyte life-stages. Age-growth data are difficult to obtain as, similar to monocotyledons, tree fern structure leaves few indications of the age of an individual plant (Brock et al. 2016). Attempts to age tree ferns have used radio-carbon dating (destructive), stipe-scar counting (assuming annual frond development and senescence) and using fire scars as a historic marker to calculate recent growth rates (Tanner 1983; Ash 1987; Mueck et al. 1996; Blair et al. 2017), but none has established a universal method with which to calculate age of tree ferns.

In this chapter, I adapted an empirically evaluated forest model of northern New Zealand warm temperate evergreen mixed conifer-angiosperm forests and added a new functional type to represent the tree fern growth form. The spatially explicit model described by Morales & Perry (2017) represents broadleaved-podocarp forest communities commonly found in northern New Zealand with species functional types modelled on the behaviour of three canopy species (Beilschmiedia tawa, Lauraceae; Laurelia novae-zealandiae, Atherospermataceae; Dacrydium cupressinum, Podocarpaceae), one small tree (Hedycarya arborea, Monimiaceae), and two understorey species (Melicytus ramiflorus, Violaceae; Piper excelsum, Piperaceae). The model has been rigorously evaluated against field plot data, and a thorough sensitivity analysis conducted on it. These evaluations showed that while the model accurately represented the structural characteristics (size classes of individuals) of forest fragments, it under-predicted mean individual stem size, and over-predicted stem density (B. tawa by 83%; L. novae-zealandiae by 112% and D. cupressinum by 747%). Producing an over-abundance of small individuals is a problem previously identified in forest models in New Zealand, and has been assumed to be a failure to represent the long periods (e.g. several decades) of suppression in shade many New Zealand trees can exhibit (Develice 1988; Thrippleton et al. 2014). Shade-intolerant tree species were also suppressed or lost from the model relatively earlier than expected (Morales & Perry 2017). The species of tree fern identified as most representative of the understorey of lowland broadleaved-podocarp forests of northern New Zealand (forest type for which the Morales & Perry (2017) model was parameterised) was Cyathea dealbata (Cyatheaceae) (Brock et al. 2016). Tree fern growth rates vary significantly depending on geographic location (Blair et al. 2017); however, other than light the Morales & Perry (2017) model does not consider an abiotic
filter (e.g. soil conditions or topography), so to develop age vs. height growth curves for *Cyathea dealbata* I pooled growth data from across a range of environments in northern New Zealand.

After adapting the original model to include a growth form model for tree ferns, the objectives of this study were to answer the following questions in the context of published hypotheses regarding the long-term influences of tree fern presence in forests:

1. Do tree ferns, where present in differing abundances, differentially influence the relative abundances of angiosperms and gymnosperms? [In response to: Gymnosperm opportunities are reduced in a forest with tall ferns, when competing with angiosperms; Coomes (2005)]

2. What are the long-term effects of tree fern macro-litterfall on seedlings and saplings of vascular woody plants, and is there a corresponding response in the canopy to increased juvenile mortality? [In response to: Macro-litterfall reduces seedling and sapling abundance in the understorey influencing community structure and composition; Gillman (2001)]

### 6.3 Model description

#### 6.3.1 Overview of the Morales & Perry (2017) Model

The Morales & Perry (2017) model is a spatially explicit individual-based model (SEIBM) designed to represent long-term dynamics of podocarp-*B. tawa* forest fragments of a 16 ha forest (grid: 100 x 100, 4 x 4 m cells; NetLogo 5.3.1, Wilensky & Evanston 1999). The model was parameterised using literature and field estimates, and evaluated against published descriptions of forest stand structures (parameters detailed in Table 6.1). The forest structure was initialised as a spatially random pattern; at each model time-step a series of ecological routines were followed: seed dispersal (from both within and beyond the grid), mortality, gap formation, recruitment, growth and seedling/sampling demography (Fig. 6.1; adapted from Morales & Perry 2017). The model was designed to consider the long-term (> 1,000 years) effects on forest dynamics of habitat fragmentation, fencing to prevent stock trampling of seedlings/saplings, random destructive disturbance events, and also the effects of herbivory and restoration plantings; these effects were not considered in the experiments described here. Morales and Perry (2017) provide full ODD (Overview, Design concepts, and Details) model documentation.
Table 6.1. Species life-history parameters. Values in bold are those parameters refined and/or added to the Morales & Perry (2017) model.

<table>
<thead>
<tr>
<th>Parameter name</th>
<th>Parameter description</th>
<th>Beilschmiedia tawa</th>
<th>Laurelia novae-zelandiae</th>
<th>Dacrydium cupressinum</th>
<th>Hedycarya arborea</th>
<th>Melicytus ramiflorus</th>
<th>Piper excelsum</th>
<th>Cyathea dealbata</th>
<th>Kunzea robusta</th>
</tr>
</thead>
<tbody>
<tr>
<td>growth-form</td>
<td>Growth form identifier – woody vascular plant (1) vs. tree fern (2)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>max-hgt</td>
<td>Maximum height (m)</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>15</td>
<td>12</td>
<td>6</td>
<td>10</td>
<td>15</td>
</tr>
<tr>
<td>max-dbh</td>
<td>Maximum DBH (m)</td>
<td>1.2</td>
<td>1.2</td>
<td>2</td>
<td>0.5</td>
<td>0.6</td>
<td>0.3</td>
<td>0.45</td>
<td>0.9</td>
</tr>
<tr>
<td>max-age</td>
<td>Maximum age (years)</td>
<td>450</td>
<td>450</td>
<td>800</td>
<td>100</td>
<td>60</td>
<td>60</td>
<td>250</td>
<td>150</td>
</tr>
<tr>
<td>shade-tolerance</td>
<td>Shade tolerance of species, relative position on light gradient</td>
<td>0.25</td>
<td>0.25</td>
<td>0.35</td>
<td>0.4</td>
<td>0.55</td>
<td>0.4</td>
<td>0.25</td>
<td>0.9</td>
</tr>
<tr>
<td>repro-height</td>
<td>Minimum height for propagule set (m)</td>
<td>5.6</td>
<td>5.6</td>
<td>5.6</td>
<td>4.1</td>
<td>3.8</td>
<td>3.4</td>
<td>2</td>
<td>4.1</td>
</tr>
<tr>
<td>repro-age</td>
<td>Minimum age for propagule set (years)</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>gap-maker</td>
<td>Make a gap on dying (Boolean)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>supp-tolerance</td>
<td>Level of suppression (proportion of optimal growth five-year average) below which mortality risk increases</td>
<td>0.35</td>
<td>0.35</td>
<td>0.4</td>
<td>0.5</td>
<td>0.5</td>
<td>0.8</td>
<td>0.35</td>
<td>0.8</td>
</tr>
<tr>
<td>supp-mortality</td>
<td>Annual mortality rate for suppressed trees</td>
<td>0.025</td>
<td>0.025</td>
<td>0.1</td>
<td>0.125</td>
<td>0.125</td>
<td>0.125</td>
<td>0.025</td>
<td>0.125</td>
</tr>
<tr>
<td>seedling-survival</td>
<td>Proportion of seedlings that survive each year</td>
<td>0.5</td>
<td>0.5</td>
<td>0.4</td>
<td>0.5</td>
<td>0.6</td>
<td>0.6</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>sapling-survival</td>
<td>Proportion of saplings that survive each year</td>
<td>0.7</td>
<td>0.7</td>
<td>0.6</td>
<td>0.7</td>
<td>0.8</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td>seedling-transition</td>
<td>Proportion of seedlings that become saplings</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
<td>0.07</td>
<td>0.07</td>
<td>0.1</td>
<td>0.04</td>
<td>0.04</td>
</tr>
<tr>
<td>seedling-inhibition</td>
<td>Proportion by which seedling abundance is reduced in patch</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.5</td>
<td>0.0</td>
</tr>
<tr>
<td>external-species</td>
<td>Probability multiplier for propagule rain (anemo/endozoochory)</td>
<td>0.005</td>
<td>0.005</td>
<td>0.005</td>
<td>0.02</td>
<td>0.02</td>
<td>0.02</td>
<td>0.02</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Figure 6.1. Flow-chart representing the sequence of ecological processes in the modified model (adapted from Morales & Perry 2017); modifications are shown in red, grey boxes show processes not used in this study. Dashed lines represent processes that can be turned on and off.
6.3.2 Modifications – parameterising tree ferns

Height-increment growth data for *C. dealbata* were obtained from permanent vegetation plots in the Kauaeranga Valley in the Coromandel and at the University of Auckland’s Huapai reserve (Fig. 6.2; Ogden & Buddenhagen 1994). Height measurements were taken of 292 tagged *C. dealbata* tree ferns that had first been measured between 5 and 38 years prior to their re-survey. Tree ferns were measured on the uphill side of the trunk between the base and the top of the caudex to within a 5 cm accuracy. The previous height measurements were subtracted from current height, to derive annual height increments based on number of years since previous measurement. I derived a height increment (ΔH) model through an iterative model selection process and quantile regression. I used an optimal growth rate (95th percentile) as the SEIBM calculates growth rates of individuals based on an optimal rate that is then reduced through competitive interactions with plants in neighbouring patches. The model that best fitted the height increment data was a negative exponential model:

\[
\Delta H = 0.268 \times e^{(-0.105 \times H)} \text{ m yr}^{-1}
\]

Tree fern growth was represented with this height-increment model (H/ΔH; m yr\(^{-1}\)). A Boolean growth-form flag was introduced for each species in the model to determine whether the tree (ΔD; m yr\(^{-1}\)) or tree fern (H/ΔH; m yr\(^{-1}\)) model was used both in growth increment and suppression-related mortality (mortality increases under long periods of slow growth; Morales & Perry, 2017).

