Plant traits and their role in determining forest community structure along a soil fertility gradient

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Abstract

Previous studies have shown that changes in community composition in mature kauri forests are driven by topographical gradients. The extent to which functional traits influence the patterns detected in these forests has not been well-studied. The overall objective of this thesis was to enhance our understanding of what drives community assembly in these forests by testing the importance of functional traits in mediating the relationship between environmental factors and community composition.

Puketī Forest (Northland, New Zealand) was selected as the study site because rapid turnover of species composition occurs over very strong topographic and edaphic gradients. Community composition was determined using forty permanent 400 m^2 plots that spanned the full gradient in soil properties and topographic variation. Leaf, height and wood traits were measured in thirty of these plots on three individuals (> 10 cm dbh) for each species on each plot. A total of 30 species were studied; the criteria for a species to be included was that the species had to attain a relative abundance of at least 0.05 within a single plot and occur on at least 10 percent of the forty plots sampled. Fully-expanded, mature, healthy, well-lit leaves were collected from the canopy using a pole pruner, shotgun or slingshot. Cores were collected using an increment borer. The relationships between community-weighted mean traits and environmental gradients were analysed using linear regression.

Results showed that there is a continuous compositional change along this environmental gradient and consequently there are few visually abrupt changes that occur between forest types. The exception to this is the kauri-dominated stands that are found in low fertility environments that are present on ridges. Soil variables and topography were found to be correlated, and the environmental variables that explain the majority of the variation in the community composition and functional trait data were soil carbon: nitrogen ratio, total soil phosphorus and soil pH, rather than topography.

Trait – environment regressions showed that traits are filtered along the soil fertility gradient. Species that have high SLA, high leaf and litter nitrogen, low leaf thickness, large seeds and low wood densities were found in the more fertile environments, which have a low soil carbon: nitrogen ratio, high total soil phosphorus and a high pH, such as a gully habitat. At the other end of this gradient, species that have low SLA, low leaf and litter nitrogen, high leaf thickness, small seeds and high wood densities were present in less fertile environments, which have a high soil carbon: nitrogen ratio, low total soil phosphorus and a low pH, such as a ridge top habitat.

Functional diversity indices indicate that the strength of environmental filtering changes along the soil fertility gradient. These indices show that trait variability does vary along the soil fertility gradient and that there are different community assembly processes operating in different places. The strength of the soil fertility as an environmental filter is strongest in low fertility soils, as environmental filtering results in convergence towards traits that confer a resource-retaining strategy.

Previous studies in kauri forests have shown changes in community composition to be determined by topography. This study has shown that these well-known patterns are driven by the filtering of leaf and wood traits along the topographically-driven soil fertility gradient.

Keywords: Puketī Forest, community assembly, leaf traits, wood traits, environmental filtering, functional diversity, topography, environmental gradient, kauri, *Agathis australis*.

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Chapter One: Introduction

1.1 Overview

To successfully restore an ecosystem requires a fundamental understanding of the ecological characteristics of the species, together with the knowledge of how they assemble, interact and function as a community (Pywell et al. 2003). Therefore, given the increasing impact of humans on the environment, the clarification of the processes that influence the species composition, diversity and traits that make up a community and accurate predictive models of species abundance has never been greater and consequently has become one of the most important quests in ecology. However, there appears to be a lack of consensus on the processes that influence community assembly and which ecological principles should be used to develop these models (Keddy 1992, HilleRisLambers et al. 2012, Laughlin et al. 2012). Although community ecology is often perceived as a "mess", due to the vast number of processes that can underlie the observed patterns (Lawton 1999, Vellend 2010), I sought to determine the importance of functional traits in mediating the relationship between environmental factors and community composition and the significance of environmental filtering in the context of a species-rich, old-growth kauri forest. Environmental filtering is a process that selects individuals with functional traits that yield the highest fitness and performance within a given environment (Keddy 1992). This process increases functional similarity of species within a community, resulting in trait convergence (Gourlet-Fleury et al. 2011, Lasky et al. 2013).

1.2 Plant diversity and global distribution

There are more than 250,000 vascular plant species worldwide undertaking similar processes of acquiring resources (water, light and nutrients) in order to photosynthesise and reproduce (Wright et al. 2004). However, the distribution of these plants throughout the world is not random. This is because evolutionary processes determine the species pool within a particular area and then filters act to determine the distribution and abundances of these species within the regional species pool (Grime 1977). The individuals that are not filtered out by the spatial variation in filters such as climatic conditions, due to having desirable traits for a certain region, will then undergo further filtering through disturbance and biotic interactions until a community has established. Climate acts on a broad scale and is one of the first limiting factors in plant distribution, whereas other ecosystem filters such as soil fertility act on a much finer, regional scale (Diaz et al. 1999).

In terms of latitude, there is a broad change in biomes and species diversity, ranging from tropical evergreen rainforest at the equator, to tropical deciduous forest, to desert or savannah, to temperate deciduous forests, to grassland, to evergreen coniferous forests and arctic tundra. There is also a broad change in biomes along altitudinal gradients ranging from tropical forest, to deciduous forest, to evergreen forest, to alpine tundra (Desonie 2008). Species found in one biome will have different traits and therefore different ecological strategies to those species found in other biomes, due to the difference in environmental conditions and resource availability (Westoby et al. 2002).

The change in the composition of species and ecological strategies can occur on much smaller scales, such as along soil fertility gradients within an ecosystem. Mason et al. (2012) showed that there is a shift in plant strategies from resource-retaining on the sites with low phosphorus, to resource-acquiring strategies such as high growth rates, high nutrient investments in leaves and low leaf lifespan on sites with high levels of soil phosphorus.

1.3 What are traits?

The concept of traits was first proposed by Darwin (1859). However, Darwin’s use of the term trait was mainly to describe the performance of an individual. The modern definition of a trait, proposed by Violle et al. (2007), is “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation”.

The meaning and use of the word trait varies throughout the literature. Papers such as Petchey et al. (2004) and Eviner (2004) show the misperception about the term and definition of a trait. Petchey et al. (2004) manipulated plant species and functional group richness and then measured 11 different traits to determine if they could explain differences in biomass production. However, of the 11 traits that were used, only eight comply with the definition proposed by Violle et al. (2007). The remaining three traits: vegetation cover, canopy height and standing biomass, do not refer to an individual trait, but rather to the study area. Eviner (2004) investigated eight plant species and determined if their traits influenced bio-geochemical cycling. Within this experiment there were many traits (e.g. soil temperature and soil moisture) that applied to an ecosystem level, not an individual plant.

There are many different types of traits used to describe plants, however not all of them are mutually exclusive. The main types of traits that are referred to in the literature, which are relevant to this study are: functional, response and effect. Functional traits are those that strongly impact an individual's fitness or performance. They are the ecological attributes of a species that relate both to strategies of resource capture and to the effect of that species on the overall pool of resources in the ecosystem (McGill et al. 2006, Funk et al. 2008). Examples of functional traits are plant height, specific leaf area and seed size (Westoby 1998). Response traits are those that respond to changes in environmental factors and as a result many functional traits are also considered response traits. These traits are important in determining the resilience of an ecosystem. Effect traits are those that are related to the effects of a plant on ecosystem functioning. Lavorel and Garnier (2002) show that effect traits involved in changes in primary productivity along a nutrient gradient strongly overlapped with those involved in the response of species to the gradient (response traits). This shows that traits are not mutually exclusive of each other.

1.4 Plant ecological strategies and functional traits

Functional traits influence their environment by affecting ecological processes such as litter decomposition, competition, light availability, soil fertility, temperature and precipitation. The traits that each plant possesses will therefore determine their ability to establish, survive and reproduce in a particular environment (Suding et al. 2008, Freschet et al. 2011). Functional traits are also used as indicators to help determine the ways in which species obey assembly rules. Assembly rules specify which subset of species would tolerate specified environmental conditions and form a community. Assembly rules work through eliminating sets of traits (and therefore species that possess them), which are unsuitable to that environment. The species that comprise the community are those that have suitable traits for the specified conditions. Another important concept is the response rule, which determines how the species composition will respond when environmental factors are changed. Examples of this are forest clearing, fire or intensified grazing. It is important to re-examine the initial species and sets of traits once variables and environmental factors have been changed, because species with different sets of traits that are more suitable to the changed environment can replace those already present (Keddy 1992).

Ecological differences among plant species arise due to the different ways that plants acquire the same major resources such as light, water, carbon dioxide and nutrients. As a result of this, leaves, stems, roots, and seeds vary between species in the way that they are constructed, their lifespan and in the proportion of resources that are allocated to them (Westoby et al. 2002). The variation in these traits is explained using ecological strategies. Ecological strategies are identified by referencing a number of characteristics including morphological features, resource allocation, phenology, response to stress and nutrient acquisition (Grime 1977, Craine 2005). For example, continuous variables, such as specific leaf area can be high, low or anywhere in between, which is the same for a variety of foliar, wood and whole-plant traits. When studying ecological strategies it is useful to compare more than one trait, because it allows one to locate the position of an individual or a species within a multidimensional trait space.

Grime’s CSR (competitor, stress-tolerator and ruderal) triangle, developed in 1977, was one of the first ecological strategy models. This triangle was developed in response to stress and disturbance, which are two external factors that limit plant biomass in any habitat. Stress restricts production in a given environment through shortages of light, water or nutrients. Disturbance is the partial or total destruction of plant biomass through activities such as herbivory, wind, soil erosion, and fire. The idea of this triangular model was to allow plants with different dimensions of the CSR strategies to be modelled and compared in a single figure. Plants with a competitive strategy are more suited to low stress with low disturbance environments, stress tolerant plants to high stress with low disturbance environments and ruderal plants to low stress with high disturbance environments. It is important to note that these three strategies are the extremes as there are a wide range of strategy variations within this triangular model (Grime 1977). However, this model is not able to easily compare experimental data measured from different environments and then compare them worldwide. There is no protocol for positioning species beyond these three defined reference concepts (Westoby 1998).

Westoby et al. (2002) investigated the relationship between specific leaf area and leaf lifespan (SLA-LL), seed mass and seed output (SM-SO) and leaf size and twig size (LS-TS) and maximum canopy height. Each of these strategies have trade-offs which vary climatically and within ecosystems. This study shows that species with low SLA tend to have a longer average LL. This is because leaves with low SLA, have lower leaf turnover rates because of the less favourable environments and environmental conditions that these species are exposed to. Low SLA helps to protect against wear and tear of the leaf, but low SLA costs more initially in energy and resources to create the leaf. Species with low SLA generally have a lower photosynthetic rate per unit area than those with high SLA. This allows plants with high SLA to have fast leaf turnover, allowing them to take advantage of changes in light and nutrient availability within an ecosystem. Taking advantage of changes in environmental conditions within an ecosystem is a trade-off between SLA and LL.

Another example of an ecological strategy is the trade-off between growth rate and nutrient conservation. Plants growing in nutrient rich environments produce large quantities of nutrient rich litter, which in turn releases large amounts of nutrients back into the soil, which helps to maintain high soil fertility. On the other hand, plants growing in nutrient poor environments produce small quantities of litter and, because the leaves are long-lived, plants conserve nutrients therefore accentuating the infertile environment. This trade-off is the result of the leaf traits (SLA, leaf nitrogen, leaf phosphorus and LL), which are connected to this strategy (Chapin 1980, Ordonez et al. 2009).

Mason et al. (2012) investigated foliar traits such as leaf nitrogen, leaf phosphorus, leaf thickness and tissue density, along a soil chronosequence where strong gradients in soil nutrient availability occur. The decline in leaf nitrogen and leaf phosphorus, and increase in leaf thickness and density, with decreasing soil phosphorus availability indicates a shift from a resource-acquiring strategy to a resource-retaining strategy. The shift in the resource strategy towards nutrient conservation with declining soil resource availability indicates that it is not a single trait that is involved in this change of strategy, but rather a group of traits working together. Ordonez et al. (2009) showed that there was a shift from species with low SLA, low leaf nitrogen and low leaf phosphorus on less fertile sites to species with high SLA, high leaf nitrogen and high leaf phosphorus on more fertile sites. The availability of soil nutrients is an important factor in determining the traits present and therefore the species that are found within a plant community.

There are vast numbers of vascular plant species competing for the same resources to undertake processes, such as photosynthesis, in order to ensure the continuity of future generations. Foliar traits, which are essential in these processes, are therefore fundamental in the functioning of terrestrial ecosystems (Wright et al. 2004, Craine and Dybzinski 2013). Within growth forms or functional groups there is a wide spectrum of variation in foliar traits. This spectrum, according to Wright et al. (2004) runs from species that have the traits which allow for the potential of quick returns on investments, such as nutrients, to species that have traits which result in a much slower rate of return. Species that have the potential for a quick rate of return have traits such as high leaf nutrient concentrations, high photosynthetic rates, short leaf lifespans and low dry mass per unit area. These traits allow species to capitalise on available resources. At the opposite end of the spectrum, species that have slower growth rates possess traits such as low leaf nutrient concentrations, low specific leaf area (SLA) and long leaf lifespans. These traits allow species to survive in environments where resources are not readily available (Chapin 1980).

Wood has several different, essential functions in plants. In a living tree, wood performs as a support function, enabling plants to grow large by supporting aboveground tissue. It also plays a role in the transfer of water and nutrients to the leaves and other growing tissues along the soil-plant-atmosphere continuum. As well as support and transport properties, wood acts as storage for nutrients, carbohydrates, defensive secondary compounds, lipids and water (Chave et al. 2009). Because wood performs multiple tasks within a single plant, there will be trade-offs in resource allocation within a plant, which can influence wood structure. These trade-offs will be the result of the environmental conditions that are present (Chave et al. 2009, Lasky et al. 2013). Wood density is considered an important functional trait by ecologists as it is related to life history strategies of tree species. Lasky et al. (2013) found that slope and wood density were strongly correlated. Low wood density was favoured on steeper slopes, whereas high wood density was favoured on low slopes and flat surfaces. This relationship is thought to occur because steep slopes are often associated with more frequent disturbances, shorter canopy heights and greater light availability. These variables favour rapid regeneration and therefore favour the traits associated with this, such as low wood density.

Gourlet-Fleury et al. (2011) observed how soil type affects species traits such as wood density. The results showed that resource poor soils favoured slower growth rates and dense wooded species, whereas resource rich soils favoured faster growth rates and light wooded species. These findings are consistent with that of Muller-Landau (2004) which also shows high disturbance areas with a high species turnover rate favoured species that have relatively low wood density and areas with low soil fertility favoured slower growing species that have high wood density.

There are many more examples of ecological strategies such as Shipley and Dion (1992), Golluscio and Sala (1993), Westoby (1998), Reich et al. (2003) and Liu et al. (2010). These strategies show that there are trade-offs between each trait and that although one strategy might be favourable in one environment, the same strategy might be disadvantageous in another environment. As a result of this, traits change along climatic and resource gradients, within and between ecosystems.