6.3.3 Modifications – early successional species

A pioneer angiosperm life form was added to the species pool considered by Morales & Perry (2017) with parameterisation based on *Kunzea robusta*, a Myrtaceuous tree species commonly associated with *C. dealbata* in early successional communities (Brock *et al.* 2018). Morphological data to parameterise this functional type were obtained from the scientific literature (Table 6.1; Burrell 1965; Smale 1994; Smale *et al.* 1995).

6.3.4 Modifications – tree fern macro-litterfall and seedling suppression

New routines were added to the model to represent increased seedling suppression underneath tree fern canopies and tree fern macro-litterfall damage to saplings:
1. Seedling suppression of up to 50% abundance relative to sites away from tree fern canopies (Chapter 5; Forbes et al. 2016) was represented by reducing seedling abundance in patches occupied by tree ferns where there is deep frond litter and a more shaded environment.

2. To represent the increased sapling damage (c. 3% per annum) that occurs underneath tree ferns due to macro-litterfall (Guariguata 1998; Gillman & Ogden 2005) a macro-litterfall procedure was developed. This procedure allows the sapling mortality rate to be reweighted under tree ferns to reflect saplings (proportions per grid cell underneath a tree fern) being killed through a dead frond falling from the tree fern crown.

Figure 6.2. Location of sampling sites (marked with a star) for Cyathea dealbata growth and reproduction data.

6.3.5 Modifications – reproduction

The parameter that describes the amount of propagule dispersed into the simulated area from beyond the model grid (i.e. the modelled landscape) was modified to differentiate between endozoochory and anemochory. This refinement was necessary with the introduction of pteridophytes into the model; propagule dispersal of tree ferns is not comparable to that of the conifer Dacrydium cupressinum, for example, with bird- dispersed arillate seed cones (Norton, Herbert & Beveredge 1988). Seed dispersal in New Zealand through endozoochory is generally over distances < 100 m (Wotton & McAlpine 2015). Although anemochorous dispersal of forest
species in NZ has not been quantified (in terms of distance travelled by seeds), long-distance dispersal of seed (> 100 m) is appreciable (1-5% likelihood) in tall canopy species (Nathan et al. 2002). Plants dispersing through endozoochory were given seedling production values 25% of that of anemochorous plants (for external-species; see Table 6.1); i.e. anemochorous plants are more likely to disperse further more often and therefore are parameterised to produce more seedlings (as a product of seeds arriving from outside the grid) in the model. The total external seed / spore rain is a function of the parameter ‘external-species’ (Table 6.1) and the prevalence of each species-type in the greater landscape outside the model grid, which is assumed proportional to relative abundance of species in model grid.

![Figure 6.3. Relationship between maximum height (m) of New Zealand woody vascular plants, and the minimum height (m) at maturity (data obtained from EcoTraits).](image)

In the Morales & Perry (2017) model version, the point at which an individual becomes reproductively mature is delimited by age alone. However, assessing reproductive maturity solely on the basis of age allows suppressed individuals to reproduce at unrealistically small sizes (Thomas 2011). I modified the representation of minimum reproductive age by including a new parameter called reproductive height; that is the minimum height, irrespective of age, at which an individual of a given species can reproduce. The reproductive height parameter was estimated using a published relationship (Thomas 2011) between maximum height of a tree
species and the minimum height at maturity. Data on the maximum height of New Zealand tree species, along with their minimum reproductive height were obtained from the EcoTraits website (Landcare Research 2005). There was a positive relationship between these variables (slope ± SE): 0.077 ± 0.008, \( p < 0.001, n = 9 \) (sample size was restricted by the minimum reproductive height data available; Fig. 6.3). Using maximum height values, minimum reproductive height values were derived (Table 6.2) for the seven spermatophyte species-types represented in the model. Minimum reproductive height for \( C. \) dealbata was established using data on crown height and sporangia production (presence / absence of sori) obtained from 178 plants in a re-measured permanent vegetation plot at Huapai (University of Auckland scientific reserve) in West Auckland (Fig. 6.4).

**Table 6.2.** Minimum reproductive height values for the eight species types. Vascular woody plant values derived from maximum height (+ 1.4 m to correct for height at which individuals are deemed trees in the model); tree fern (\( Cyathea dealbata \)) derived from field data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Maximum Height (m)</th>
<th>Minimum Height at Maturity (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Beilschmiedia tawa</em></td>
<td>35</td>
<td>5.6</td>
</tr>
<tr>
<td><em>Laurelia novae-zelandiae</em></td>
<td>35</td>
<td>5.6</td>
</tr>
<tr>
<td><em>Dacrydium cupressinum</em></td>
<td>35</td>
<td>5.6</td>
</tr>
<tr>
<td><em>Hedycarya arborea</em></td>
<td>15</td>
<td>4.1</td>
</tr>
<tr>
<td><em>Kunzea robusta</em></td>
<td>15</td>
<td>4.1</td>
</tr>
<tr>
<td><em>Melicytus ramiflorus</em></td>
<td>12</td>
<td>3.8</td>
</tr>
<tr>
<td><em>Cyathea dealbata</em></td>
<td>10</td>
<td>2.0</td>
</tr>
<tr>
<td><em>Piper excelsum</em></td>
<td>6</td>
<td>3.4</td>
</tr>
</tbody>
</table>
6.3.6 Scenario based experiments

I conducted four separate experiments to evaluate the effect of varying tree fern abundance, external propagule rain, tree fern macro-litterfall and seedling suppression (under tree ferns) on forest dynamics. High relative abundances of tree ferns are known to slow the process of succession (Walker et al. 2010), so I used a timeframe of 2,500 years in a 16 ha area, which I assumed was embedded within a larger contiguous forest (except during external propagule rain experiments). Thirty replicates of each treatment (described below) per experiment were run. To initialise the tree fern abundance scenarios under each treatment, model runs were started with different relative abundances of tree ferns, where all other species had the same initial relative abundance (remaining grid cells divided equally between species). Tree fern initial abundances were varied from 0 to 100% (of model grid cells) in 10% increments spanning the range of possible tree fern densities in the landscape.

To establish the effect of modified external propagule rain parameters, and to consider the effects on forest structure and composition of long-term persistence of tree ferns in contiguous...
areas of forest compared to isolated (complete propagule dispersal failure), smaller fragments of forest, simulations with and without external propagule rain were conducted.

The importance of seedling suppression, and tree fern macro-litterfall as a driver of sapling death and subsequent forest dynamics was evaluated by running two experiments. The first increased seedling suppression in patches occupied by tree ferns to 50% (field-observed levels; as per Chapter 5). Macro-litterfall was examined by varying the probability of sapling loss underneath tree ferns from macro-litterfall (i.e. on top of background mortality) from 0 to 100% by 20% increments. To initialise these evaluations tree fern relative abundance was set at 50%, which is a mean relative abundance of tree ferns in New Zealand lowland broad-leaved podocarp forest: 49 ± 28% (n = 18; Brock et al. 2016), with all other species equal in relative abundance. The disturbance regime in this model was from tree-fall; where dying individuals belonged to a gap-maker species then on the death of the individual a gap is created that potentially extends to grid-cells other than its own (Morales & Perry 2017).

6.3.7 Analysis

I explored the dynamics of a 16 ha forest by running the model 30 times for 2,500 years varying only those parameters described above (model parameters detailed in Table 6.1). I graphically analysed mean abundance, height, and age values of the tree fern C. dealbata and the seven other species: main late-successional canopy dominants (Dacrydium cupressinum, Beilschmiedia tawa, Laurelia novae-zelandiae), small tree species (Hedycarya arborea), and the early successional and understorey species (K. robusta, P. excelsum, M. ramiflorus). To establish species-level change in abundance over time, pairwise t-tests were used to compare the mean values (abundance, height, DBH) among centuries to identify where species abundances stabilise as an indicator of the ‘endpoint’ of the successional process in each simulation. Mean abundance values after 1,000 years were calculated to provide intra-specific comparison, and canopy height variance calculated (1,000 years provides a useful comparison to data presented in Morales & Perry, 2017). Inferential statistical analyses were not undertaken because the data produced by simulations have arbitrarily high levels of replication, reducing the relevance of a p-value. Furthermore the nature of experimentation in simulations invalidates the premise of the null hypothesis (that there is no difference between parameter values) (White et al. 2014); the relative magnitude of difference between simulations was therefore evaluated visually.
6.4 Results

6.4.1 Effect of tree fern abundance

The overall response to increasing tree fern abundance was an increase in the length of time required for the densities of the dominant canopy species *B. tawa*, *L. novae-zelandiae* and *D. cupressinum* to stabilise (Table 6.3). *Hedycarya arborea* and *Melicytus ramiflorus* generally declined and became locally extinct earlier with greater initial tree fern density. All canopy dominant species grew taller and had greater DBH with greater tree fern initial abundance treatments; across all species the mean height of individuals generally increased with the initial relative abundance of tree ferns up to 80%, after which it decreased. Mean age of individuals varied across species (canopy dominants increasing in age vs small trees and understorey species decreasing in age) in response to increasing tree fern abundance.

*B. tawa* and *L. novae-zelandiae* took increasingly longer (up to 900 years longer) to reach a stable abundance as initial tree fern abundance increased (Table 6.3). Although densities were relatively lower in tree fern dominant (≥ 50%) systems, mean DBH and height of *B. tawa* and *L. novae-zelandiae* increased by up to 50% and 25%, respectively; mean age remained relatively constant, but declined at higher tree fern abundances (≥ 80%). The mean age of the canopy angiosperms did not vary among the abundance treatments, but in simulations with ≥ 80% initial tree fern abundance, the age of the canopy trees decreased by up to 17% (Fig. 6.5). The numbers of stems per species (of canopy tree and tree fern) at 1,000 years are similar to that reported in the field data, from broadleaved-podocarp forests of northern New Zealand, of Morales & Perry (2017; Fig. 6.6).

Table 6.3. Time for main canopy species to stabilise in their population for the treatments of differing initial relative abundances of tree ferns.

<table>
<thead>
<tr>
<th>Treatment</th>
<th><em>Dacrydium cupressinum</em></th>
<th><em>Beilschmiedia tawa</em></th>
<th><em>Laurelia novae-zelandiae</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>0%</td>
<td>1,600</td>
<td>800</td>
<td>-</td>
</tr>
<tr>
<td>10%</td>
<td>1,800</td>
<td>1,000</td>
<td>-</td>
</tr>
<tr>
<td>20%</td>
<td>1,800</td>
<td>1,100</td>
<td>-</td>
</tr>
<tr>
<td>30%</td>
<td>2,000</td>
<td>1,600</td>
<td>-</td>
</tr>
<tr>
<td>40%</td>
<td>2,200</td>
<td>2,100</td>
<td>-</td>
</tr>
<tr>
<td>50%</td>
<td>2,300</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>60%</td>
<td>2,500</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>70%</td>
<td>2,300</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>80%</td>
<td>2,200</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>90%</td>
<td>2,000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>100%</td>
<td>1,800</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
In contrast to the canopy angiosperms, the conifer *D. cupressinum* decreased in abundance over time across all the tree fern abundance treatments. However, *D. cupressinum* remained relatively more abundant, and the average height, age and DBH were higher (by 159, 280 and 250%, respectively, comparing 0% to 100% initial abundance of tree ferns), where tree ferns were relatively more abundant (Fig. 6.5). The mean age of *D. cupressinum* did decrease when tree ferns had an initial relative abundance of ≥ 90%; however, the individuals present in the forest were considerably older (by 800%, \(n = 30\) (tree ferns absent), \(n = 60\) (tree ferns ≥ 90%) than those in systems where tree ferns were absent.

Overall, the abundance, mean age, mean height and mean DBH of the understorey tree *H. arborea* decreased (53%, 50%, 24% and 17%, respectively) with increasing tree fern presence, although in the first two centuries the species grew up to 30% taller in simulations with greater relative abundances of tree ferns. The abundance of understorey shrub *P. excelsum* decreased with increasing tree fern abundance, yet it increased in height in stands where tree ferns were in relatively high abundance (0 -100% initial tree fern = 56% increase in height). *M. ramiflorus* appeared to experience a slight benefit from an increase in relative abundance of tree ferns, with a mean increase in abundance of 6% in the first 200 years. Likewise *K. robusta* appeared to benefit from a high abundance of tree ferns with persisting individuals being relatively taller and older (200%, 300%) than those in simulations without tree ferns (Fig 3.).
Figure 6.5. Trends of abundances, mean age, mean dbh and mean height for the eight modelled species over 2,500 simulation years with initial tree fern densities of 0, 20, 40, 60, 80, and 100%. Colours represent the following species: *B. tawa* = red; *L. novae-zelandiae* = grey; *D. cupressinum* = yellow; *H. arborea* = light green; *M. ramiflorus* = pink; *P. excelsum* = light blue; *C. dealbata* = dark green; *K. robusta* = blue. Note y-axes are variably scaled within each state variable (column).

Where tree fern initial abundance was less than 50%, tree fern abundance increased in all simulations over a period from 200 - 400 years. However, once tree fern initial relative abundance was ≥ 60% the period over which tree fern populations expanded increased from 900 to 2,500 years. This expansion and stable persistence was to the detriment of other species in the simulations as is evident in the relative abundances of the canopy dominants, which remained low over long periods of time (Table 6.3, Fig. 6.5). Mean age of tree ferns in simulations with initial tree fern abundances ≤ 50% is 321 years; in simulations with higher densities of tree ferns this increased to 550 years. Mean height of tree ferns across all simulations was 2.92 m, with a maximum height of 10.7 m.

There was a clear pattern in canopy height variance across the eleven treatments (Fig. 6.7). While initially, with increased tree fern abundance (from 0 – 10%), there was a decrease in
height variance (14%), increasing tree fern initial abundance was associated with an increase in the variance of the height of species across the simulated forest (2 - 93%).

**Figure 6.6.** Dominant canopy species density after 1,000 years in the Morales & Perry (2017) model (no tree ferns) compared to equilibrium species density values from this study (40% initial relative abundance of tree ferns treatment; Morales & Perry (2017) field data showed forests supporting approximately 44% relative abundance of stems represented by tree ferns). Coloured horizontal lines represent field data densities for the three canopy species.

**Figure 6.7.** Variance in the mean canopy heights (m) of the eight simulated species across the eleven simulations with varied tree fern presence.
Figure 6.8. Trends of abundances, mean age, mean dbh and mean height for the eight modelled species over 2,500 years of simulations external propagule rain parameter on and off. Colours represent the following species: *B. tawa* = red; *L. novae-zelandiae* = grey; *D. cupressinum* = yellow; *H. arborea* = light green; *M. ramiflorus* = pink; *P. excelsum* = light blue; *C. dealbata* = dark green; *K. robusta* = blue. Note y-axes are variably scaled within each state variable (column).

6.4.2 External propagule rain

A lack of external propagule rain in the forest simulation (i.e., representing a completely isolated fragment rather than a connected forest system) resulted in tree fern abundance declining. In simulations with external propagule rain there was a tenfold increase in the abundance of tree ferns after 1,000 years as compared to simulations without external propagule rain. In the absence of external propagule rain, *B. tawa* and *L. novae-zelandiae* increased in abundance more rapidly, compared to the simulation with external propagule rain that supported more tree ferns, and stabilised within 1,200 and 2,400 years respectively (Fig. 6.8). Both canopy angiosperms exhibited a similar response; they were taller (10%) and had larger DBH values (13%) in systems without external propagule rain. Abundance of *D. cupressinum* was relatively greater (9%) over the first 800 years in the absence of external propagule rain; however, more (72%) gymnosperms persisted in the simulation where there was external propagule rain. Of the small
trees and understorey shrubs, the main response was observed in *H. arborea*, which was relatively more (57%) abundant for the first 700 years in the absence of external propagule rain (Fig. 6.8). In comparison, without external propagule rain, the fewer *H. arborea* persisting grew taller and attained greater DBH values (200%, 86% respectively).

![Figure 6.9. Trends of abundances, age, dbh and height for the eight modelled species over 2,500 years of simulations with seedling suppression set at 0 and 50% per time-step. Colours represent the following species: B. tawa = red; L. novae-zelandiae = grey; D. cupressinum = yellow; H. arborea = light green; M. ramiflorus = pink; P. excelsum = light blue; C. dealbata = dark green; K. robusta = blue. Note y-axes are variably scaled within each state variable (column).](image-url)
6.4.3 Seedling suppression and macro-litterfall

Running the simulations with seedling suppression (of all species) in patches occupied by tree ferns reduced the abundance of tree ferns by 30% overall compared to simulations where the seedling suppression procedure was not used. *B. tawa* and *L. novae-zelandiae* increased in abundance by 29 and 35%; *D. cupressinum* increased by 17% overall. The other species were present in the model in similar abundances in both simulations (with and without seedling suppression). *B. tawa* abundance stabilises up to 500 years faster (Fig. 6.9).

Increasing the probability of the loss of a sapling underneath tree ferns (representing 50% of the stems in the model at the start of the runs) had no discernible influence on the long-term composition of the community (Fig. 6.10).