1.5 Environmental filtering and limiting similarity

Community assembly along environmental gradients is driven by two antagonistic processes that select functional traits in opposing directions (Laughlin et al. 2012). These are environmental filtering and limiting similarity. Environmental filtering selects individuals with functional traits that yield the highest fitness and performance for the given environmental conditions. This process increases functional similarity of species within a community, resulting in trait convergence. The effect of environmental filtering is that it results in a clustered community structure, where species with similar traits occur together more often than expected by chance (Kunstler et al. 2012, Laughlin et al. 2012). Examples of environmental filters include climate, topography, soil and disturbances (Freschet et al. 2011).

A study in the West Polynesian bio-geographical region investigated the effects of these two antagonistic processes on forest species and distribution. The results show that the coastal forest composition and species are relatively homogenous throughout the region. The co-occurrence of closely related species on remote oceanic islands in this region is indicative that environmental filters are structuring the species and traits found within the communities (Franklin et al. 2013).

The process of limiting similarity assumes that competitive exclusion of functionally similar species will lead to the co-existence of functionally dissimilar species, which in turn will lead to trait divergence. This is because there is a limit to the similarity and the number of competing species that can co-exist (Macarthur and Levins 1967, Laughlin et al. 2012). The limiting similarity theory is an extension of the competitive exclusion principle, which states that two species with identical niches cannot co-exist. Limiting similarity is therefore used to describe the maximum similarity in resource use patterns that is consistent with the co-existence of competing species (Abrams 1983).

Mason et al. (2012) tested whether mechanisms behind species co-existence change along a fertility gradient. The results indicated that functional divergence in plant traits was strongly positively correlated with soil phosphorus. This means that species found on high fertility soils had differing trait values, whereas species found on the less fertile soils converged on similar trait values.

The studies by Messier et al. (2010), Freschet et al. (2011), Mason et al. (2012), Franklin et al. (2013) and Lasky et al. (2013) show that the effects of limiting similarity are thought mainly to occur at smaller spatial scales, whereas the effects of environmental filtering are thought to occur at larger scales.

1.6 Trait-based community assembly models

Quantifying mechanisms that determine spatial variation, species abundance and community composition is a central goal in ecology. This is because plant ecologists seek to understand where plants grow and why they grow there (Lavorel and Garnier 2002, Lasky et al. 2013, Laughlin and Laughlin 2013). Predicting species distributions and abundances is important for understanding patterns of diversity and how ecological systems will respond to changes in climate, land use and soil chemistry (Suding et al. 2008, Albert et al. 2010).

A review by Laughlin and Laughlin (2013) compared two recent models of trait-based community assembly that predict the relative abundance of species from a regional species pool. The maximum entropy model (Maxent) proposed by

Shipley et al. (2006), is used to predict the relative abundances of every species in a regional pool based on species and community level functional traits. This model requires trait means for each species and a predicted community level trait mean based on the given environmental conditions. To gather the necessary information to predict species abundance using the Maxent model, observed species abundances are required to fit the trait-environment model, which can then be used to generate the necessary community-weighted mean traits. This model has a high level of flexibility because the data can be assembled from multiple sources and can be used in different environments. A disadvantage of the Maxent model is that it does not incorporate intraspecific trait variation and focuses only on environmental filtering. This is a sophisticated idea, however, this model has received criticism about the lack of clarity on how the model has such high explanatory power (Petchey 2010).

The second model that has recently been proposed is the hierarchical Bayesian model (Traitspace) by Laughlin et al. (2012). This model can detect the effect of environmental filtering on community structure and it incorporates trait variance and co-variance. The Traitspace model does not require community-weight mean traits or observed abundances, but rather a data set of individual trait measurements from the same plants, growing under known environmental conditions. As a result of this, the data collection for the Traitspace model is more complex than the data set needed for the Maxent model because multiple trait values are obtained from the same individual. This model also has a high level of flexibility and it is generalisable to a wide range of ecosystems (Laughlin et al. 2012, Laughlin and Laughlin 2013).

1.7 Intra and interspecific trait variability

Characterising natural variation and understanding its causes and consequences is important for developing and improving predictive models. This can then be used to help further our knowledge and understanding of community and species distributions (Messier et al. 2010). Plant traits are known to vary within (intraspecific) and between (interspecific) species. A basic assumption of plant ecology is that the difference in functional trait values is greater between species than within species (Jung et al. 2010). As a result of this, detecting the joint effects of environmental filtering and limiting similarity on a community is enhanced if the intra- and interspecific variation is incorporated into the analysis.

This is because individual plants are responding to the given environmental conditions rather than the species as a whole (Laughlin et al. 2012). Studies on trait variation can occur on three different levels. These include: within a species, among species and among communities. It is important that the variation in the traits being analysed is included to determine how the variation in a given trait changes across different ecological scales (Messier et al. 2010).

1.8 Kauri forests

The distribution and composition of species within a forest is not uniform. This is because environmental gradients such as topography, soil moisture and fertility lead to a change in vegetation composition. A study by Burns and Leathwick (1996) of vegetation - environment relationships in Waipoua Forest showed that compositional changes of vegetation within a kauri forest is linked to topography. Gradual compositional changes are evident along topographical gradients in this forest from *Rhopalostylis sapida*, *Dysoxylum spectabile*, *Corynocarpus laevigatus* and *Dacrycarpus dacrydioides* at low altitudes (high fertility) to *Beilschmiedia tarairi*, *Rhopalostylis sapida*, *Dysoxylum spectabile* and *Knightia excelsa* at mid altitudes to *Podocarpus totara*, *Quintinia serrata*, *Ixerba brexioides*, *Phyllocladus trichomanoides* and *Agathis australis* at high altitudes (low fertility). The one exception to this is kauri dominant stands, where there is an abrupt boundary change from broadleaved dominant forest to kauri dominant forest. The distinct and abrupt change to a kauri stand is due to the influence that kauri have on soil processes beneath the canopy such as reducing soil pH, slowing down of nutrient cycling processes and the formation of thick litter layers (Wyse et al. 2013). This study by Burns and Leathwick forms the foundation of my research as they determined how community composition changed along a topographically-driven soil fertility gradient. My study also aims to determine community composition changes along a gradient but with the added dimension of functional traits and also incorporating other environmental factors such as soil fertility.

1.9 Research aims and objectives

The objective of this research is to test the importance of traits in mediating the relationships between environmental factors and community composition in the context of Puketī Forest, a species-rich, old-growth kauri forest. This will be accomplished using interlinked field work that will assist in achieving the following broad research objectives:

1. Determine how the forest community composition of Puketī Forest changes along the environmental gradients and determine the relationships between soil properties and topography.
2. Determine the relationships among leaf, height, seed and wood traits within the species pool.
3. Analyse the relationships between traits and the environmental variables and determine the influence of environmental filtering on community assembly.
4. Determine whether the strength of environmental filtering changes along the soil fertility gradient.

1.10 Thesis outline

Chapter One: Introduction

This chapter provides background information on community ecology with a particular focus on plant traits, ecological strategies and community assembly models.

Chapter Two: Study site

This chapter provides a broad description of Puketī Forest including the geography, human history, climate and the different soil types. A map showing the plot locations is also included.

Chapter Three: Methodology

This chapter outlines the different methodologies that were used to collect samples. It outlines the procedures for setting up permanent plots and also the different protocols for the collection of traits.

Chapter Four: Results

This chapter presents the findings of this research project. It details how community composition, trait relationships, functional diversity indices and the influence of environmental filtering change along the soil fertility gradient.

Chapter Five: Discussion

This chapter discusses the findings of this project in context with the literature. It discusses the reasoning behind the relationships and trends that are occurring along the soil fertility gradient of Puketī Forest.

Chapter Six: Synthesis

This chapter provides a summary of the main findings from this research and the applications of this research in a broader context. Recommendations for future research are also given.

Appendix: The ecology and history of New Zealand's kauri (*Agathis australis*)

This appendix provides detail into the morphology, distribution, species interactions, regeneration and succession of kauri and kauri forests. Also outlined are the human influences on kauri, in particular the significance to Māori, early European settlers and logging and the most recent threat to these forests – kauri dieback.

Chapter Two: Study site

2.1 Study site location

Puketī Forest is located approximately 25 km west of Kerikeri, midway between the Hokianga and Whangaroa Harbours in Northland, New Zealand (Figure 2.1). The forest lies between latitudes 35^{o} 11' and 35^{o} 17'S and longitudes 173^{o} 42' and 173^{o} 48'E (Powlesland 1987, Dowding and Murphy 1994). Puketī Forest (hereafter referred to as "Puketī") covers 8066 hectares of native bush, is one of 17 forests in the Northland Forest Park and is administered by the New Zealand Government's Department of Conservation (DOC). Puketī is bordered by Omahuta Forest (6472 hectares) immediately to the west, the Manginangina Scenic Reserve (93 hectares) to the east and the Otangaroa State Forest (3821 hectares) north of the Mangakino Stream. Together, these forests form one of the largest contiguous areas of native forest in Northland (Powlesland 1987, Best and Bellingham 1991).

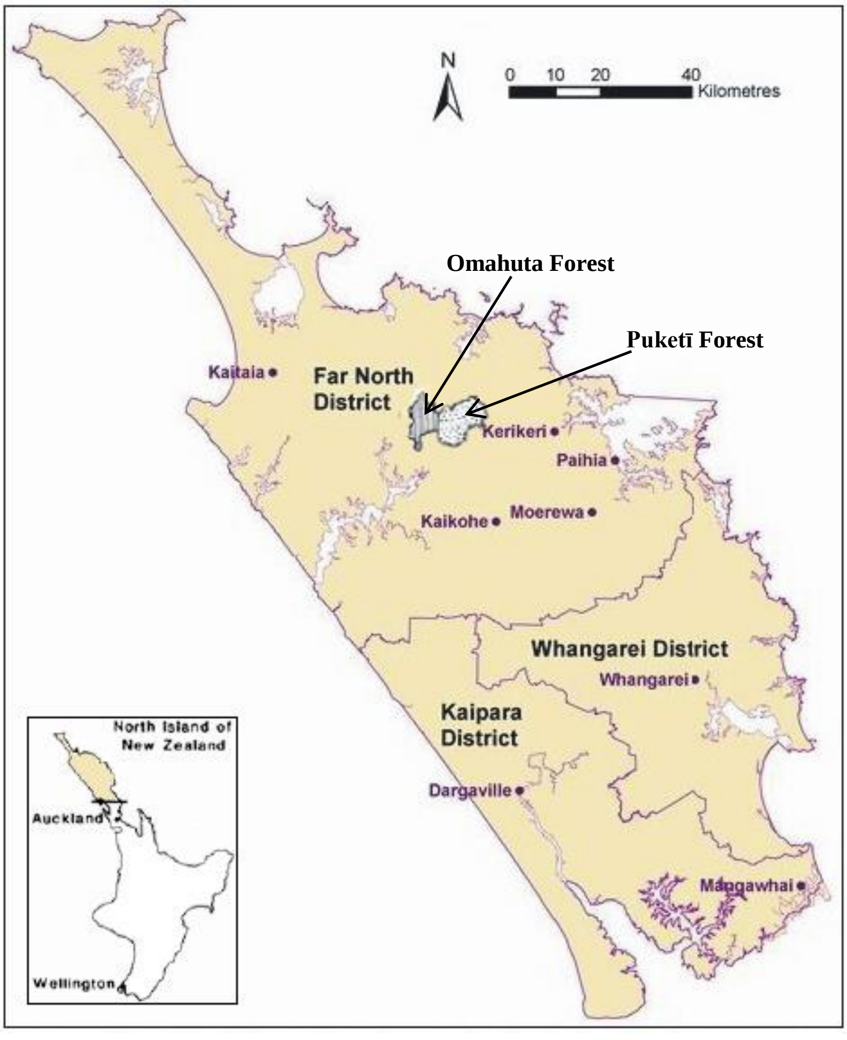

Figure 2.1: Location of Puketī State Forest in Northland, in the North Island of New Zealand (modified from Powlesland (1987) and Northland Regional Council (2007)).

Puketī and Omahuta Forest are located in the centre of the Puketī Ecological District, which covers approximately 24,000 hectares of land. The majority of this district (92%) consists of indigenous vegetation. The Puketī Ecological District is bordered by the Hokianga Ecological District to the west, the Maungataniwha Ecological District to the north and the Kerikeri Ecological District to the east (Conning and Moors 1998).

2.2 Forest composition

Puketī contains a variety of indigenous vegetation types. These are the result of the topography, logging and the subsequent succession that has occurred at these sites (Powlesland 1987). There are four commonly recognisable forest types which are: *Agathis australis* stands, podocarp – hardwood stands, hardwood stands, and *Leptospermum scoparium* shrubland.

Agathis australis stands occur in various sizes throughout Puketī, but are mainly present on ridges, where they form a tall canopy, with a sparse sub-canopy of *Ixerba brexioides*, *Halocarpus kirkii* and *Weinmannia silvicola* with scattered *Dacrydium cupressinum* and *Prumnopitys ferruginea*. The groundcover consists of thick *Gahnia xanthocarpa* and *Astelia trinervia*.

Podocarp – hardwood stands are the most extensive in the forest and occur at all altitudes and aspects. The canopy consists of a mixture of hardwoods such as *Beilschmiedia tarairi*, *Beilschmiedia tawa, Weinmannia silvicola, Knightia excelsa* and *Dysoxylum spectabile*, with less frequent *Agathis australis, Dacrycarpus dacrydiodes*, *Dacrydium cupressinum, Phyllocladus trichomanoides* and *Podocarpus cunninghamii* occurring as emergent trees. The understory and ground cover is very diverse and commonly occurring species include *Geniostoma ligustrifolium* var. *ligustrifolium, Coprosma grandifolia, Hedycarya arborea, Melicytus ramiflorus, Melicytus macrophyllus, Rhopalostylis sapida, Cyathea dealbata* and *Dicksonia squarrosa*.

Hardwood stands commonly occur within the gully areas of Puketī. The dominant canopy species include *Beilschmiedia tarairi*, *Beilschmiedia tawa, Laurelia novae-zelandiae, Dysoxylum spectabile, Weinmannia silvicola* and *Knightia excelsa*. The understory and ground cover are similar to that of the podocarp – hardwood stand but with increased abundance of *Cyathea dealbata, Dicksonia squarrosa* and *Rhapalostylis sadipa*.

Leptospermum scoparium shrubland is present on the areas of land that have been clear felled and/or burnt. The main vegetation species are *Leptospermum scoparium, Knightia excelsa, Weinmannia silvicola* and *Geniostoma ligustrifolium* var. *ligustrifolium*. The ground cover is a mixture of *Gahnia xanthocarpa* and fern species (Ecroyd 1982, Powlesland 1987, Best and Bellingham 1991, Dowding and Murphy 1994).

2.3 Geographical features

2.3.1 Drainage

Puketī drains into two different catchment areas. It forms the larger portion of the catchment of the Waipapa River, which divides Omahuta Forest from Puketī and drains to the southwest, into the Hokianga Harbour. Small tributaries in the south of Puketī drain into the Waihoanga River and then also into the Hokianga Harbour. The northern sides of Puketī drain into the Kaeo River and out into the Whangaroa Harbour (Best and Bellingham 1991).