Figure 6.10. Trends of abundances, age, dbh and height for the eight modelled species over 2,500 years of simulations with sapling mortality ranging from 0, 20, 40, 60, 80, to 100% per time-step. Colours represent the following species: *B. tawa* = red; *L. novae-zelandiae* = grey; *D. cupressinum* = yellow; *H. arborea* = light green; *M. ramiflorus* = pink; *P. excelsum* = light blue; *C. dealbata* = dark green; *K. robusta* = blue. Note y-axes are variably scaled within each state variable (column).
6.5 Discussion

The Morales & Perry (2017) model that I adapted is one of a small number of simulation models that specifically consider New Zealand indigenous forest dynamics (Develice 1988; Hall & Hollinger 2000; Kunstler et al. 2009; Thrippleton et al. 2014). The version described here is the first spatial model of New Zealand indigenous forests to have a tree fern growth form parameterised with tree fern demographic data using a non-DBH based growth model.

The first aim of this project was to develop a growth-form model for tree ferns that realistically represents their patterns of growth: increase in height without secondary growth (lateral thickening), and constant canopy width throughout life. Overall the model produced realistic outputs with individual *C. dealbata* attaining heights of up to 10 metres and ages between 300-500 years (Mueck et al. 1996; Bystriakova et al. 2011a; Brock et al. 2016). Ageing understorey tree ferns is a complex and expensive challenge, and to date there are no published age data for New Zealand species. While the occasional individual tree fern in the simulation achieving a longevity in excess of 500 years is unlikely in reality, the problem of individual persistence in low-light levels is not restricted to the tree ferns and is an element of the model that has previously been acknowledged as requiring refinement (Morales & Perry 2017). The data used to parameterise the tree fern height growth curve (ΔH) in the model came from 292 individuals in forest stands of different ages; although it is probable that inaccurate height recording of tree ferns over 6 m tall limits the accuracy of the height-growth curve particularly for tall ferns. In terms of the response of the simulated forest species to the presence of the tree ferns, the addition of tree ferns overall reduced the canopy dominants’ mean density. After 1,000 simulation years and across all initial tree fern abundances, mean *B. tawa* density is $131.4 \pm 101.6$ (ind/ha), *L. novae-zelandiae* is $156.7 \pm 123.1$, and *D. cupressinum* is $7.0 \pm 3.0$ stems, closely replicating the species densities observed in northern NZ forests described (2017).

Increasing the relative abundances of tree ferns in the simulations increased the length of time before overall *B. tawa* abundance stabilised. *L. novae-zelandiae* was approaching a stable abundance towards the end of an undisturbed 2,500 year period as tree ferns and *D. cupressinum* abundance declined. *D. cupressinum* stabilises at low numbers in the simulation; this species is characterised by low relative abundance (1% of stems), but relatively large individuals, consistent with the findings of Morales & Perry (2017) and the ecology of the species (in the absence of large disturbances; Ogden & Stewart 1995). That the mean height, DBH and age of these scattered, large gymnosperms increases with increasing relative abundance of tree ferns
compared to the angiosperms, suggests that these trees are growing relatively more slowly than their angiosperm competitors (Bond 1989). In general, the increase in height and DBH of the conifer canopy dominant types suggests a release from competitive suppression; a plausible explanation for this pattern is that by introducing shorter, relatively long-lived species (tree ferns) into the simulation, the density and uniformity of the canopy is reduced and so they experience less competition from taller neighbouring individuals. There is also potential for a reduction in juvenile mortality as fewer canopy gaps form due to a reduction in the number of canopy trees (this does not appear to be countered by the relative increase in macro-litterfall). Increasing variability in canopy height (Fig. 6.7) also suggests that with increasing tree fern relative abundance, there is a greater range of inter-specific growth rates. The greater range of growth rates is mirrored in the small trees and in the understorey where, likely due to decreased light competition, *H. arborea, M. ramiflorus* and *P. excelsum*, although displaced by tree fern abundance, grow larger in simulations with a greater abundance of tree ferns. This pattern suggests that small trees and understorey angiosperms benefit from the variation of the canopy and light environments that arises as height complexity increases. Furthermore, although as an early successional species *K. robusta* is rapidly lost (<200 years) from the forest community (in the absence of large-scale disturbances), where it does re-establish in canopy gaps, this species also grows taller and older, in systems with higher relative abundances of tree ferns. A future modification with regard to the response of understorey species to tree fern presence might be to include the ability of seedlings of some species to respond positively to macro-litterfall, e.g. to represent the increased growth rates observed in *H. arborea* after experimental pinning, mimicking the effect of fallen, dead fronds (Gillman et al. 2003).

Shade intolerant gymnosperms, along with their angiosperm counterparts, are therefore subjected to lesser light competition where tree ferns form the understorey as tree ferns both capture space in the model (reducing canopy stem density) yet remain relatively shorter in stature than the canopy dominants (opening up an otherwise dense canopy structure). Where tree ferns are present, gymnosperms, although suppressed in the regeneration niche (Bond 1989; Coomes et al. 2005), will persist longer and grow larger than when in communities dominated by angiosperms, which suggest of a significant competitive dynamic in native broadleaved-podocarp forests.

An interesting counterpoint to the outputs of the Morales and Perry (2017) model is the reduction in canopy tree densities at 1,000 years in this study. In the experimental treatment where the model is initialised with 40% relative abundance of tree ferns, the values for numbers of stems
per hectare are similar to empirical data on stand structure (as reported in Morales & Perry 2017).

Increasing seedling suppression to 50% (field-observed levels; Chapter 5) reduced tree fern abundance indicating negative density dependence (NDD) of *C. dealbata* in the simulations, comparable to that observed in *C. caracasana* in southern Ecuador by Chacón-Labella *et al.* (2014). Contrary to previous suggestions that suppression of seedlings underneath tree ferns reduces gymnosperm establishment, NDD effects on *C. dealbata* may actually reduce the competitiveness of tree ferns in the seedling community (tree ferns appear to consistently recruit under tree ferns; Morales *et al.* (2016)) and permit increased numbers of saplings of the three main canopy species to advance to maturity. The simulation outcomes suggest that the influence of macro-litterfall on community assembly, while spatially limiting the regeneration niche (Clark & Clark 1989; Gillman & Ogden 2001), has relatively little effect on canopy composition over the longer-term. This pattern suggests that the main contribution of tree ferns to successional processes is by capturing space in the landscape early on, and then persisting for periods of up to 500 years and significantly lengthening the time required for canopy dominant species to stabilise in the forest community. Similar inhibitory processes of tree ferns, reducing the establishment of woody plant species, have been observed in early successional communities (over a 7.3 year period) in Puerto Rico (Walker *et al.* 2010). Furthermore, tree ferns do not behave like the angiosperm understorey species *P. excelsum* and *M. ramiflorus* in this forest but rather increase in their abundance for the first several hundred years in every simulation. This dynamic is consistent with field observations made by Richardson *et al.* (2014) and Bellingham *et al.* (1998) with the understorey tree ferns *C. dealbata* and *C. smithii* in forests that have received prior disturbance. Local dominance by tree ferns after disturbance is likely a significant driver of forest community dynamics, and while slowing the stabilisation of dominant canopy species, also reduces inter and intra-specific competition driving the development of a tall angiosperm canopy with emergent gymnosperms.

The amount of external propagule rain is a difficult parameter to estimate for most species. There is little information on *Cyathea* spore dispersal, other than the studies undertaken by Conant (1978) showing a leptokurtic dispersal pattern of spores in understorey tree ferns over a 30 m distance (greatest spore density within 7.5 m of parent tree fern). Likewise, there is little information on likely dispersal distances of anemochorous canopy trees, although Nathan *et al.* (2002) present data to suggest that distances of greater than 100 m are achieved for between 1 and 5% of seed dispersal events. Most of the data that are available, however, consider...
endozoochorous tree taxa seed to typically disperse less than 100 m in New Zealand forests (Thorsen, Dickinson & Seddon 2009; Wotton & McAlpine 2015; Pegman, Perry & Clout 2017). Tree fern persistence and increase in abundance in the understorey is a clear response to propagule dispersal; more data on dispersal and gametophyte success would better inform the processes behind the spatial and temporal patterns of tree fern dominance in the landscape.

6.6 Conclusion

The outcomes of the in-silico experiments undertaken with this model suggest that tree ferns can strongly influence the structure and composition of New Zealand forests. Although the deep shade cast by tree ferns may reduce the abundance of shade-intolerant gymnosperms in the seedling bank, seedling suppression reducing the tree fern regeneration overall increases the likelihood of gymnosperms establishing. Furthermore, where tree ferns and established gymnosperms co-occur, the former also facilitate the latter through decreasing canopy stem density and, subsequently, light competition. Sub-canopy and understorey angiosperms appear to be similarly facilitated by reduced competition from tree ferns in the seedling bank, increased vertical complexity and altered light competition regimes. Finally, a less homogenous canopy may also facilitate a competitive release for canopy angiosperms.