2.3.2 Topography

Puketī contains a mosaic of steeply dissected topography (Figure 2.2). The distinguishing features include the northern ridges, Mokau (Omataroa) (300 – 460 m asl), Mangehorehore (300 – 460 m asl), the southern Pirau Ridge (360 – 460 m asl) and the southwest elevated plateau with the highest land point (460 – 539 m asl). The plateau and ridges are flanked with steep, irregular valleys and long spurs. Another distinguishing feature is the Waipapa River, which flows at a gentle gradient from the north east border at 100 m asl, through to 30 m asl in the west of Puketī. The overall rough topography and dense bush means that much of Puketī Forest is only accessible on foot (Best and Bellingham 1991).

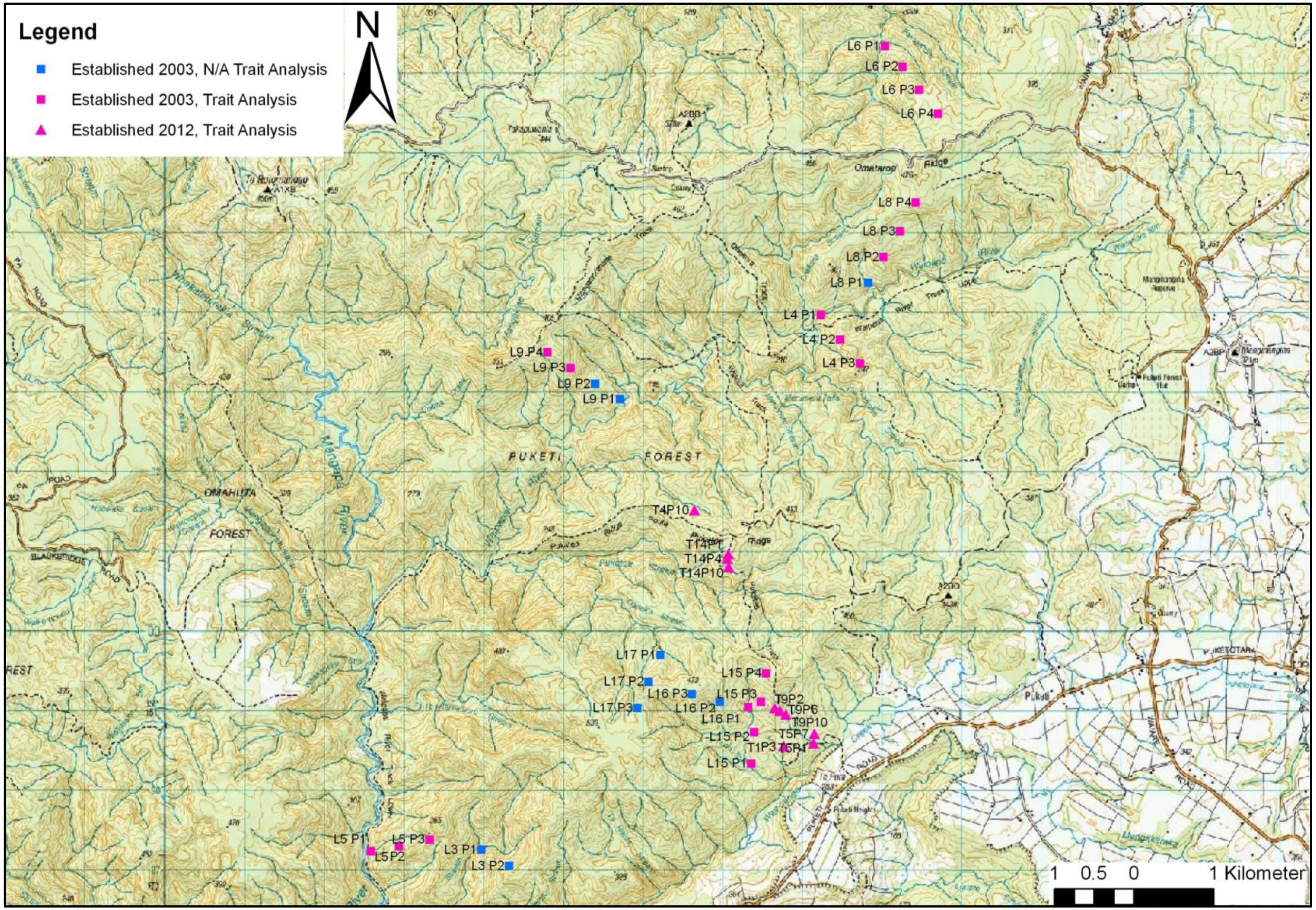

Figure 2.2: Topographic map of Puketī Forest showing the locations of the plots sampled.

2.4 Northland climate

Northland is a warm temperate location and is only 80 km across at its widest point. As a peninsula with low elevation and close proximity to the sea, the climate of this area is characterised by warm, humid summers and mild winters, with only a few light frosts each year. The prevailing wind is from the south west, however tropical cyclones give rise to north-easterly winds.

The 2012 – 2013 summer has been very dry in comparison with previous years, with the January rainfall total being less than 10 percent of the normal. The February rainfall was less than 50 percent and March rainfall was 20 percent of the normal amount in Northland. As at the 1 April 2013 a total of 31 mm of rain had fallen in Northland, which is less than 25 percent of the normal rainfall for this period. Drought was declared in Northland on 27 February 2013, following extreme soil deficits of more than 130 mm (NIWA National Climate Centre 2013).

2.4.1 Rainfall

The mean annual rainfall of Northland ranges from approximately 800 mm to above 2000 mm. The wettest months are the winter months of June, July and August. Droughts are common during the summer period, with high pressure weather systems resulting in hot, humid and windy conditions for several weeks or months (Northland Regional Council 2007).

The long term median annual total rainfall from 1981 – 2010 (Figure 2.3) shows that the annual total rainfall in Puketī varies from 1500 mm to above 2000 mm on the higher peaks. indicating that Puketī is one of the wettest areas of the Northland Region (NIWA 2012a).

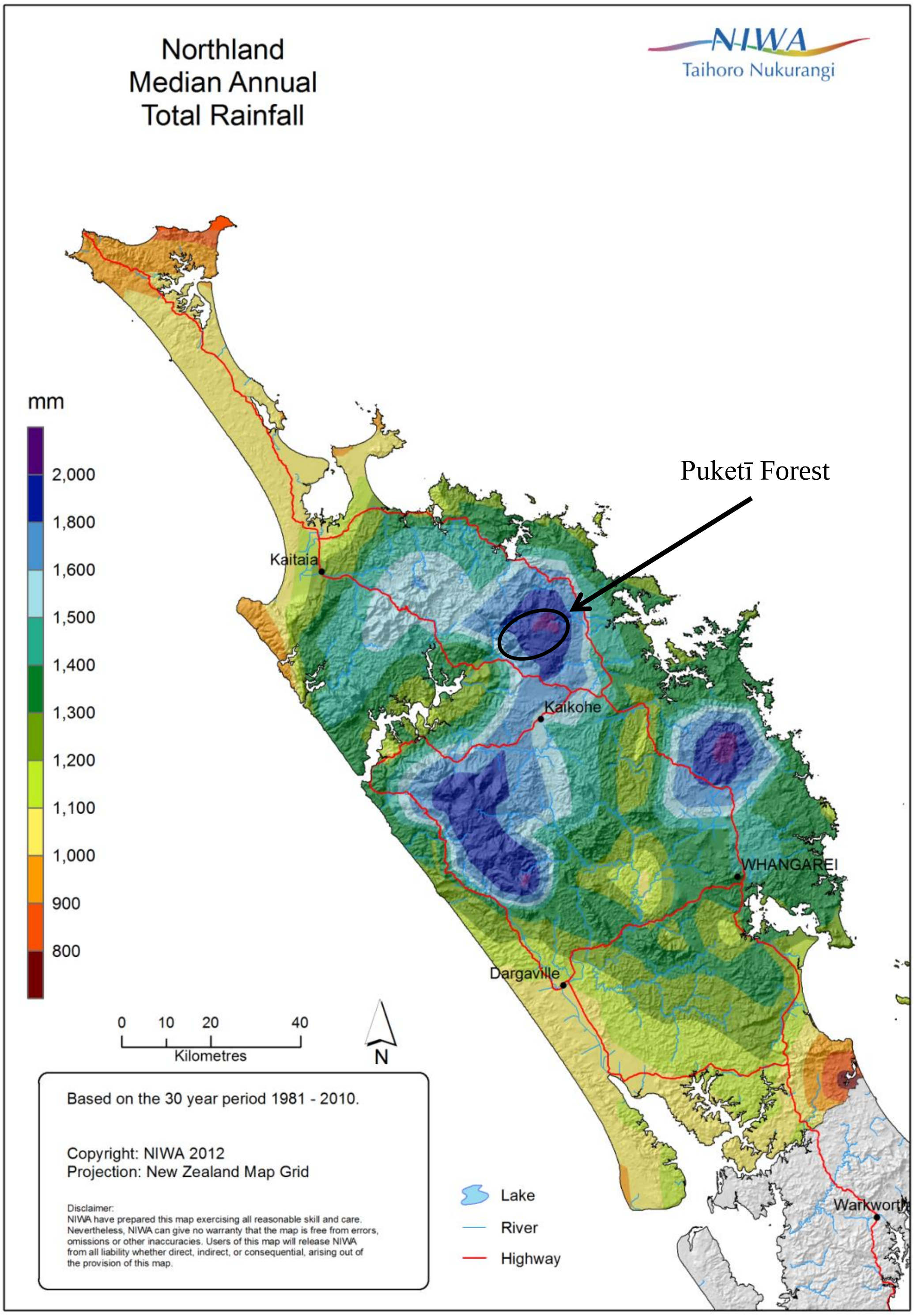

Figure 2.3: Northland median annual rainfall (NIWA 2012a).

2.4.2 Temperature

The long term median annual average temperature from 1981 – 2010 (Figure 2.4) in Puketī Forest falls between 13°C and 15°C (NIWA 2012b).

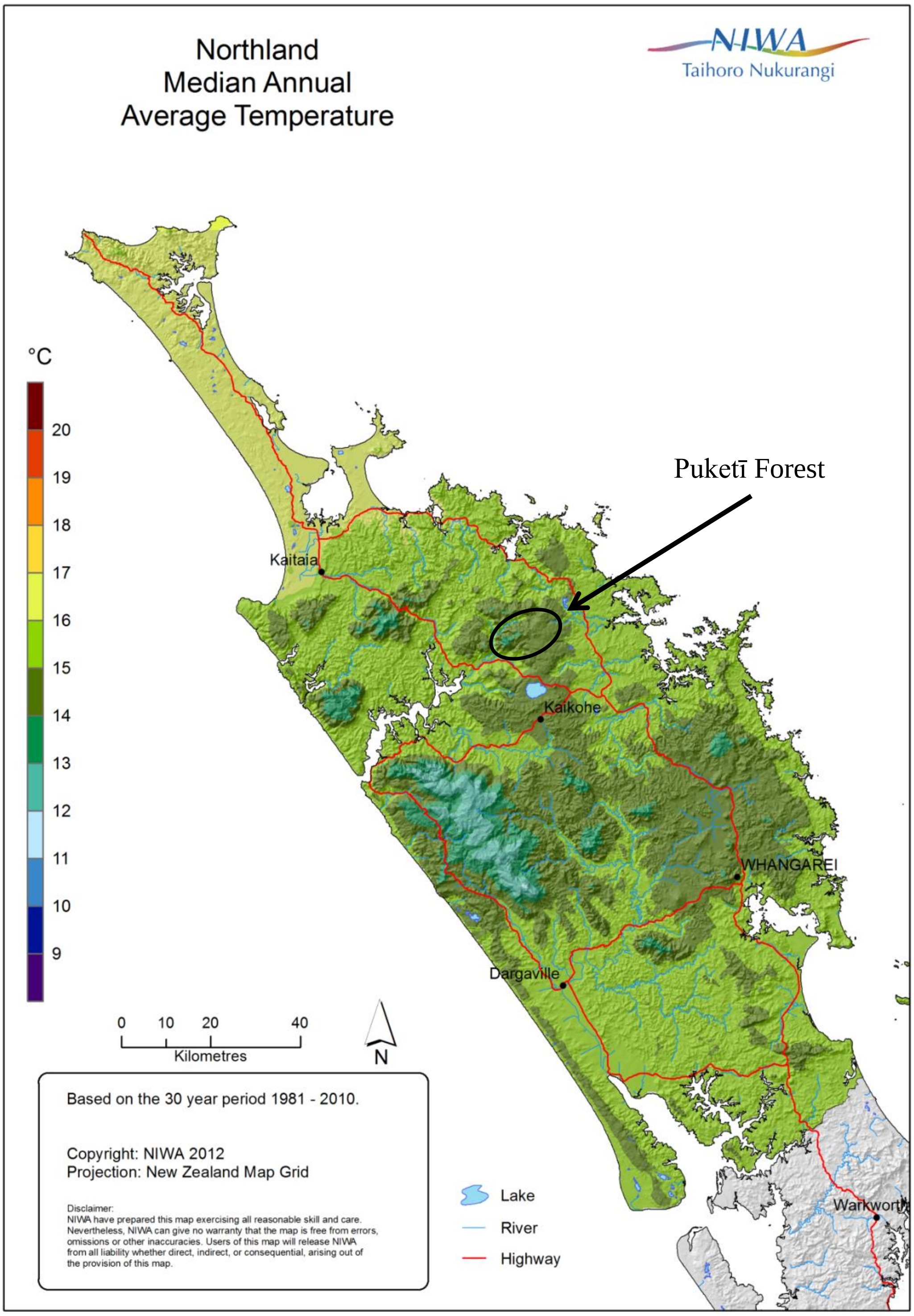

Figure 2.4: Northland median annual average temperature (NIWA 2012b).

2.5 Soils

The Northland region consists of a wide variety of land uses, soil types and landforms, varying from young active sand dunes along the coastal margins, to old greywacke, hills and volcanic peaks in the inland areas. The low relief and warm, moist climate of Northland has resulted in the soils being dominated by strongly leached, mature, heavy clays, with thin topsoils.

The cover of the original indigenous forest has strongly influenced Northland's soil properties (Northland Regional Council 2007). Trees with acidic litter, such as *Agathis australis*, *Podocarpus cunninghamii* and *Dacrydium cupressinum*, have produced strongly leached soils, while broadleaf trees, such as *Vitex lucens*, *Dysoxylum spectabile* and *Beilschmieda tarairi*, have returned nutrients back to the soil through rapid decomposition of leaves and branches, resulting in fertile topsoils.

The soil of Puketī are predominately Te Ranga yellow-brown steep land soil (TRS as shown in Figure 2.5), which is a clay loam and stony clay loam (Sutherland et al. 1980). The Te Ranga soil is excessively to somewhat excessively, drained. It requires low to moderate management to avoid structural breakdown of the soil profile and has a low to moderate risk of undergoing surface soil erosion when covered in forest (Sutherland et al. 1979, Hicks 1995).

The other soils found in Puketī are the Marua clay loam (MRH) and Tikitohe gravelly silt loam (TVH), which are also yellow-brown earth soils. Both of these soil types are well to moderately well drained and have a low risk of undergoing surface soil erosion when covered in forest. The MRH requires moderate management to avoid structural breakdown of the soil profile, whereas the TVH only requires low management. All three soil types (TRS, MRH and TVH) are categorised as moderately to strongly leached (Sutherland et al. 1980, Hicks 1995).