Previous simulation models of indigenous New Zealand forest dynamics have consistently over-estimated stem density and under-estimated the size of canopy trees. By including tree ferns, an abundant life-form in northern New Zealand forests, and appropriately representing their distinct growth form, this model produces emergent patterns more representative of indigenous forest structure and composition. This study highlights the important of including different life-forms in forest models, particularly when they are long-lived and present at high relative densities. Furthermore, accurate representation of the growth patterns of these different life-forms is key to disentangling the effect that these life-forms have on the other species-types present in forests.
Chapter 7

Synthesis

7.1 Context

In Chapter 2, a synthesis of the ecology of New Zealand’s tree ferns, I highlighted nine knowledge gaps in our understanding of the ecology of tree ferns. The knowledge gaps were divided into sporophyte (carbon and water relations, nutrient ecophysiology, growth and mortality, spore viability and dispersal distances, effect on community assembly, accurate representation in forest simulation models) and the role of the gametophyte (niche and nutrient ecophysiology). This thesis addresses four of these knowledge gaps (in bold) by:

1. Determining how environmental filters influence tree fern gametophyte establishment,
2. Identifying how pioneering tree ferns influence community development,
3. Determining patterns and mechanisms of influence of understorey tree ferns on forest seedling communities; and,
4. Resolving the long-term effects of tree fern presence in temperate rainforest.

This thesis presents laboratory experiments manipulating environmental conditions for developing gametophytes; field surveys to obtain data on the selective effect on seedling recruitment by tree fern canopies; and, modelling forest systems to compare regeneration in the presence and absence of tree ferns in the community (as per Chapter 2). Due to practical limitations in time and space, I focused on a limited number of tree fern species (three species of the genus *Cyathea*) and the northern forests of New Zealand in this thesis. Further work could expand this research in more southern locations in New Zealand, and particularly with species in the genus *Dicksonia*, the other major genus of tree ferns in New Zealand with different ecological characteristics (e.g. frost tolerance, clonal stand development; Silvester 1964; Blaschke 1988).

7.2 Environmental filters influencing tree fern establishment

Gametophytes of various fern species develop relatively faster in locations with higher resources, both available phosphorus in the substrate and irradiance levels, suggesting these resources, assuming development rate correlates with mortality, are key limitations on
establishment (Greer 1993; Reis Moura et al. 2012; Pittermann et al. 2013). The morphology of fern gametophytes is uniform across growth environments and they are therefore considered suitable for experimental work (Farrar et al. 2008); however, I am not aware of any literature that describes experiments with gametophytes in controlled experimental conditions. In this thesis, I present first attempts to explore gametophyte ecology in this way.

The first aim of this thesis was to identify how environmental factors, in particular soil available phosphorus (orthophosphate) and irradiance, influence the establishment of the gametophyte life stage of *Cyathea medullaris, C. dealbata* and *C. smithii*. In Chapter 3, I quantified the development rates of gametophytes of the three *Cyathea* species and their differential response to controlled environmental conditions in which phosphate and light were varied. In two of the three species, the niche of the gametophyte tree fern was broadly similar to the niche of the sporophyte tree fern, suggesting limited environmental selection at the sporophyte stage. In general gametophytes of pioneer species (*C. medullaris*) of tree fern have broader environmental tolerances than understorey (*C. dealbata* and *C. smithii*) gametophyte tree ferns. I also show that gametophyte development can be modelled using a simple Markov model, providing further evidence that gametophytes show a predictable and consistent ontogeny across diverse environmental conditions (as suggested in Farrar et al. 2008).

Experimental study of the gametophyte development rates of *C. medullaris, C. dealbata* and *C. smithii* showed that phosphorus and irradiance strongly influence the development rates of the gametophyte tree ferns of these species. The niche of the gametophyte and sporophyte life-stages of *C. medullaris* and *C. dealbata* is similar; however, gametophyte and sporophyte preferences for *C. smithii* appear to decouple along a phosphorus gradient (gametophyte growth rates are highest at orthophosphate concentrations higher than those in which most sporophytes are recorded). *C. medullaris*, a pioneer species (see Chapter 4), has a gametophyte life-stage with growth rates indicative of a broad tolerance to a range of orthophosphate concentrations and irradiance levels. The two understorey tree ferns *C. dealbata* and *C. smithii* have significantly different growth rates under the same experimental conditions suggesting that one species could out-compete the other where rates of gametophyte development determine competitive outcomes (i.e. independent of resource availability). Further research should consider gametophyte interactions by experimentally considering inter-specific competition between gametophyte tree ferns, and conducting field surveys coupled with genetic identification as per Nitta et al. (2017), to establish the range of conditions under which gametophytes of these species naturally establish.
7.3 Tree fern influence in early successional forest communities

Early successional tree fern studies have only previously been described from tropical countries including Colombia and Puerto Rico (Arens & Sánchez Baracaldo 2000; Shiels 2006; Weaver 2008; Walker et al. 2010). In these ecosystems, tree ferns are described as inhibitory and as slowing down successional processes (Grubb 1977; Walker et al. 2010; Richardson et al. 2014). Tree ferns have also been described as producing a recalcitrant understorey, where changes in the disturbance regime, in particular increases in the rate of herbivory or fire, have promoted tree ferns to abnormal dominance (Jane & Pracy 1974; Royo & Carson 2006). More specifically, tree ferns can suppress the establishment and regeneration of conifers (Norton 1991; Duncan 1993; Coomes et al. 2005). Furthermore, high basal areas (> 21.2 m² ha⁻¹) of C. dealbata appeared to delay or prevent anticipated changes in forest structure over time (e.g., declining basal area, increasing stem diameter, basal area and above-ground biomass), resulting in ‘arrested successions’ (Richardson et al. 2014).

The second aim of this thesis was to determine whether succession under tree ferns follows a different trajectory to that under kānuka (Kunzea robusta) and then to identify the abiotic and biotic controls on any such differences. The characteristics of tree fern (C. medullaris) and kānuka ecosystems are analysed in Chapter 4. I studied vegetation plot data of early-successional communities from across the Auckland region to compare the vegetation communities associated with these two different pioneer species and, while accounting for abiotic influences, establish a pattern of tree fern influence in early successional forest.

The results of the study in Chapter 4 show compositional differences in vegetation communities associated with the pioneers C. medullaris and K. robusta. These two pioneer species separate along an environmental gradient of soil-moisture, aspect and slope, and once established, pioneer tree ferns, along with understorey C. dealbata (present in both systems), directly influence the vascular plant seedling community that develops beneath their canopies. The two pioneer vegetation communities are characterised by different plant species and functional types: notophyll species (e.g., Beilschmiedia tarairi, Hedycarya arborea) are associated predominantly with C. medullaris and nanophyll species (e.g., Phyllocladus trichomanoides, Leucopogon fasciculatus) are most commonly associated with K. robusta. Shade-tolerant conifers (e.g. Prumnopitys ferruginea) are faithful associates of tree fern dominated ecosystems. I found no evidence that conifer or angiosperm regeneration was suppressed in areas with high tree fern basal area, suggesting that the presence of tree ferns per se is not a limiting factor on
the establishment of woody vascular species. Instead, historic disturbance, and loss of dispersal (Kelly et al. 2010) and increased seed predation by exotic mammals (Perry et al. 2015), all of which reduce competition with and therefore favour tree ferns, may be the key drivers of previously described arrested successions. Further consideration should be given to the disturbance-tolerance traits (surviving macro-litterfall) of those species commonly developing in association with high tree fern densities e.g. *Hedycarya arborea*, *Melicytus ramiflorus* and *Geniostoma ligustrifolium*. *H. arborea* in particular has been shown to respond positively and increase growth rates after being pinned down by macro-litterfall (Gillman et al. 2003).

7.4 Patterns and mechanisms of influence of understorey tree ferns on forest seedling communities

Tree ferns can influence seedling and sapling communities through macro-litterfall, shading, effects on nutrient cycling, allelopathy and the provision of additional establishment surfaces (Froude 1980; Burton & Mueller-Dombois 1984; Enright & Ogden 1987; Gillman et al. 2004). Studies utilizing artificial seedlings have shown that macro-litterfall damage to seedlings is relatively low in New Zealand relative to the tropics (2% vs 41%; Young et al. 2014; Gillman 2016). Rates of damage significantly increase underneath macro-litterfall producing species (Gillman & Ogden 2005). The direct impacts of macro-litterfall in New Zealand accounted for up to 14% of conifer and angiosperm seedling mortality along 100 m transects (Gillman & Ogden 2001; Gillman et al. 2004). There is evidence that tree fern shading suppresses shade intolerant woody seedlings e.g. *Podocarpus totara* (Forbes et al. 2016). Similarly, this has been observed in Hawai‘i where understorey *Cibotium glaucum* suppressed seedlings of shade intolerant *Metrosideros polymorpha* (Burton & Mueller-Dombois 1984). Enright and Ogden (1987), Richardson (2005) and Froude (1980) provide evidence that in New Zealand tree ferns produce leaf litter high in nitrogen that breaks down relatively slowly, and alkaloids that potentially suppress seed germination of woody vascular species. Tree ferns can also provide an establishment surface for epiphytic seedlings and saplings with up to 60% of canopy *Weinmannia racemosa* in southern New Zealand forests establishing in this manner (Gaxiola et al. 2008).

The third aim of this thesis was to determine the effect of understorey tree ferns on forest structure and composition. In this study I focused solely on *C. dealbata* to avoid any potentially confounding covariables from differing frond-shedding processes among tree fern taxa and any
variation in possible allelopathic effects (see Chapter 2). I undertook field survey work to establish patterns of seedling and angiosperm : gymnosperm abundance in relation to the local presence or absence of tree ferns. I then experimentally manipulated the conditions in tree fern micro-sites to determine the mechanisms by which tree ferns influence the forest seedling communities.

This chapter presents analyses showing that tree ferns do affect woody seedling densities in their local neighbourhood. Seedling communities under tree ferns do not differ in composition from those away from tree fern canopy drip-lines; however, both angiosperms and gymnosperms are reduced equally in density beneath fern canopies. Tree fern micro-sites are characterised by relatively deep macro-litter (up to 20 cm) and are subjected to heavy shading (sub-tree fern PAR: $9.6 \pm 9.9 \mu\text{mol m}^{-2}\text{s}^{-1}$) as tree ferns filter up to 50% photosynthetic active radiation in the understorey (ambient PAR: $30.4 \pm 56.7 \mu\text{mol m}^{-2}\text{s}^{-1}$). Frond removal consistently resulted in the establishment of shade intolerant conifer seedlings (e.g. *Podocarpus totara*). Further work should include a tree fern removal treatment in vegetation plots in indigenous forests to compare understorey response to tree fern presence, in seedlings and saplings. Furthermore, tagged seedlings, terrestrial and epiphytic, should be monitored over longer time periods to allow survival and transition to older life-stages along a tree fern density gradient to be quantified.

### 7.5 Long-term effects of tree fern presence in temperate rainforest

A key hypothesised impact of increased tree fern abundance in mature podocarp-angiosperm forests is the suppression of shade-intolerant species, in particular conifers (Coomes *et al.* 2005; *Forbes et al.* 2016). Forest conifers in New Zealand are described as long-lived colonisers; that is, species that arrive early in succession (soon after disturbance) and persist in the ecosystem as mature adults in limited numbers (Ogden 1985; Ogden & Stewart 1995). Understorey tree ferns establish at a similar time to tree ferns in successional communities and, as can be seen in Chapter 5, lower the probability of new conifers establishing underneath their canopies (Wardle 1974; Chapter 4; Burns & Smale 1990; Norton 1991; Duncan 1993).

The final aim of this thesis was to use a spatially explicit individual-based model to simulate the long-term effects of tree fern presence in the forest understorey, building on information obtained in Chapter 5. Again this study focused on *C. dealbata* as it is the most common understorey tree fern in northern New Zealand forests; in particular, this species was the most
frequently recorded (73% of stems) species in the forests used to parameterise the original model (Morales & Perry, 2017). I established a new tree fern growth algorithm based on new field data of height increment. Previous approaches have relied on diameter increment, which is misleading for tree ferns with their stable canopy diameter, even as stems enlarge and get taller. My representation of the growth form of tree ferns slowed their modelled height-growth and significantly increased their densities in the modelled forest compared to the emergent densities of the only other model representing New Zealand forests that includes tree ferns and reports on their performance (LANDCLIM; Thrippleton et al. (2014)).

The most interesting result of the simulation experiments is the unexpected positive response of the conifer species-type to increasing tree fern density in the forests. Conifers persisted up to 500 years longer, and grew up to an average of 12 m taller in systems with high initial densities of tree ferns when compared to simulations with no tree ferns present. Angiosperms also responded positively to increased tree fern density, as although fewer individual angiosperms were present in the canopy compared to modelled forests without tree ferns, the reduced density of canopy trees in the simulated forest with tree ferns reduced competition for light in the canopy (driven by increasing stem density of tree ferns). Incremental increases in tree fern density resulted in increasingly variable canopy height structure, which led to increased irradiance heterogeneity and generally reduced levels of competition facilitating all canopy tree species present in the simulated forest. A second surprising outcome was that the suppression of woody seedlings in patches occupied by tree ferns did not slow successional processes (as suggested in Chapter 4), but rather canopy species benefitted (increases in mean age and height) and abundances stabilized in the canopy earlier. Tree fern seedlings appear to be most affected by seedling suppression underneath tree ferns, an emergent pattern suggesting negative density dependence processes in *C. dealbata* (as observed in the field by Chacón-Labella et al. 2014). Further work on these models should introduce an age-mortality function, seedling and sapling outputs (the model outputs do not currently provide an opportunity to monitor patterns of non-mature individuals), environmental heterogeneity (topography and soils), and explore the importance of landscape-level disturbance regimen.

### 7.6 Management implications

Overall, my thesis has shown that tree ferns have a complex and influential role in the indigenous temperate rainforests of New Zealand. These forests have been significantly reduced (up to 75%
compared to prehuman extent) through anthropic fire and clearance for agriculture (McGlone 1989). In response to this, in many parts of New Zealand local community groups are working to re-establish and restore forest communities. A common practice for replanting temperate rainforest is to plant a mixture of the angiosperms *Leptospermum scoparium* and/or *Kunzea robusta* as prominent pioneer and nursery species, along with early-successional canopy species. As discussed in Chapter 4, tree ferns, particularly *Cyathea medullaris* may be a more suitable nursery species for the restoration of indigenous temperate rainforest in steeper, less dry conditions because these are the conditions in which this species naturally occurs as a pioneer. Further research to enhance colonization by *C. medullaris* would prove beneficial to these projects and lower the risk of establishment failure (Eleutério & Pérez-Salicrup 2009). Likewise, understanding how to establish understory *C. dealbata* and *C. smithii* may prove beneficial to managed forests in developing deep litter layers that encourage the re-development of indigenous detritivore communities.

As a counterpoint to the use of tree ferns to contribute positively to habitat restoration, commercial plantation forest managers may wish to remove *Cyathea dealbata* (and other tree fern species) from the understory of commercial plantations and indigenous forests under productive management to encourage natural regeneration of indigenous canopy tree species, particularly if gymnosperms are a desired resource.

### 7.7 Conclusions

Tree ferns, as with keystone and foundation species, influence abiotic conditions in their microsites and influence the structure and composition of the forest communities of which they are a component. However, their influence is not restricted to top-down filtering of irradiance levels and macro-litterfall. This thesis presents the first evidence from simulated data to show that tree ferns also, unusually for the understory, have a bottom-up effect and can facilitate growth and productivity in the canopy by reducing canopy stem density and thus reducing intra- and interspecific competition for light resources. Contrary to the popular understanding that tree ferns have an entirely antagonistic relationship with the gymnosperms I suggest that the research presented here indicates that the two clades may have a relatively beneficial relationship. The research I present in this thesis suggests that tree ferns have substantial influences on the structure and composition of many New Zealand native forests.
### Appendix 1


<table>
<thead>
<tr>
<th>Tree fern</th>
<th>Forest / Scrub Community</th>
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| C. colensoi | Lophozonia menziesii forest¹²  
Lophozonia menziesii - Griselinia littoralis - Myrsine divaricata / Coprosma foetidissima forest⁶  
Lophozonia menziesii - Fuscospora fusca - Fuscospora solandri forest⁶  
Weinmannia racemosa - Lophozonia menziesii forest¹² |
| C. cunninghamii | Agathis australis forest⁶  
Dracophyllum arboreum forest⁸ |
| C. dealbata | Agathis australis – Phyllocladus trichomanoides forest⁷  
Cyathea dealbata - Melicytus ramiflorus - Freycinetia baueriana - Ripogonum scandens forest⁶  
Knightia excelsa – Weinmannia racemosa – Cyathea dealbata forest⁸  
Kunzea ericoides - Cyathea dealbata – (Leptospermum scoparium) / Leucopogon fasciculatus - (Coprosma rhamnoides) forest and tall shrubland⁶  
Kunzea ericoides scrub¹  
Leptospermum scoparium scrub²  
Melicytus ramiflorus - Cyathea smithii - Dicksonia squarrosa - Carpodetus serratus (Beilschmiedia tawa) forest⁶  
Pseudopanax arboreus – Dicksonia squarrosa – Cyathea spp. – Melicytus ramiflorus bush⁸  
Weinmannia racemosa - Cyathea dealbata - Knightia excelsa (Beilschmiedia tawa) / Leucopogon fasciculatus forest⁶  
Weinmannia silvicola – Beilschmiedia tawa / Freycinetia banksii forest⁶ |
| C. kermadecensis | Metrosideros kermadecensis – Ascarina lucida var lanceolata forest⁸ |
| C. medullaris | Agathis australis forest⁸  
Dacrydium cupressinum – Beilschmiedia tawa – Metrosideros robusta forest¹¹  
Dracophyllum arboreum forest⁸  
Kunzea ericoides scrub⁸  
Laurelia novae-zelandiae – Beilschmiedia tawa – Dacrycarpus dacrydoides forest⁸ |
| C. milnei | Metrosideros kermadecensis – Ascarina lucida var lanceolata forest⁸ |
| C. smithii | Dacrycarpus dacrydiodes – Coprosma rotundifolia – Podocarpus totara forest¹  
Dacrycarpus dacrydiodes forest⁸  
Fuscospora fusca forest⁶, ¹²  
Lophozonia menziesii forest⁸, ¹²  
Melicytus ramiflorus - Cyathea smithii - Dicksonia squarrosa - Carpodetus serratus (Beilschmiedia tawa) forest⁶  
Metrosideros umbellata – Weinmannia racemosa – Dacrydium cupressinum forest¹⁰  
Weinmannia racemosa - Cyathea smithii - Prumnopitys ferruginea / Blechnum discolor forest⁶  
Weinmannia racemosa – Griselinia littoralis – Pseudowintera colorata / Blechnum discolor forest⁶ |
| D. fibrosa | Weinmannia racemosa – Beilschmiedia tawa forest⁸ |
| D. lanata var. hispida | Agathis australis forest⁸ |
D. lanata var. **Fuscospora cliffortiodes** forest