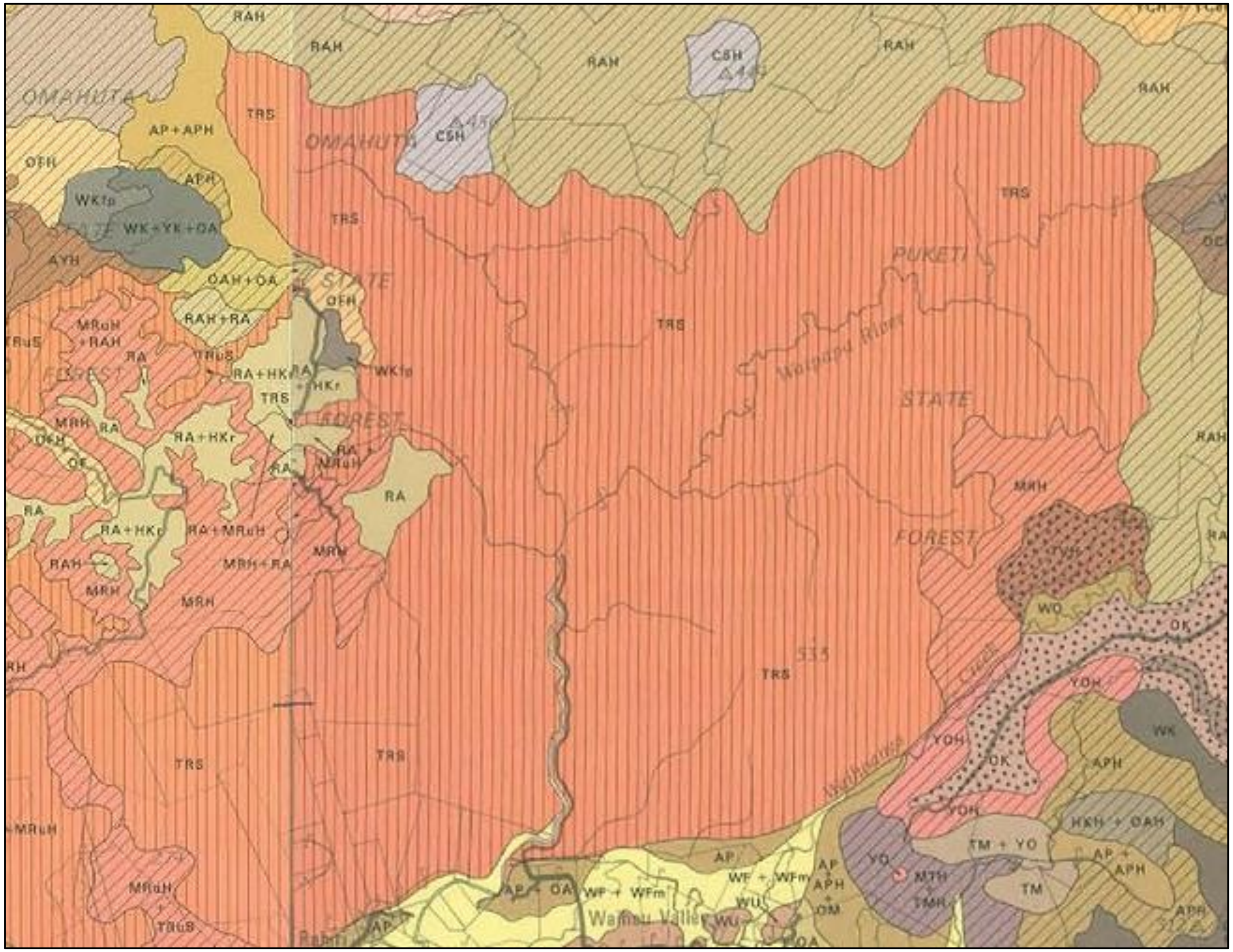

Figure 2.5: Soil composition of Puketī Forest and the surrounding landscape (stitched together from Sutherland et al. (1979) and Sutherland et al. (1980)).

2.6 Human history

2.6.1 Māori and early European settlers

Puketī Forest is a place of strong spiritual significance to the tangata whenua. In pre-colonial times there were many Māori settlements scattered around Puketī, which was evident by the abandoned cultivation sites where crops such as taro were grown. The forest was a source of natural resources for Māori and early European settlers. These resources include timber for carving and construction, fibrous plants for clothing and weaving and foods such as karaka fruit and tubers. In 1859 the Crown bought Puketī from the Māori owners and in 1933 it was designated as a State Forest (Best and Bellingham 1991).

2.6.2 Logging

In the 1860's, commercial kauri (*Agathis australis*) logging began along the banks of the Waipapa River for ship spars. Extensive logging in the Waipapa River and Taita Stream headwaters occurred intermittently from 1870 to 1915. The timber felled in these areas was floated downstream to the Hokianga Harbour using dams, remains of which are still present. In 1900 – 1910 the forest in the east of Puketī around the headwaters of the Puketotara Stream, Waikape Stream, Puruwharawhara Stream and in the north, near Waihoanga Stream, was clear felled, and the timber transported using bullock and stream trains. During this time, large areas of kauri and podocarp forest were also logged in the west, around the Mangakino Stream and Collin's Creek.

Little logging of either kauri or podocarp forest occurred during World War II, however kauri logging recommenced in 1965 in the head of the Waipapa River and in the Puruwharawhara area and continued through until 1973. During this time, there was a change in the logging process, from clear felling to leaving trees with a diameter of less than 100 cm. This change in the logging process coincided with the announcement of the 1973 Kauri Policy, which stated forest workers were to select only mature kauri for logging. Logging in various areas of Puketī occurred according to this policy, from 1973 until 1980. In 1985, a revised Kauri Policy prohibited felling of kauri in State Forests, except for specific cultural purposes, for which Ministerial approval is required (Best and Bellingham 1991).

2.6.3 Kauri gum

Kauri gum fossicking was a common pastime for the forest workers, and in 1920, licences were issued to allow for the fossicking and the selling of gum. However, bleeding of live kauri trees became commonplace and many mature trees were badly damaged. This created entry points for pathogens, and consequently trees were mutilated and large kauri trees were killed. As a result of these consequences for kauri, bleeding trees for gum was banned in 1952 (Best and Bellingham 1991).

Chapter Three: Methodology

3.1 Community composition data

3.1.1 Plot size and location

Community composition of Puketī Forest was determined using forty permanent 400 m^2 (20 m x 20 m) plots, which is the commonly accepted plot size for lowland forest in New Zealand (Hurst and Allen 2007). The locations of the forty plots that were used in this research project are shown in Figure 2.2. Thirty of these plots were established along random transects within Puketī Forest in 2003, and were re-measured in 2011. All forty of these plots (both pink and blue) were used for the community composition analysis, whereas only thirty of these plots (pink) were sampled for traits, due to time constraints. The following method describes the protocol for the establishment of the ten additional permanent plots that were measured in November 2012, following the methodology of Hurst and Allen (2007).

Peter Bellingham (Landcare Research) and colleagues established a series of 9 m^2 plots along transects throughout the forest in 2011 to study seedling regeneration dynamics. The ten additional permanent plots were established over the top of ten of these seedling plots because soil properties were already collected from these sites. These additional plots were intentionally located on ridges or in gullies to maximise the range of topographic variation among the 40 plots. These transects were chosen because the soil fertility was known at these locations. The plots were therefore established over existing seedling plots to allow comparisons between soil fertility gradients, trait and community data.

3.1.2 Permanent plot layout

The following section describes the set up and layout of a 20 m x 20 m permanent plot (Figure 3.1). The corner pegs A, D, M and P, were marked using white permolat (150 mm x 50 mm), engraved with the appropriate corner letters and threaded over aluminium pegs (400 mm x 6.34 mm). The centre of the 24 seedling plots, as shown by the “x” in Figure 3.1, was marked using red permolat (150 mm x 25 mm), threaded over smaller (300 mm x 4.76 mm) aluminium seedling pegs. Each piece of red permolat was engraved with the corresponding number from 1 - 24. Finally, each 5 m interval (as shown along the A - P boundary) was marked using a small aluminium peg, tied with pink flagging tape. Figure 3.2 shows an example of a corner, seedling and side peg. To reduce the possibility of the permolat sliding off the top of the peg, the top was bent over. The plot was positioned so that the A - D boundary was orientated along the contour of the slope, to allow the A - P boundary to run parallel to the transect line.

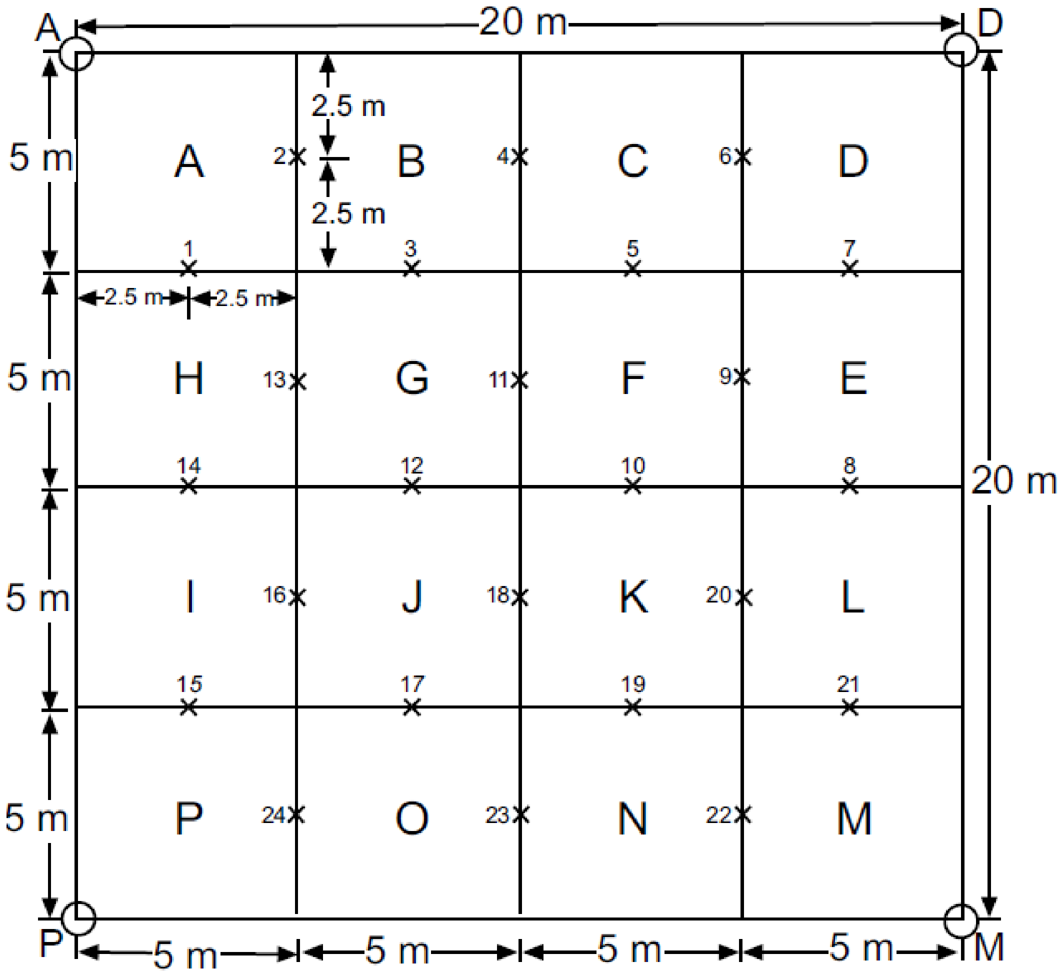

Figure 3.1: The layout of a 20 m x 20 m permanent plot (Hurst and Allen 2007).

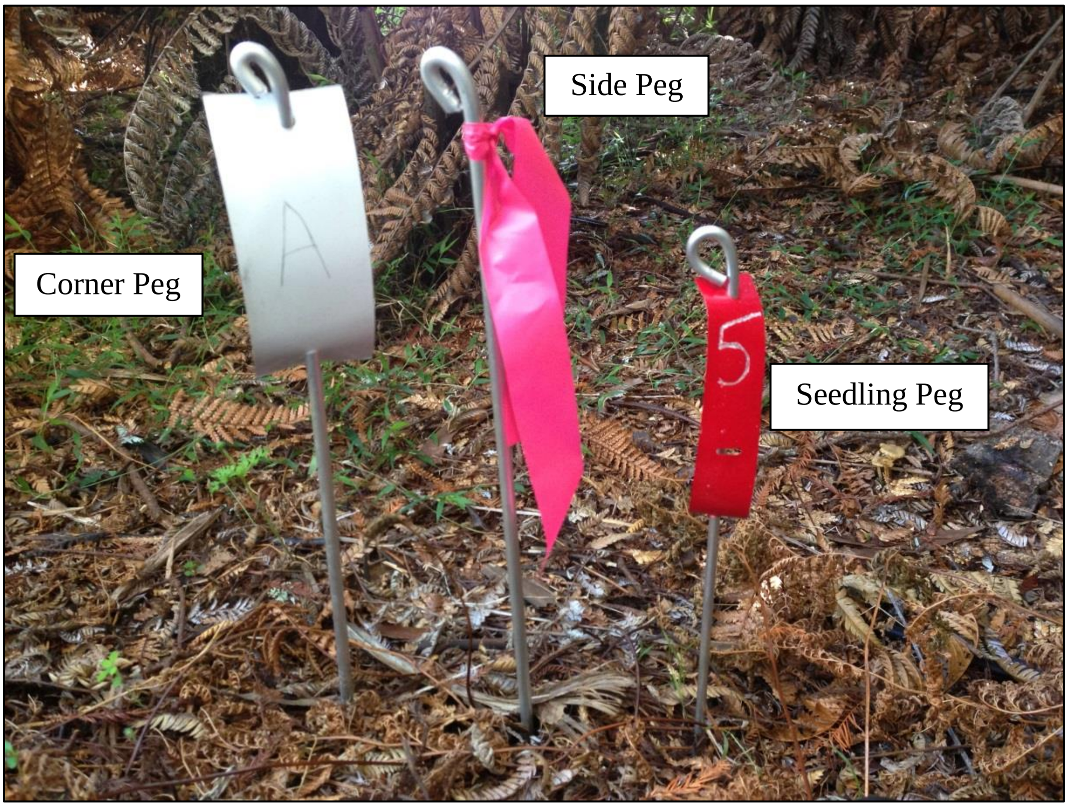

Figure 3.2: Example of a corner, side and seedling peg used along the boundaries of a plot.

Sighting compasses were used to lay out the boundary tapes to ensure that the tapes met at right angles at the corner pegs. All tapes were laid as close to the ground as possible to clearly define the plot area. Tapes were laid in such a way that they followed the contour of the ground and were as straight as possible. Trees that were encountered along plot boundaries were included when greater than 50 % of the tree was rooted within the plot, otherwise they were excluded. The plot was then subdivided into sixteen, 25 m^2 (5 m x 5 m) subplots (A - M), along the 5 m intervals (Figure 3.1).

To help with re-finding corner pegs, a strip of white permolat was nailed to a suitable tree outside the plot near each corner (A, D, M and P). Each strip of permolat was labelled with the appropriate corner letter, distance and the bearing to the peg.

3.1.3 Data collection

The collection of the community composition data involved the completion of the stem diameter and sapling sheet, the understory subplot sheet and the reconnaissance sheet. The stem diameter data required all living tree stems ≥ 2.5 cm dbh (diameter breast height, 135 cm) and tree ferns with stems ≥ 135 cm high and ≥ 2.5 cm dbh, rooted within the plot, to be tagged with a tree tag at dbh, within the sixteen subplots. The species, dbh and tree tag number were then recorded for every tree and tree fern that met this criteria. Diameter at breast height was measured to calculate basal area (m^2 ha^{-1}) of each species in each plot. Sapling counts of all species $\geq$ 35 cm in height, but < 2.5 cm dbh were tallied in each subplot. Tree ferns were tagged with 75 mm flat-head galvanised nails and trees with 50 mm flat-head galvanised nails. All nails used to tag trees and tree ferns remained protruding from the trunk to allow for growth.

Understory subplot measurements were recorded at each of the twenty four, circular, seedling plots. The subplot area was defined using a non-elastic length of string tied to the seedling peg. This string was pulled tightly and then knotted 49 cm along to define the 0.75 m^2 area. The string was tied loosely around the peg so that it moved freely around, in a circular motion. Each plant that was encountered by the string was identified and recorded in the appropriate height tier (< 15 cm, 16 – 45 cm, 46 – 75 cm, 76 – 105 cm or 106 – 135 cm).

The reconnaissance permanent plot was completed for the whole 20 m x 20 m plot. Plot identification information and site characteristics, such as GPS coordinates, slope, aspect, drainage, canopy cover, percentage litter, bare ground and rock were recorded. The plots varied in physiography from ridges, terraces, faces to gullies. For further information about the reconnaissance permanent plot method, refer to Hurst and Allen (2007): A permanent plot method for monitoring indigenous forests: field protocols.

Plant species were recorded using the currently accepted taxonomic name and using a six-letter species code unique to each species, for example *Weinmannia silvicola* was abbreviated to WEISIL.

3.1.3.1 Protocol for plot data clean up and selection of species to include in the trait analysis

Certain woody species contribute little to basal area and some only occur in a few plots therefore the criteria for a species to be included in the community composition and trait analysis was that the species had to have a stem diameter greater than 10 cm, attain a relative abundance of 0.05 within a single plot and occur on at least 10 percent of the forty plots sampled. However, exceptions were made for *Ackama rosaefolia, Dacrycarpus dacrydioides, Halocarpus kirkii, Ixerba brexioides, Leptospermum scoparium* and *Metrosideros robusta* because trait data was available for each of these species. Of the 50 species encountered 30 were included in the community composition analysis.

3.2 Trait data collection

To quantify the relationship between environmental factors and functional traits (Table 3.1) leaf, wood, bark, and whole-plant traits were sampled from tree species that occur in the plots within Puketī forest following standard trait measurement protocols (Pérez-Harguindeguy et al. 2013). The objective was to collect traits on three individuals from each species that occurred in each plot. Extra individual trees were sampled if the species was uncommon, hard to find, or only found in certain habitats, such as *Agathis australis* on ridge top plots and *Laurelia novae-zelandiae* in gully plots. In total trait data was collected from 762 individuals.

Table 3.1: Functional traits and their corresponding units.

Functional Trait	Abbreviation	Unit
Leaf thickness	Leaf thickness	mm
Leaf density	Leaf density	mg mm^{-3}
Specific leaf area	SLA	mm^{2} mg^{-1}
Leaf dry matter content	LDMC	mg(dry) mg(fresh)$^{-1}$
Wood density	Wood density	mg mm^{-3}
Wood dry matter content	TDMC	mg(dry) mg(fresh)$^{-1}$
Bark thickness : dbh ratio	Bark : dbh	mm(bark) mm(dbh)$^{-1}$
Maximum dbh	Max dbh	cm
Maximum height	Max height	m
Bark thickness	Bark thickness	mm
Leaf nitrogen	Leaf N	%
Leaf phosphorus	Leaf P	%
Litter nitrogen	Litter N	%
Litter phosphorus	Litter P	%
Nitrogen re-sorption	N resorption	%
Phosphorus re-sorption	P resorption	%
Seed mass (dry)	Seed mass	mg

3.2.1 Leaf traits

Fully-expanded, mature, healthy, well-lit leaves were collected from three trees of each species in thirty of the forty permanent plots that spanned the full gradient in soil properties and topographic variation. The number of leaves, leaflets or photosynthetic units (hereafter, collectively termed ‘leaves’) collected depended on the size and area of the leaves. Ten leaves were collected for *Cyathea dealbata, Cyathea medullaris, Dicksonia squarrosa, Phyllocladus trichomanoides, Podocarpus cunninghamii* and *Prumnopitys ferruginea* because they were small. Thirty leaves were collected for *Leptospermum scoparium* trees because they were extremely small. Three leaves were collected from all other species.

There were three different methods that were used to collect leaves from the canopies of trees. The first and preferred method was to use a 4 m or 8 m long telescopic pole pruner to cut leaves off branches. The second method was to use a 12 gauge shotgun to shoot leaves off branches from the extremities of a tree when the pole pruner was unable to reach (size 2, 35 gram steel shot was used). In areas where the shotgun was not permitted and leaves could not be reached using the telescopic pruners the slingshot method was used. This involved using a Barnett Diablo slingshot to launch a guide wire, which was made up of a 2 oz lead sinker attached to 30 lb braid, over an extremity branch, approximately 1 – 2 cm in diameter. The sinker was then removed from the guide wire and a 40 m rope with a 2 m razor wire section in the middle was then pulled back up over the branch and the branch was sawn off. The slingshot method was mainly used to collect samples off kauri growing in areas with open understories in the locations where the shotgun was not permitted.

Once the leaves were collected, the thickness of three leaves was measured in the field using digital callipers regardless of the number of leaves collected. Primary and secondary veins were avoided when measuring the leaf thickness. Leaves were then stored in air-tight plastic bags to minimise water loss until the combined area was measured using a Bio-Science CI-202 portable laser leaf area meter and the combined fresh weight measured using a Mettler-Toledo PB3002-S DeltaRange portable analytical balance. Measurements were made once the field crew returned back to the accommodation from the field. This was generally within seven hours from the time of collection.

Further information that was collected from each tree sampled was the height, using a Haglöf Vertex IV hypsometer, the dbh and the tag number (if present).

The leaf traits that were calculated are leaf thickness, leaf area, leaf density, leaf dry matter content (LDMC) and specific leaf area (SLA) (Table 3.1). Leaf thickness (mm) is a key component in leaf density and in determining the physical strength of the leaves. This was calculated by averaging the three leaf thicknesses measured using digital callipers in the field. Leaf area (mm^2) is the most common measurement for leaf size and is defined as the one-sided area of a leaf. Leaf area of fresh leaves was calculated using a portable laser leaf area meter. Leaf density ($mg\ mm^{-3}$) is the measure of dry mass per unit fresh volume of a leaf. It is calculated by dividing the dry mass (mg) by the volume (mm^3) of the leaves (volume = leaf area x leaf thickness). LDMC was calculated by dividing the dry weight (mg) by the fresh weight (mg) of the leaves. SLA ($mm^2\ mg^{-1}$) is a function of leaf area and dry mass. This was calculated by dividing the one-sided area (mm^2) of the fresh leaves by their dry weight (mg) (Pérez-Harguindeguy et al. 2013).

3.2.2 Leaf and litter chemical analysis

For one tree of each species sampled on every plot, extra leaves and freshly fallen litter were collected for total leaf and litter nitrogen (N) and total leaf and litter phosphorus (P) analysis. A total of 248 leaf samples and 248 litter samples were analysed. These values were then used to calculate the percentage re-sorption efficiency (Table 3.1). The leaves and litter were dried at 60 ^{o}C for a minimum of one week and then ground into a fine powder using a Retsch MM 2000 grinder. The amount of leaves and litter collected varied depending on species, but enough material was collected in order to have 1 g of ground leaves and 1 g of ground litter. Ground samples were then sent to the Landcare Research Environmental Chemistry Laboratory in Palmerston North for flow injection analysis using a Lachat QuikChem 8000 series (test number and protocol 206).

3.2.3 Seed traits

Seed dry mass (mg) was measured on each of the 30 species by Sarah Richardson from Landcare Research, using herbarium records from the Allan Herbarium in Christchurch. An estimate of fern spore mass was used in this analysis and spores will henceforth be collectively referred to as seeds.

3.2.4 Wood and bark traits

Wood samples were collected to quantify wood density (i.e., stem specific density). Tree cores were collected using a Suunto increment borer with hardened steel bits on trees > 10 cm dbh. The diameter of the borer was 5.15 mm and the length was 30 cm. A single core contained an outer section of bark, with the remainder being wood. One core per tree was taken at breast height. The length of the core varied depending on the diameter of the tree, but was such that the core reached pith or was the length of the corer, if the diameter of the tree was large. The bark was then removed from the core and the thickness of the bark was measured using digital callipers. The bark was then discarded. The length of the wood core was measured and it was then stored in an appropriately labelled plastic straw.

The wood and bark traits that were calculated are wood density (stem specific density), twig dry matter content and bark thickness (Table 3.1). Stem specific density (mg mm^{-3}) is a section of the main stem of a plant divided by the volume of the same section. This was calculated by dividing the dry mass of the core (mg) by the volume (area x length) of the core (mm^3). Twig dry matter content was calculated by dividing the dry weight (mg) by the fresh weight (mg) of the twig. Fresh weights of the cores and twigs were measured at the end of each sampling day (Pérez-Harguindeguy et al. 2013). The bark thickness to dbh ratio, defined here as the portion of the stem that is external to the wood or xylem was calculated by dividing the bark thickness measured from the core (mm) by the dbh of the stem (mm). This measurement is useful for determining the proportion of external bark a tree has per mm of internal wood.

3.2.4.1 Protocol for kauri wood density adjustment

The permit that I was granted did not allow permission to core kauri in Puketī. As a result of this, I sampled kauri twigs using telescopic pole pruners, a shotgun, or a slingshot. Twigs were stripped of their bark in order to compare twig wood density with trunk wood density. Two diameters (smallest and largest) were measured at the middle of a straight twig to account for the variability in the shape. The length of each twig was also measured. To estimate trunk wood density from twig wood density a predictive model was developed using both of these variables measured on 25 kauri individuals in the Huapai Forest Reserve (University of Auckland).

The direct relationship between twig wood density and trunk wood density of kauri in the Huapai Forest was weak, but the relationship between twig wood density and the difference between twig and trunk wood density within an individual (Figure 3.3) was significant, positive and linear ($R^2 = 0.53$, $p < 0.0001$). This means that the denser the twig wood density, the greater the difference between twig and trunk wood density.

The twig wood density measurements from the kauri in Puketī were then adjusted according to the predicted difference between twig and trunk wood density to calculate trunk wood density. Using this relationship the average predicted wood density of kauri in Puketī was virtually identical to the measured average trunk wood density in Huapai Forest.

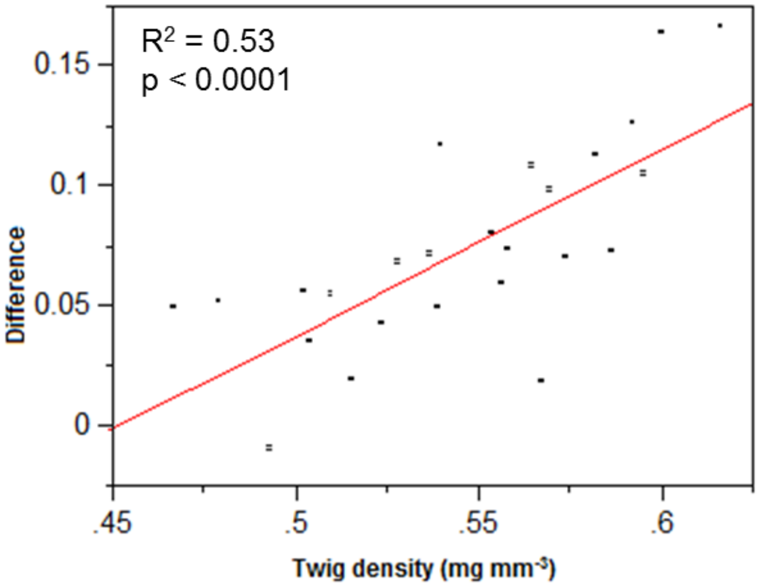

Figure 3.3: Relationship between twig wood density and the difference between twig and trunk wood density within an individual kauri tree from Huapai Forest Reserve (difference = -0.353195 + 0.7815093 twig wd).

3.3 Soil properties

Soil samples were collected by Peter Bellingham from Landcare Research in 2011 from the 3 m x 3 m seedling plots and the thirty 20 m x 20 m permanent plots in Puketī. Both types of plots were divided into quarters and one soil sample per quarter was collected using a 3 cm diameter corer, to a depth of 15 cm. The four samples were then pooled. All recognisable organic material was scraped away before the core was taken. Mineral and organic horizons visible within the core were not separated.

3.3.1 Soil and environmental variables

The soil variables (Table 3.2) that were measured or calculated from the soil samples collected at each plot are pH (Landcare Environmental Chemistry Laboratory test method 106 (i), Radiometer PHM210 pH meter with a Radiometer pHC2401-8 electrode), organic carbon and total nitrogen (method 114 using a Leco CNS2000 Analyser), total phosphorus and organic phosphorus (method 130, flow injection analysis using a Lachat QuikChem 8000 series), soluble phosphorus (method 128, flow injection analysis using a Lachat QuikChem 8000 series), calcium, magnesium, potassium, sodium (method 143, atomic absorption spectroscopy using a Varian SpectrAA-220FS), cation exchange capacity (method 144 (ii)), base saturation (amount of basic cations that occupy the cation exchange sites, divided by the total cation exchange capacity (Bases ÷ CEC × 100 = base saturation %) and carbon to nitrogen ratio. Additional environmental variables (Table 3.2) that were measured at each of the plots are altitude (m), aspect (degrees from north), slope (degrees) and topographic index. A high topographic index indicates that the topography is steeply sloping, for example a gully habitat. A low topographic index indicates that the area is gently sloping such as a ridge top. Topographic index is a continuous variable.

3.4 Data analysis

This section describes the analyses and protocols that were undertaken to achieve the four objectives outlined in Chapter One.

3.4.1 Community composition

To determine the relationship between environmental factors and community composition a non-metric multidimensional scaling analysis using a Bray-Curtis distance measure was carried out in PC-ORD. A scree plot showing stress as a function of dimensionality was generated in order to determine the dimensionality of this ordination. A two dimensional ordination was chosen to represent community composition because the first two axes resulted in a greater reduction of stress (inverse measure of fit to the data) than the later four axes, therefore two dimensions represented the elbow in the scree plot.