| D. squarrosa | Beilschmiedia tawa - Weinmannia racemosa - Melicytus ramiflorus / Ripogonum scandens forest²  
Dacrycarpus dacrydiodes – Weinmannia racemosa forest³  
Dacrycarpus dacrydiodes forest⁹  
Dacrydium cupressinum – Prumnopitys taxifolia / Beilschmieda tawa – Elaeocarpus hookerianus forest⁸  
Dacrydium cupressinum / Beilschmieda tawa / (Melicytus ramiflorus – Dicksonia squarrosa – Pseudopanax arboreus) forest⁸  
Fuscospora fusca forest⁸, ¹²  
Leptospermum scoparium scrub²  
Lophozonia menziesii forest⁸, ¹²  
Melicytus ramiflorus - Cyathea smithii - Dicksonia squarrosa - Carpodetus serratus (Beilschmieda tawa) forest⁶  
Metrosideros umbellata – Weinmannia racemosa – Dacrydium cupressinum forest¹⁰  
Pseudopanax arboreus – Dicksnoia squarrosa – Cyathea spp. – Melicytus ramiflorus bush⁸ |
Appendix 2

Figure A2.1. nMDS ordination of the vegetation data using frequency data; stress on the ordination is 0.21. PERMANOVA $F_{1-164}$: 29.12, $P < 0.001^{***}$

Figure A2.2. nMDS ordination of the vegetation data using presence absence data; stress on the ordination is 0.20. PERMANOVA $F_{1-164}$: 12.22, $P < 0.001^{***}$
Figure A2.3. nMDS ordination of the vegetation data using BA data with *C. medullaris* and *K. robusta* data removed; stress on the ordination is 0.24.
Table A2.1. Indicator species of *Cyathea medullaris* / *Cyathea dealbata* and *Kunzea robusta* / *Cyathea dealbata* forests in the tree / sapling data (species grouped in the table by position in forest and/or taxa: canopy, subcanopy and tree fern). The predictive value (Pred. Val.) is the probability that any vegetation plot belongs to the successional community given the presence of this species (an indicator species). Sensitivity (Sens.) is the probability of finding the species in vegetation plots belonging to the successional community. The final two columns of figures state the strength and significance of the association of each species with the successional community.

<table>
<thead>
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<tr>
<td>Hedycarya arborea</td>
<td>0.949</td>
<td>0.763</td>
<td>0.851</td>
<td>0.001 ***</td>
<td></td>
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<td>Olearia rani</td>
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<td>0.673</td>
<td>0.001 ***</td>
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<tr>
<td>Dysoxylum spectabile</td>
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<td>0.390</td>
<td>0.607</td>
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<tr>
<td>Knightia excelsa</td>
<td>0.719</td>
<td>0.593</td>
<td>0.653</td>
<td>0.001 ***</td>
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<td>0.237</td>
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<td>Vitex lucens</td>
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<td>0.203</td>
<td>0.439</td>
<td>0.015 *</td>
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<td>0.841</td>
<td>0.186</td>
<td>0.396</td>
<td>0.045 *</td>
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<tr>
<td>Laurelia novae-zelandiae</td>
<td>0.773</td>
<td>0.102</td>
<td>0.280</td>
<td>0.037 *</td>
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<tr>
<td>Melicytus ramiflorus</td>
<td>0.850</td>
<td>0.949</td>
<td>0.898</td>
<td>0.001 ***</td>
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<tr>
<td>Rhopalostylis sapida</td>
<td>0.902</td>
<td>0.644</td>
<td>0.762</td>
<td>0.001 ***</td>
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<td>Coprosma grandifolia</td>
<td>0.873</td>
<td>0.627</td>
<td>0.740</td>
<td>0.001 ***</td>
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<td>Schefflera digitata</td>
<td>0.988</td>
<td>0.407</td>
<td>0.634</td>
<td>0.001 ***</td>
<td></td>
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<td>Brachyglossis repanda</td>
<td>0.864</td>
<td>0.322</td>
<td>0.528</td>
<td>0.001 ***</td>
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<td>0.851</td>
<td>0.186</td>
<td>0.398</td>
<td>0.026 *</td>
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<td>0.102</td>
<td>0.319</td>
<td>0.005 **</td>
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<tr>
<td>Piper excelsum</td>
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<td>0.068</td>
<td>0.260</td>
<td>0.016 *</td>
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<td>Rhabdothamnus solandri</td>
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<td>0.068</td>
<td>0.260</td>
<td>0.011 *</td>
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<td>Cyathea medullaris</td>
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<td>Cyathea dealbata</td>
<td>0.735</td>
<td>0.983</td>
<td>0.850</td>
<td>0.001 ***</td>
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<tr>
<td>Dicksonia squarrolsa</td>
<td>0.914</td>
<td>0.576</td>
<td>0.726</td>
<td>0.001 ***</td>
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<tr>
<td>Cyathea smithii</td>
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Table A2.2. Indicator species of *Cyathea medullaris* / *Cyathea dealbata* and *Kunzea robusta* / *Cyathea dealbata* forests in the seedling data (species grouped in the table by position in forest and/or taxa: canopy, subcanopy and tree fern). The predictive value (Pred. Val.) is the probability that any vegetation plot belongs to the successional community given the presence of this species (an indicator species). Sensitivity (Sens.) is the probability of finding the species in vegetation plots belonging to the successional community. The final two columns of figures state the strength and significance of the association of each species with the successional community.

<table>
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<tr>
<th>Species</th>
<th>Pred. Value</th>
<th>Sensitivity</th>
<th>Stat</th>
<th>Sig. Value</th>
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<td><strong>Cyathea medullaris / Cyathea dealbata Forest</strong></td>
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<td>0.817</td>
<td>0.661</td>
<td>0.735</td>
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<td>Knightia excelsa</td>
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<td>0.569</td>
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<td>Dysoxylum spectabile</td>
<td>0.750</td>
<td>0.254</td>
<td>0.437</td>
<td>0.016 *</td>
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<td>Prumnopitys ferruginea</td>
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<td>0.203</td>
<td>0.409</td>
<td>0.016 *</td>
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<td>0.702</td>
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<td>0.408</td>
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<td>Laurelia novae-zelandiae</td>
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<td>0.344</td>
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<td>Rhopalostylis sapida</td>
<td>0.830</td>
<td>0.797</td>
<td>0.813</td>
<td>0.001 ***</td>
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<td>0.664</td>
<td>0.644</td>
<td>0.654</td>
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<td>Geniostoma ligustrifolium</td>
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<td>0.458</td>
<td>0.599</td>
<td>0.010 **</td>
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<td>0.549</td>
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<td>0.153</td>
<td>0.372</td>
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<td>0.153</td>
<td>0.371</td>
<td>0.003 **</td>
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<td>0.119</td>
<td>0.344</td>
<td>0.002 **</td>
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<td>0.306</td>
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<td>0.068</td>
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<td>0.014 *</td>
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<td>0.427</td>
<td>0.017 *</td>
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<td>Phyllocladus trichomanoides</td>
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<td>0.336</td>
<td>0.570</td>
<td>0.001 ***</td>
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<td>0.346</td>
<td>0.567</td>
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<td>0.290</td>
<td>0.525</td>
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<td>0.150</td>
<td>0.371</td>
<td>0.030 *</td>
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<td>0.828</td>
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<td>Leucopogon fasciculatus</td>
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<td>0.505</td>
<td>0.662</td>
<td>0.001 ***</td>
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<td>Olearia furfuracea</td>
<td>0.982</td>
<td>0.280</td>
<td>0.525</td>
<td>0.002 **</td>
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<td>Coprosma spathulata</td>
<td>0.968</td>
<td>0.262</td>
<td>0.503</td>
<td>0.020 *</td>
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<td>Leptospermum scoparium</td>
<td>0.980</td>
<td>0.150</td>
<td>0.383</td>
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<td>0.150</td>
<td>0.365</td>
<td>0.037 *</td>
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<td>0.102</td>
<td>0.321</td>
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<td>0.746</td>
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Appendix 3
Table A3.1. Environmental data: range of soil nutrients (5% -Median - 95%) across the experiment locations by treatment