Relationships between soil properties and topography were determined using linear regression models in R-Project version 3.0.1.

3.4.2 Trait relationships among species

To determine the trait relationships among species a principal component analysis using a correlation matrix and distance based biplot for the vectors was carried out in PC-ORD. Eigenvectors and eigenvalues were recorded from this analysis. A two dimensional ordination was chosen to represent this data because the eigenvalue of the first two axis were greater than the broken-stick eigenvalue (McCune and Grace 2002). However, there could be as many as five dimensions in this ordination as four eigenvalues are greater than one and the fifth is close to one.

The relationships between leaf, height, seed and wood traits were determined using linear regression models in R-Project.

3.4.3 Trait – environment relationships

To determine the relationships between community-weighted mean leaf, height, seed and wood functional traits and environmental factors, linear regression models in R-Project were used.

Individual level functional traits (SLA and wood density) and soil properties were analysed using regression models in R-Project. All trait values such as SLA that were measured on the 762 individual trees were plotted against the soil variable. Separate regression models were then determined for each individual species that occurred on more than one plot and then an overall regression (all species included) for this relationship was determined.

The main environmental variables which explain how traits change along the environmental gradient were soil C:N ratio, total soil phosphorus and soil pH, rather than topography. This was determined using a backwards stepwise multiple linear regression analysis in STATISTICA. As a result of this analysis, the trait relationships are only shown in relation to these three soil properties.

3.4.3.1 Protocol for the removal of kauri from plots to determine the influence of environmental filtering

To determine whether the acidic litter produced by kauri trees was influencing trait – environment relationships, all plots that contained kauri were removed from the analysis and a subset community-weighted mean trait matrix created. Regression analyses were then carried out to determine if the relationships were affected by the presence of kauri. This is shown on the regression models through the use of solid black circles which represent plots without kauri and open circles which represent plots that include kauri. The solid line on these graphs represents the fitted regression line including plots with kauri and the dashed line represents the fitted regression line for just the plots that do not have kauri present.

3.4.4 Functional diversity

Distance-based functional diversity indices (dbFD) were calculated using the FD package in R-Project. Linear regression models were then used to determine the relationships between these indices and environmental variables.

Table 3.2: Soil and environmental properties with their corresponding units and Landcare Environmental Chemistry Laboratory test method.

Soil or environmental variable	Abbreviation	Average ± SE	Range	Unit	Landcare Environmental Chemistry Test
pH	pH	4.73 ± 0.10	3.63 – 6.32	-	Method 106 (i)
Organic carbon	OrgC	9.79 ± 0.89	2.55 – 25.22	%	Method 114
Total nitrogen	TotalN	0.45 ± 0.03	0.10 – 0.83	%	Method 114
Carbon to nitrogen ratio	C:N ratio	20.84 ± .90	12.63 – 36.58	-	-
Total phosphorus	TotalP	376.21 ± 23.84	160.13 – 833.26	mg kg^{-1}	Method 130
Organic phosphorus	OrgP	340.19 ± 21.71	128.96 – 762.70	mg kg^{-1}	Method 130
Soluble phosphorus	SolubleP	36.03 ± 2.52	10.33 – 71.42	mg kg^{-1}	Method 128
Calcium	Ca	4.35 ± 0.69	0.41 – 19.53	cmol(+) kg^{-1}	Method 143
Magnesium	Mg	3.13 ± 0.24	0.71 – 7.99	cmol(+) kg^{-1}	Method 143
Potassium	K	0.47 ± 0.03	0.08 – 1.09	cmol(+) kg^{-1}	Method 143
Sodium	Na	0.43 ± 0.05	0.10 – 1.71	cmol(+) kg^{-1}	Method 143
Cation exchange capacity	CEC	32.42 ± 1.69	12.80 – 60.17	cmol(+) kg^{-1}	Method 144 (ii)
Base saturation	Basesat	26.60 ± 2.96	9.71 – 92.6	%	-
Altitude	Altitude	277 ± 16	70 – 502	m	-
Aspect	Aspect	82 ± 8	0 - 160	^{o} from North	-
Slope	Slope	26 ± 1	5 - 42	^{o} (degrees)	-
Topographic index	TopoIndex	17.4 ± 0.8	8.4 – 30.9	-	-

Chapter Four: Results

4.1 Objective 1: Community composition

Puketī Forest has a total average basal area of 48 m^2 ha^{-1} and a range between 15 – 92 m^2 ha^{-1} for the 30 study species. The total average stem density was 1025 per hectare with a range from 475 – 1725 stems per hectare. The species with the highest stem densities are *Cyathea dealbata, Rhopalostylis sapida* and *Halocarpus kirkii* the species that had the largest average basal area were *Agathis australis, Metrosideros robusta* and *Halocarpus kirkii* (Table 4.1).

A two dimensional ordination of the composition of the forest was chosen to represent this data set due to the first two axes resulting in a greater reduction of stress than the later four axes (Table 4.2 and Figure 4.2) (McCune and Grace 2002). The total stress of this two dimensional ordination is 17.51. The environmental variables that explain the majority of the variation along axis 1 ($R^2 = 0.54$) are the soil C:N ratio, soil pH, topographic index and soil phosphorus. The variables that explain the variation in the distribution of species along axis 2 ($R^2 = 0.22$) are magnesium, potassium and cation exchange capacity. As a result of the large number of species that have been analysed and the wide variation in relationships that topography (Figure 4.3) and soil variables have with each other (Figure 4.4) there is continuous change in community composition along this environmental gradient.

There are a number of recognisable forest types in Puketī, however due to the continuous compositional change along this environmental gradient there are visually, few abrupt changes that occur in forest type. The exception to this is the kauri-dominated stands that are found in low fertility environments on the ridge tops. The NMS ordination separates out the species that are found in the kauri-dominated stands, because ridge top habitats generally have a high C:N ratio, low pH and low phosphorus (Figure 4.1). Species that are found within these environmental conditions include: *Agathis australis, Ixerba brexioides, Quintinia serrata* and *Halocarpus kirkii* (Refer to Table 4.1 for species codes).

The most extensive forest type in Puketī is the podocarp – hardwood forests. This is the forest type that represents the transition from the hardwood (gully) forest type to the kauri-dominated stands. Because of the transitional nature of this forest type and the broad range of values for the environmental variables, the species community is typically dominated by generalist species that include: *Beilschmiedia tarairi*, *Knightia excelsa*, *Weinmannia silvicola* and *Dysoxylum spectabile* (Refer to Table 4.1 for species codes).

The last major forest type is the hardwood stands, which are found in gully habitats and generally have a low C:N ratio, high pH and high soil phosphorus (Figure 4.1). Species that are typically associated with only gully habitats include: *Laurelia novae-zelandiae, Melicytus ramiflorus, Corynocarpus laevigatus* and *Rhopalostylis sapida* (Table 4.1). However, there is no abrupt change between the species composition of the hardwood and podocarp – hardwood stands due to the transitional nature of the podocarp – hardwood stands and the overlap that occurs in environmental conditions and generalist species between these two forest types.

Table 4.1: Species names, six letter codes, basal area per hectare (mean ± standard error) and stem density per hectare (mean ± standard error) of the 30 study species in Puketī Forest. These were calculated using stems that were > 10 cm dbh.

Species	Six letter species code	Average basal area/hectare (m^2 ha^{-1}) ± SE	Range of basal area/hectare (m^2 ha^{-1})	Average stem density/ hectare (stems ha^{-1}) ± SE	Range of stem density/hectare (stems ha^{-1})
Ackama rosaefolia	ACKROS	0.7 ± 0.1	0.6 – 0.9	40 ± 6	25 – 50
Agathis australis	AGAAUS	32.7 ± 9.2	0.2 – 80.9	120 ± 40	25 – 350
Beilschmiedia tarairi	BEITAR	9.5 ± 1.4	0.3 – 22.3	134 ± 22	25 – 550
Beilschmiedia tawa	BEITAW	4.1 ± 1.0	0.2 – 15.1	56 ± 10	25 – 175
Corynocarpus laevigatus	CORLAE	1.3 ± 0.4	0.5 – 3.0	30 ± 5	25 – 50
Cyathea dealbata	CYADEA	5.5 ± 0.8	0.3 – 18.2	286 ± 38	25 – 975
Cyathea medullaris	CYAMED	3.5 ± 1.1	1.2 – 6.2	75 ± 29	25 – 175
Cyathea smithii	CYASMI	2.3 ± 0.9	0.4 – 4.2	169 ± 79	25 – 350
Dacrydium cupressinum	DACCUP	7.7 ± 3.5	1.0 – 27.1	31 ± 4	25 – 50
Dacrycarpus dacrydioides	DACDAC	8.9 ± 0	0 - 8.9	25 ± 0	0 - 25
Dicksonia squarrosa	DICSQU	1.0 ± 0.3	0.2 – 3.4	81 ± 13	25 – 150
Dysoxylum spectabile	DYSSPE	3.6 ± 0.7	0.7 – 9.2	123 ± 19	25 – 225
Elaeocarpus dentatus	ELADEN	1.6 ± 0.3	0.3 – 6.7	43 ± 5	25 – 100
Halocarpus kirkii	HALKIR	11.9 ± 3.6	6.2 – 18.6	217 ± 30	175 – 275
Hedycarya arborea	HEDARB	1.0 ± 0.2	0.2 – 2.2	52 ± 10	25 – 175
Ixerba brexioides	IXEBRE	4.3 ± 0.7	3.4 – 5.7	183 ± 30	125 – 225
Knightia excelsa	KNIEXC	3.2 ± 0.4	0.2 – 7.6	63 ± 8	25 – 200
Laurelia novae-zelandiae	LAUNOV	4.5 ± 1.3	0.5 – 10.7	34 ± 7	25 – 75
Leptospermum scoparium	LEPSCO	0.7 ± 0.5	0.2 – 1.2	50 ± 25	25 – 75
Melicytus ramiflorus	MELRAM	1.8 ± 0.4	0.2 – 5.2	85 ± 17	25 – 225
Metrosideros robusta	METROB	19.3 ± 11.4	5.6 – 41.9	42 ± 8	25 – 50
Nestegis lanceolata	NESLAN	1.2 ± 0.5	0.3 – 3.3	31 ± 6	25 – 50
Olearia rani	OLERAN	2.0 ± 0.7	0.9 – 4.4	80 ± 33	25 – 200
Phyllocladus trichomanoides	PHYTRI	3.1 ± 1.1	1.3 – 7.1	110 ± 47	25 – 225
Podocarpus cunninghamii	PODCUN	9.3 ± 2.8	0.5 – 27.9	61 ± 11	25 – 150
Prumnopitys ferruginea	PRUFER	5.8 ± 0.9	1.8 – 11.3	33 ± 6	25 – 100
Quintinia serrata	QUISER	3.2 ± 1.8	0.9 – 8.6	100 ± 67	25 – 300
Rhopalostylis sapida	RHOSAP	4.2 ± 1.0	0.3 – 22.4	258 ± 55	25 – 1200
Vitex lucens	VITLUC	4.0 ± 2.1	1.1 – 10.4	56 ± 12	25 – 75
Weinmannia silvicola	WEISIL	7.1 ± 0.8	0.7 – 17.2	154 ± 26	25 – 800
Total		47.7 m^2 ha^{-1}	14.6 – 91.8 m^2 ha^{-1}	1025 stems ha^{-1}	475 – 1725 stems ha^{-1}

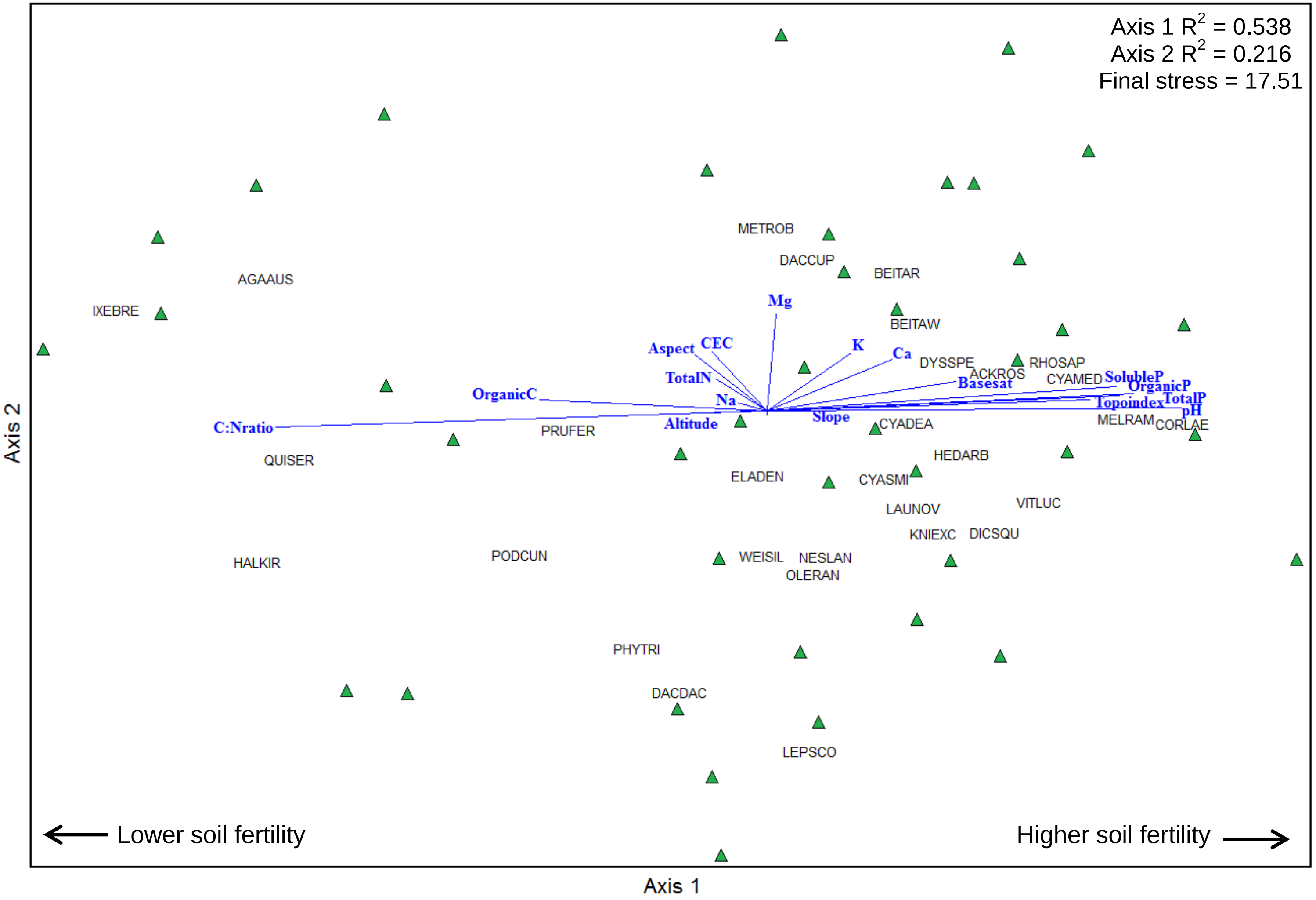

Figure 4.1: Non-metric multidimensional scaling ordination showing compositional differences among plots in Puketī Forest, relative to soil and environmental variables. Refer to Table 4.1 for species names.