<table>
<thead>
<tr>
<th>Environmental Data</th>
<th>Control (T1)</th>
<th>Frond and litter removal (T2)</th>
<th>Frond removal only (T3)</th>
<th>Litter removal only (T4)</th>
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<td>Soil conditions</td>
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<td>Cation Exchange Capacity (meq 100g⁻¹)</td>
<td>10.9 – 21.1 – 27.4</td>
<td>12.4 – 19.3 – 26.8</td>
<td>10.9 – 18.7 – 29.6</td>
<td>10.8 – 20.1 – 24.9</td>
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<tr>
<td>pH</td>
<td>4.2 – 4.7 – 5.6</td>
<td>3.9 – 4.5 – 5.8</td>
<td>4.1 – 4.8 – 5.7</td>
<td>4.2 – 5.8 – 5.8</td>
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<tr>
<td>Organic Matter (%)</td>
<td>11.5 – 26.0 – 88.5</td>
<td>12.7 – 25.2 – 87.7</td>
<td>11.2 – 23.4 – 80.3</td>
<td>9.7 – 26.7 – 76.5</td>
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<td>Sulfur (ppm)</td>
<td>10.0 – 13.5 – 18.1</td>
<td>10.0 – 14.0 – 18.1</td>
<td>10.0 – 14.0 – 18.0</td>
<td>10.0 – 13.5 – 16.1</td>
</tr>
<tr>
<td>Phosphorus mg kg⁻¹</td>
<td>4.0 – 6.0 – 10.0</td>
<td>4.0 – 6.0 – 12.1</td>
<td>3.0 – 5.0 – 11.1</td>
<td>4.0 – 5.0 – 10.1</td>
</tr>
<tr>
<td>Bray I</td>
<td>0.5 – 1.0 – 5.1</td>
<td>0.5 – 2.0 – 5.1</td>
<td>0.5 – 1.0 – 3.0</td>
<td>0.5 – 1.0 – 4.0</td>
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<tr>
<td>Nitrogen</td>
<td></td>
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<td></td>
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<tr>
<td>NO₃ (ppm)</td>
<td>0.1 – 0.1 – 2.8</td>
<td>0.1 – 0.1 – 3.1</td>
<td>0.1 – 0.1 – 0.5</td>
<td>0.1 – 0.1 – 2.8</td>
</tr>
<tr>
<td>NH₄ (ppm)</td>
<td>4.9 – 15.0 – 34.8</td>
<td>4.6 – 13.5 – 26.3</td>
<td>4.0 – 11.7 – 26.9</td>
<td>3.9 – 12.2 – 30.0</td>
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<tr>
<td>Calcium</td>
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<td></td>
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<tr>
<td>mg kg⁻¹</td>
<td>417.8 – 1,165.0 – 1,907.3</td>
<td>316.8 – 869.0 – 1,972.3</td>
<td>368.3 – 950.0 – 1,972.0</td>
<td>480.0 – 982.0 – 1,923.4</td>
</tr>
<tr>
<td>%</td>
<td>15.8 – 24.0 – 40.1</td>
<td>11.4 – 20.4 – 43.1</td>
<td>13.7 – 24.3 – 40.5</td>
<td>15.4 – 23.1 – 41.7</td>
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<tr>
<td>Magnesium</td>
<td></td>
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<tr>
<td>mg kg⁻¹</td>
<td>165.2 – 309.5 – 795.0</td>
<td>151.6 – 300.0 – 738.5</td>
<td>183.8 – 287.0 – 667.8</td>
<td>162.5 – 301.0 – 682.9</td>
</tr>
<tr>
<td>%</td>
<td>7.8 – 12.8 – 25.0</td>
<td>7.2 – 13.6 – 23.8</td>
<td>8.7 – 15.1 – 25.8</td>
<td>8.6 – 14.0 – 29.4</td>
</tr>
<tr>
<td>Potassium</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>mg kg⁻¹</td>
<td>98.9 – 146.5 – 266.4</td>
<td>98.9 – 140.5 – 288.3</td>
<td>90.8 – 146.0 – 264.8</td>
<td>87.4 – 146.0 – 282.5</td>
</tr>
<tr>
<td>%</td>
<td>1.2 – 1.9 – 3.4</td>
<td>1.4 – 2.0 – 3.5</td>
<td>1.5 – 2.1 – 3.0</td>
<td>1.5 – 1.9 – 3.2</td>
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<tr>
<td>Sodium</td>
<td></td>
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<td></td>
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<tr>
<td>mg kg⁻¹</td>
<td>49.7 – 87.5 – 164.3</td>
<td>56.0 – 88.5 – 140.4</td>
<td>56.0 – 81.5 – 139.65</td>
<td>52.0 – 88.0 – 141.2</td>
</tr>
<tr>
<td>%</td>
<td>1.3 – 1.8 – 3.5</td>
<td>1.3 – 1.9 – 3.1</td>
<td>1.3 – 2.0 – 2.7</td>
<td>1.4 – 1.9 – 3.1</td>
</tr>
<tr>
<td>H⁺ %</td>
<td>26.9 – 51.0 – 61.2</td>
<td>21.0 – 55.0 – 66.0</td>
<td>23.7 – 49.0 – 63.1</td>
<td>21.0 – 49.0 – 61.1</td>
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<tr>
<td>Boron (mg kg⁻¹)</td>
<td>0.3 – 0.6 – 0.8</td>
<td>0.3 – 0.5 – 0.8</td>
<td>0.3 – 0.6 – 0.9</td>
<td>0.4 – 0.6 – 0.8</td>
</tr>
<tr>
<td>Iron (mg kg⁻¹)</td>
<td>58.0 – 238.5 – 386.3</td>
<td>52.5 – 226.0 – 451.3</td>
<td>65.3 – 280.0 – 476.4</td>
<td>80.6 – 214.0 – 417.5</td>
</tr>
<tr>
<td>Manganese (mg kg⁻¹)</td>
<td>8.9 – 28.0 – 109.2</td>
<td>6.0 – 23.0 – 86.2</td>
<td>5.9 – 21.0 – 79.2</td>
<td>7.9 – 24.5 – 87.8</td>
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<tr>
<td>Copper (mg kg⁻¹)</td>
<td>0.6 – 0.8 – 7.2</td>
<td>0.6 – 0.9 – 6.5</td>
<td>0.6 – 0.8 – 4.4</td>
<td>0.6 – 0.8 – 4.7</td>
</tr>
<tr>
<td>Zinc (mg kg⁻¹)</td>
<td>1.8 – 3.6 – 8.1</td>
<td>1.7 – 3.2 – 6.8</td>
<td>1.5 – 2.8 – 5.9</td>
<td>1.5 – 3.4 – 6.6</td>
</tr>
<tr>
<td>Aluminium (mg kg⁻¹)</td>
<td>233.2 – 815.5 – 1,137.6</td>
<td>270.7 – 765.0 – 1,153.7</td>
<td>342.8 – 830.0 – 1,314.3</td>
<td>299.8 – 739.0 – 1,210.7</td>
</tr>
</tbody>
</table>
Table A3.2. Environmental data: range of biophysical conditions (5% - Median - 95%) across the experiment locations by treatment

<table>
<thead>
<tr>
<th>Environmental Data</th>
<th>Control (T1)</th>
<th>Frond and litter removal (T2)</th>
<th>Frond removal only (T3)</th>
<th>Litter removal only (T4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil Moisture</td>
<td>13.3 – 36.3 – 49.5</td>
<td>12.9 – 38.7 – 50.1</td>
<td>13.6 – 39.0 – 50.4</td>
<td>13.0 – 38.1 – 49.7</td>
</tr>
<tr>
<td>Tree fern height</td>
<td>1.4 – 2.8 – 4.6</td>
<td>1.2 – 3.2 – 5.5</td>
<td>1.4 – 3.1 – 4.9</td>
<td>0.9 – 2.5 – 4.7</td>
</tr>
<tr>
<td>Tree fern canopy width</td>
<td>2.4 – 3.7 – 5.3</td>
<td>2.7 – 4.3 – 5.4</td>
<td>2.7 – 4.1 – 5.1</td>
<td>2.3 – 3.7 – 5.5</td>
</tr>
<tr>
<td>Slope</td>
<td>9.0 – 17.0 – 27.0</td>
<td>7.0 – 16.5 – 26.2</td>
<td>6.0 – 16.0 – 24.1</td>
<td>7.0 – 16.0 – 26.1</td>
</tr>
<tr>
<td>Mean litter depth (at commencement)</td>
<td>1.2 – 4.3 – 11.5</td>
<td>1.7 – 4.6 – 9.1</td>
<td>1.7 – 4.5 – 9.0</td>
<td>0.7 – 4.4 – 12.4</td>
</tr>
<tr>
<td>Asp North</td>
<td>-1.0 - -0.2 – 0.9</td>
<td>-1.0 - -0.4 – 0.9</td>
<td>-1.0 - -0.3 – 0.9</td>
<td>-2.0 - -0.3 – 1.0</td>
</tr>
<tr>
<td>Asp East</td>
<td>-0.9 – 0.1 – 0.9</td>
<td>-0.9 – 0.1 – 0.9</td>
<td>-0.9 – 0.1 – 0.9</td>
<td>-0.9 – 0.2 – 0.9</td>
</tr>
</tbody>
</table>
References


Bowkett, L. (2011) *Epiphytic relations of the soft tree fern Dicksonia antarctica Labill. and the vascular plant species utilising its caudex*. PhD, University of Tasmania, Hobart.


Dingley, J.M. (1940) *Some observations on the New Zealand representatives of the genus Dicksonia*. University of New Zealand.