Table 4.2: Non-metric dimensional scaling test results comparing stress in relation to dimensionality.

	Stress in real data			Stress in randomised data (Monte Carlo test, 250 runs)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	30.269	46.038	56.226	39.460	52.396	56.273	0.0040
2	17.496	18.268	21.226	21.226	27.609	39.878	0.0040
3	12.569	12.874	15.707	15.707	18.405	20.811	0.0040
4	9.502	9.753	11.774	11.774	13.755	24.806	0.0040
5	7.759	7.956	9.341	9.314	10.638	12.198	0.0040
6	6.403	6.534	6.957	7.383	8.504	9.793	0.0040

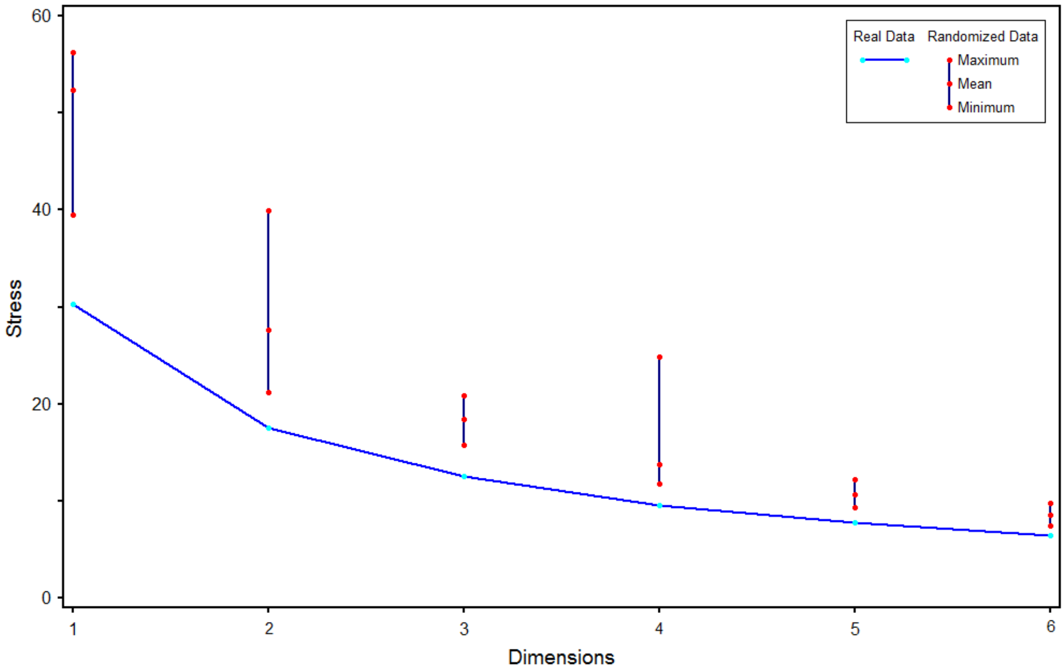

Figure 4.2: Scree plot showing stress as a function of dimensionality for the community composition data analysis.

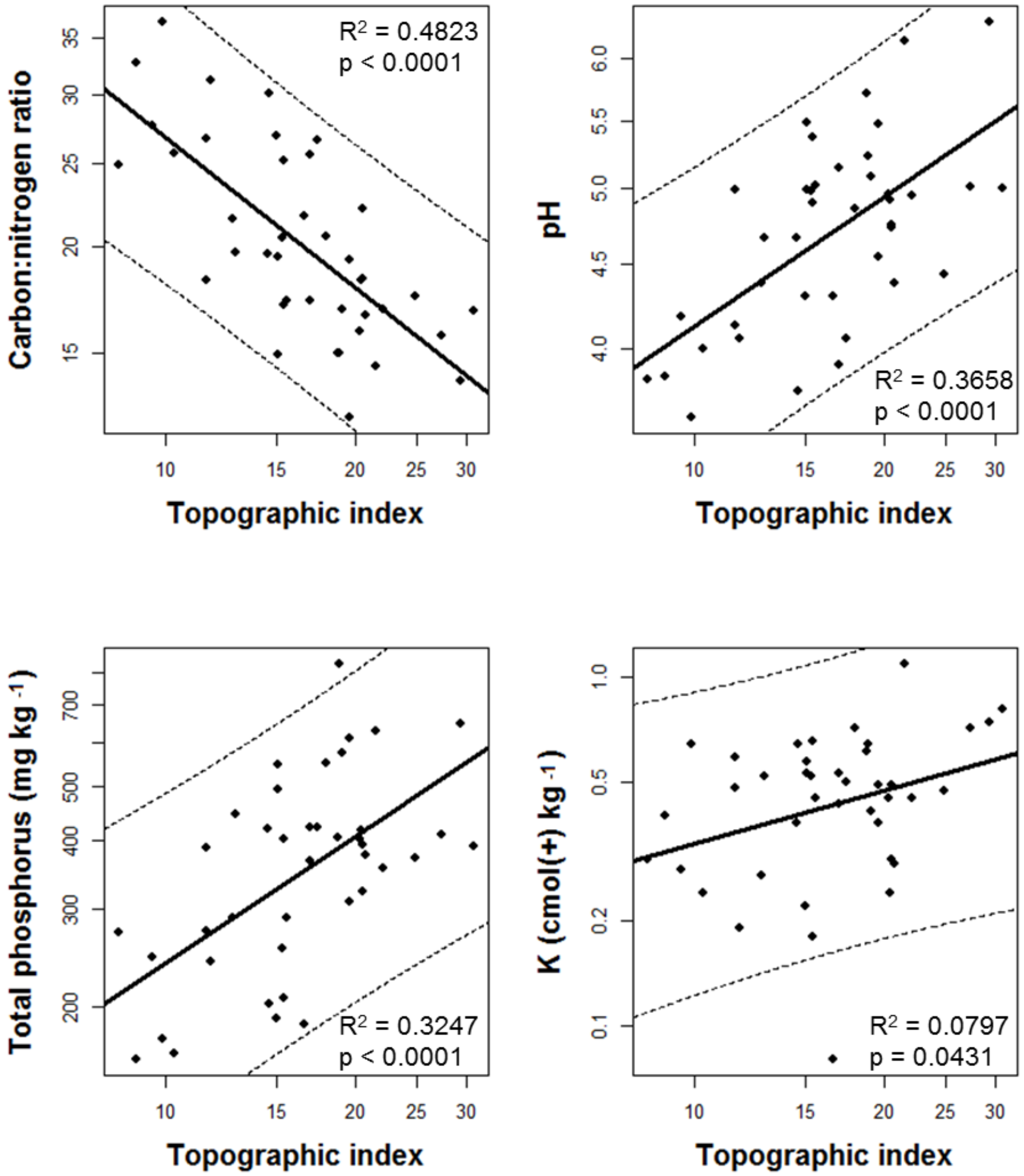

Figure 4.3: Regression of topographic index and soil carbon: nitrogen ratio, soil pH, total soil phosphorus (mg kg^{-1}) and soil K (cmol(+) kg^{-1}). Each circle represents a one of the 40 plots sampled along the environmental gradient. The solid line represents the fitted regression line and the dashed lines represent the prediction intervals.

The soil environmental variables measured on these 40 plots were correlated with topography (Figure 4.3). There were negative relationships between topographic index and soil C:N ratio (R^2 = 0.48, p < 0. 0001) and a positive relationship between topographic index and soil pH (R^2 = 0.37, p < 0. 0001), total soil phosphorus (R^2 = 0.32, p < 0. 0001) and soil K (R^2 = 0.08, p = 0. 0431).

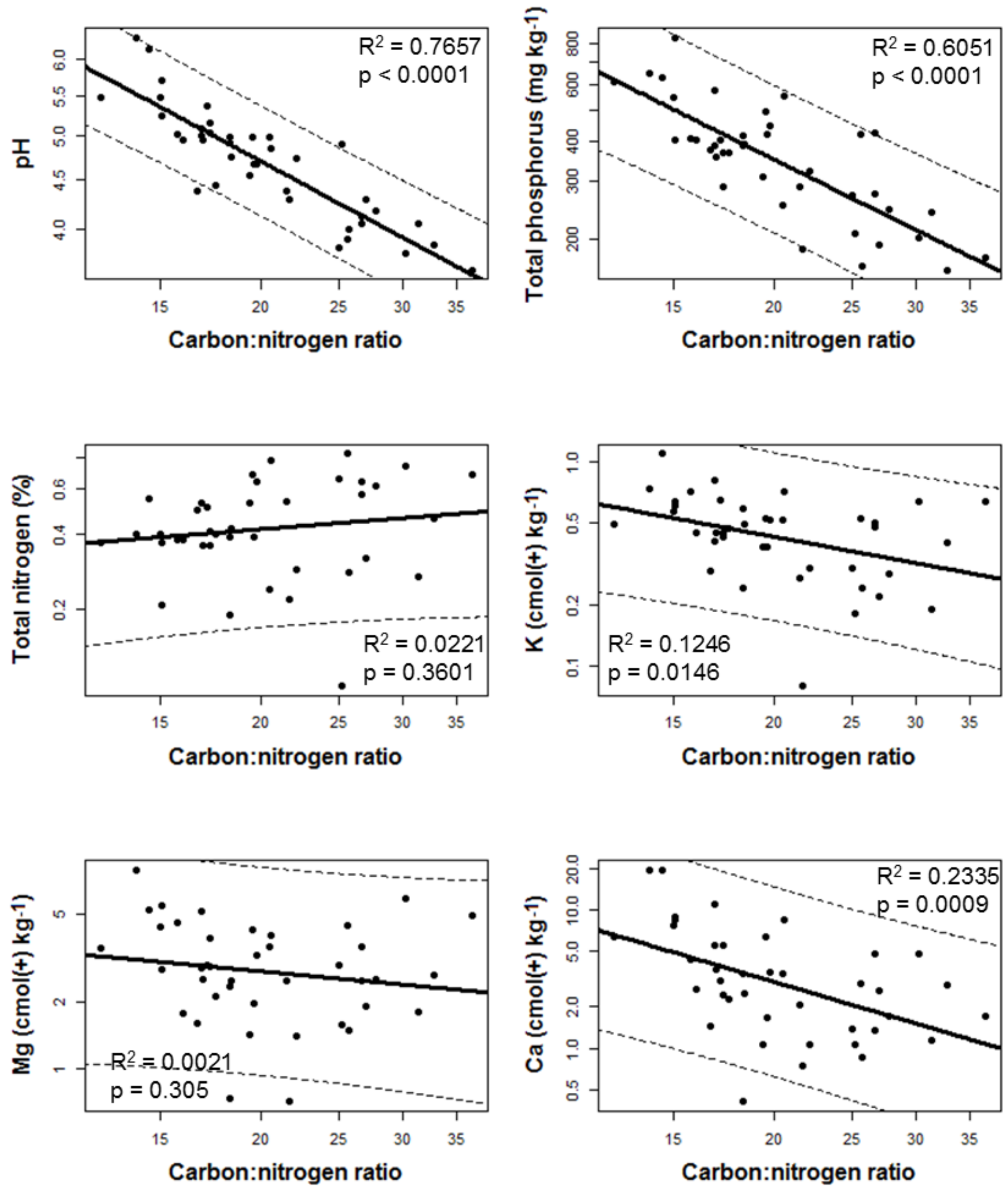

Figure 4.4: Regression of soil carbon: nitrogen ratio and soil pH, total soil phosphorus (mg kg^{-1}), total soil nitrogen (%), soil K (cmol(+) kg^{-1}), soil Mg (cmol(+) kg^{-1}) and soil Ca (cmol(+) kg^{-1}). Each circle represents a one of the 40 plots sampled along the environmental gradient. The solid line represents the fitted regression line and the dashed lines represent the prediction intervals.

Many of the environmental variables measured on these 40 plots were correlated. The negative relationships between soil C:N ratio and pH (R^2 = 0.77, p < 0. 0001), total soil phosphorus (R^2 = 0.61, p < 0. 0001), K (R^2 = 0.12, p = 0. 0146) and Ca (R^2 = 0.23, p = 0. 0009) varied in strength from very strong to weak (Figure 4.4). The relationships between soil C:N ratio and total soil nitrogen (R^2 = 0.02, p = 0. 3601) and Mg (R^2 = 0.002, p = 0. 305) were not significant.

4.2 Objective 2: Trait relationships among species

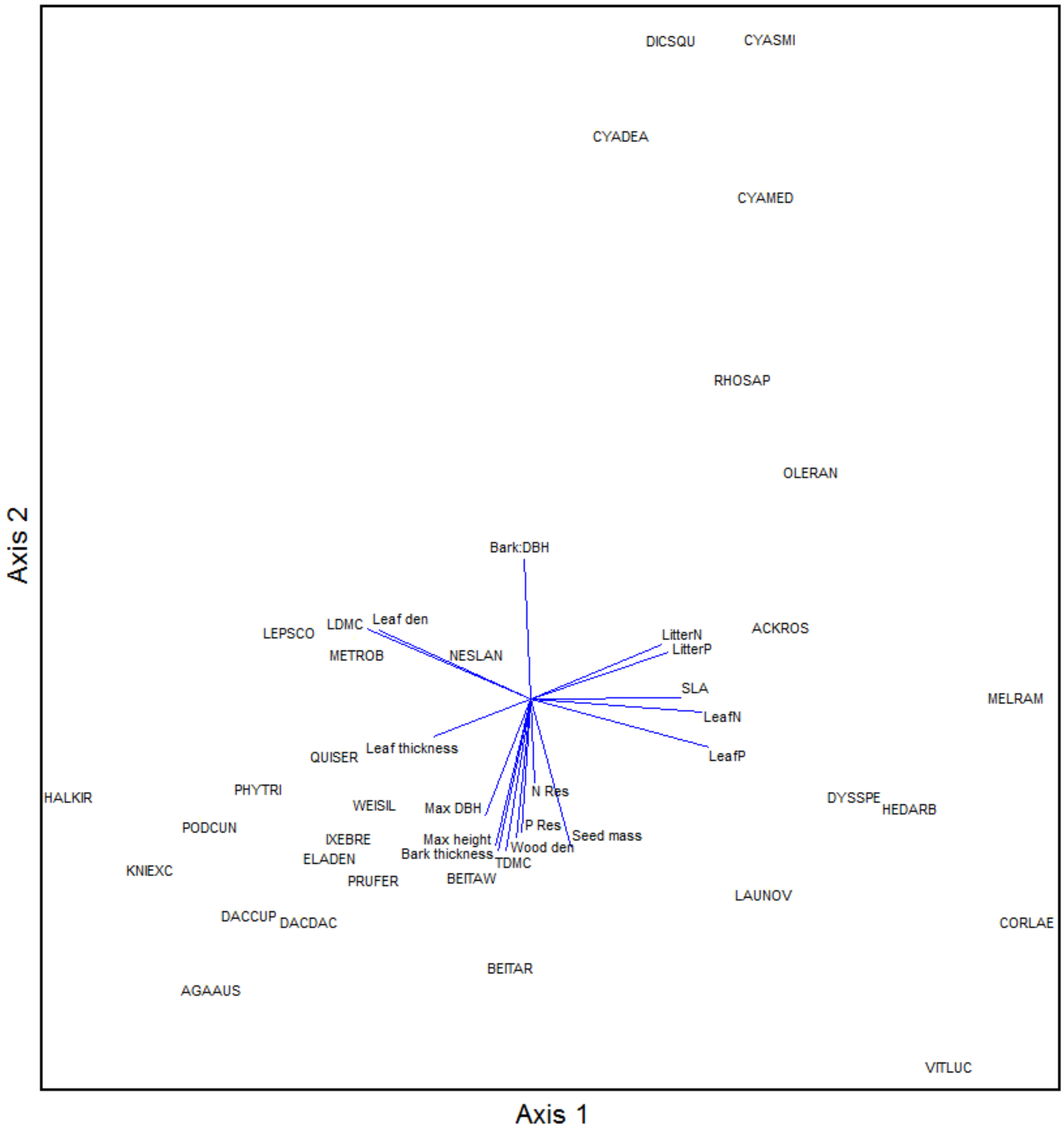

Figure 4.5: Ordination showing the relationship between wood, foliar, seed and whole plant traits and species (varimax rotation to maximise SLA along axis 1). Refer to Table 4.1 for species names.

The principle component analysis (Figure 4.5) illustrates how wood, leaf, seed and whole plant traits are correlated with each other and how these traits varied between species. A two dimensional ordination was chosen to represent the trait relationships among species data because the eigenvalue of the first two axis are greater than the broken-stick eigenvalue (Table 4.3). This indicates that these two axes are significant as these axes contain more information than expected by chance and therefore should be considered for interpretation. However, there could be as many as five dimensions in this ordination as four eigenvalues are greater than one and the fifth is close to one.

The eigenvectors of this ordination are reported in Table 4.4. However, it is important to note that these vectors are not directly applicable to Figure 4.5, because that ordination has a varimax rotation of -43^{o} to maximise SLA along axis 1, making this a leaf trait axis and axis 2 a wood, seed and height trait axis.

Functional traits are related and are not all independent of each other. For example SLA was positively correlated with leaf nitrogen and negatively correlated with traits such as leaf thickness and leaf density (Figure 4.6). Leaf nitrogen was positively correlated with litter nitrogen, leaf phosphorus and litter phosphorus (Figure 4.7). Traits such as wood density were positively correlated with twig dry matter content, seed mass and maximum height (Figure 4.8).

As a result of these relationships there are three functional groupings of species. The bottom left group (Figure 4.5) is made up of gymnosperms such as *Halocarpus kirkii*, *Dacrydium cupressinum*, *Podocarpus cunninghamii* and *Agathis australis* and angiosperms such as *Elaeocarpus dentatus*, *Knightia excelsa* and *Beilschmiedia tawa*, which have associations and trait overlap with these species. These species group together due to having traits such as thick leaves, low SLA, low litter nitrogen and litter phosphorus (Table 4.5). This group of species is typically associated with the slope and ridge habitats.

The bottom right group is made up of species that are typically associated with gully habitats such as *Vitex lucens*, *Corynocarpus laevigatus*, *Laurelia novae-zelandiae*, *Melicytus ramiflorus* and *Dysoxylum spectabile* and the traits are reflective of a high fertility environment such as thin leaves, high SLA, high leaf nitrogen, high leaf phosphorus, low leaf density, and low leaf dry matter content (LDMC) (Table 4.5).

The last group of *Dicksonia squarrosa*, *Cyathea dealbata*, *Cyathea smithii*, *Cyathea medullaris* and *Rhopalostylis sapida* are the tree ferns and palm species that were included in this study. They are grouped together due to the very small amount or lack of bark and low wood densities. These species also have traits such as high leaf nitrogen, high litter phosphorus, high SLA, low seed mass and low leaf thickness (Table 4.5), which are characteristic of high fertility environments.

Table 4.3: Eigenvalue and variance for the first 10 axes of the principle component anaylsis for wood, foliar, seed and whole plant traits.

Axis	Eigenvalue	% of variance	Cum. % of variance	Broken-stick eigenvalue
1	7.064	41.553	41.553	3.440
2	3.994	23.491	65.045	2.440
3	1.785	10.501	75.546	1.940
4	1.383	8.136	83.682	1.606
5	0.971	5.714	89.396	1.356
6	0.531	3.122	92.518	1.156
7	0.475	2.796	95.314	0.990
8	0.265	1.558	96.872	0.847
9	0.153	0.899	97.771	0.722
10	0.116	0.684	98.455	0.611

Table 4.4: Eigenvectors for the first four axes of Figure 4.5. It is important to note that Figure 4.5 has a varimax rotation of -43^{o}.

Trait	Eigenvector			
	1	2	3	4
Max dbh	-0.263	-0.126	-0.250	-0.288
Max height	-0.290	-0.193	-0.216	-0.113
Leaf thickness	-0.223	0.091	-0.398	-0.388
Bark thickness	-0.298	-0.206	-0.160	0.126
SLA	0.257	-0.235	0.259	0.285
Leaf density	-0.151	0.357	0.157	0.055
LDMC	-0.166	0.378	0.016	0.096
TDMC	-0.283	-0.219	-0.047	0.383
Wood density	-0.243	-0.214	-0.001	0.484
Bark: dbh	0.212	0.248	0.059	-0.138
Leaf N	0.272	-0.293	0.039	-0.115
Leaf P	0.226	-0.363	-0.023	-0.156
Litter N	0.308	-0.114	-0.272	-0.025
Litter P	0.307	-0.138	-0.307	-0.003
N resorption	-0.127	-0.149	0.537	-0.343
P resorption	-0.226	-0.214	0.388	-0.282
Seed mass	-0.166	-0.314	0.011	-0.098

Table 4.5: Trait values for the 30 species sampled in Puketī Forest. Values represent mean ± standard error.

Species	Six letter species code	SLA (mm^2 mg^{-1})	Leaf thickness (mm)	Leaf N (%)	Max height (m)	Seed size (mg)	Wood density (mg mm^{-3})
					(S. Richardson, Landcare)		
Ackama rosaefolia	ACKROS	17.01 ± 4.42	0.20 ± 0.02	1.25	12	0.03	0.41 ± 0.03
Agathis australis	AGAAUS	4.43 ± 0.11	0.51 ± 0.01	0.72 ± 0.03	40	1.88	0.47 ± 0.00
Beilschmiedia tarairi	BEITAR	8.10 ± 0.22	0.28 ± 0.02	1.38 ± 0.03	22	1868.35	0.54 ± 0.00
Beilschmiedia tawa	BEITAW	9.95 ± 0.27	0.17 ± 0.00	1.23 ± 0.04	25	1069.07	0.57 ± 0.01
Corynocarpus laevigatus	CORLAE	13.84 ± 0.60	0.29 ± 0.01	3.00 ± 0.21	20	1980.00	0.55 ± 0.01
Cyathea dealbata	CYADEA	10.13 ± 0.31	0.18 ± 0.01	1.27 ± 0.05	10	0.0008	0.22 ± 0.01
Cyathea medullaris	CYAMED	7.37 ± 2.10	0.42 ± 0.14	1.48 ± 0.15	20	0.0008	0.16 ± 0.01
Cyathea smithii	CYASMI	15.68 ± 1.99	0.15 ± 0.01	1.59 ± 0.10	8	0.0008	0.19 ± 0.01
Dacrydium cupressinum	DACCUP	3.02 ± 0.17	1.03 ± 0.05	0.66 ± 0.03	40	6.19	0.46 ± 0.01
Dacrycarpus dacrydioides	DACDAC	2.41 ± 0.13	0.79 ± 0.02	1.07	50	30.34	0.41 ± 0.03
Dicksonia squarrosa	DICSQU	10.63 ± 0.67	0.19 ± 0.01	1.44 ± 0.09	7	0.0008	0.25 ± 0.00
Dysoxylum spectabile	DYSSPE	15.05 ± 0.40	0.20 ± 0.00	1.93 ± 0.08	16	85.47	0.49 ± 0.01
Elaeocarpus dentatus	ELADEN	6.38 ± 0.25	0.26± 0.01	0.94 ± 0.02	21	656.32	0.48 ± 0.01
Halocarpus kirkii	HALKIR	0.99 ± 0.05	1.64 ± 0.03	0.65 ± 0.01	25	5.84	0.50 ± 0.02
Hedycarya arborea	HEDARB	13.31 ± 0.39	0.25 ± 0.01	2.08 ± 0.16	15	188.93	0.55 ± 0.01
Ixerba brexioides	IXEBRE	8.55 ± 0.24	0.27 ± 0.01	0.73 ± 0.09	17	5.08	0.54 ± 0.00
Knightia excelsa	KNIEXC	5.39 ± 0.17	0.35 ± 0.01	0.64 ± 0.03	30	20.11	0.55 ± 0.00
Laurelia novae-zelandiae	LAUNOV	11.59 ± 0.76	0.34 ± 0.02	1.54 ± 0.08	36	9.61	0.41 ± 0.01
Leptospermum scoparium	LEPSCO	6.67 ± 0.25	0.25 ± 0.01	0.93 ± 0.09	10	0.09	0.72 ± 0.01
Melicytus ramiflorus	MELRAM	19.73 ± 0.76	0.18 ± 0.01	2.34 ± 0.11	10	1.21	0.44 ± 0.01
Metrosideros robusta	METROB	5.60	0.29	0.89	30	0.05	0.64
Nestegis lanceolata	NESLAN	6.74 ± 0.32	0.29 ± 0.02	1.20 ± 0.14	15	34.57	0.70 ± 0.04
Olearia rani	OLERAN	18.04 ± 2.74	0.20 ± 0.02	0.98	8	0.07	0.52 ± 0.02
Phyllocladus trichomanoides	PHYTRI	5.44 ± 0.26	0.32 ± 0.02	0.76 ± 0.13	25	2.94	0.56 ± 0.01
Podocarpus cunninghamii	PODCUN	3.94 ± 0.16	0.44 ± 0.03	0.63 ± 0.03	24	12.15	0.49 ± 0.01
Prumnopitys ferruginea	PRUFER	6.14 ± 0.33	0.28 ± 0.01	0.81 ± 0.05	30	397.42	0.51 ± 0.01
Quintinia serrate	QUISER	9.65 ± 0.42	0.22 ± 0.02	0.72 ± 0.05	12	0.03	0.52 ± 0.01
Rhopalostylis sapida	RHOSAP	8.12 ± 0.22	0.22 ± 0.01	1.65 ± 0.06	10	239.62	0.15 ± 0.01
Vitex lucens	VITLUC	21.58 ± 2.45	0.17 ± 0.01	2.10 ± 0.24	20	521.31	0.73 ± 0.05
Weinmannia silvicola	WEISIL	9.67 ± 0.29	0.22 ± 0.01	0.96 ± 0.03	20	0.005	0.52 ± 0.01

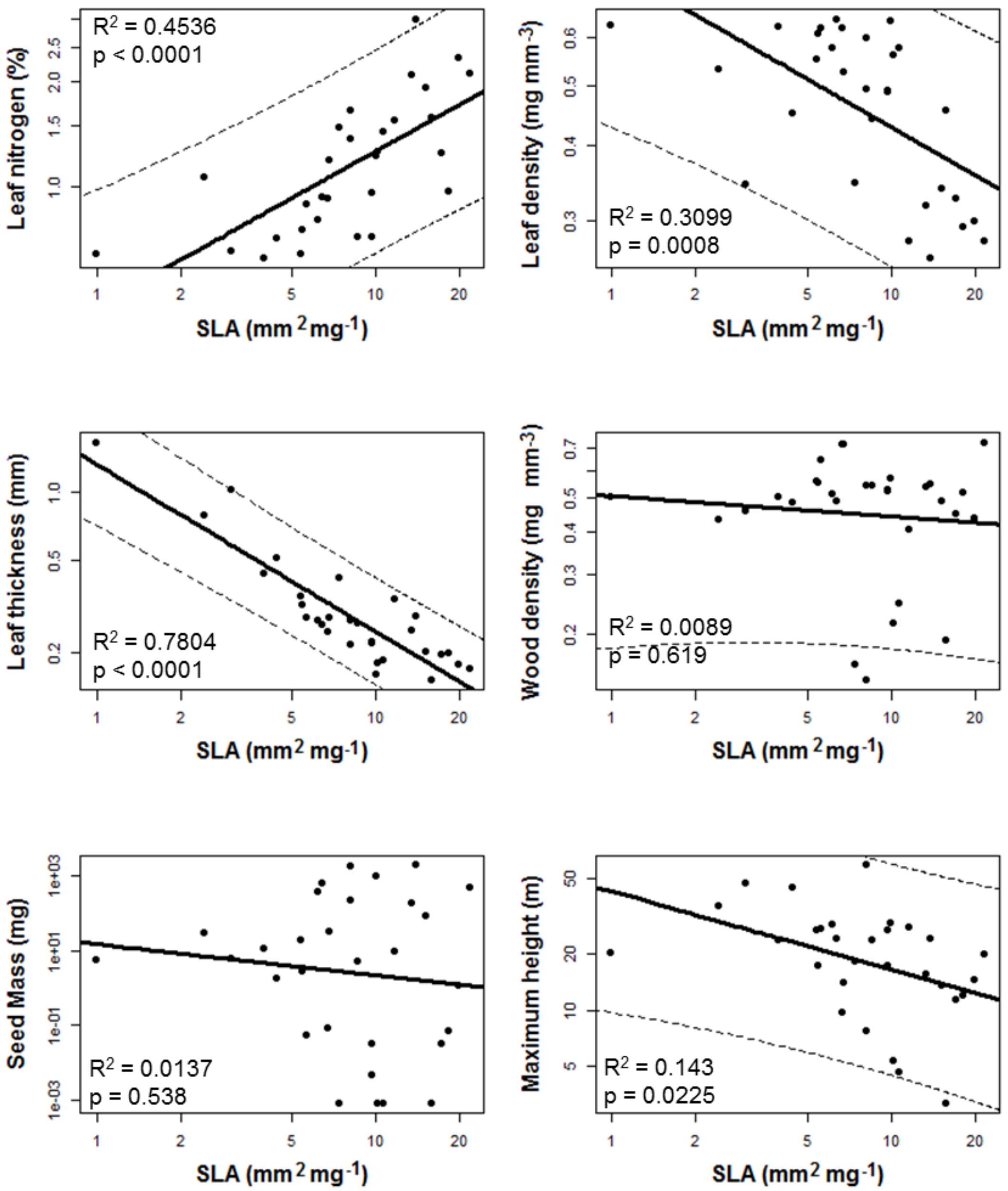

Figure 4.6: Regression of SLA (mm^2 mg^{-1}) and leaf nitrogen (%), leaf density (mg mm^{-3}), leaf thickness (mm), wood density (mg mm^{-3}), seed mass (mg) and maximum height (m). Each circle represents the average trait value for one of the 30 species sampled (Refer to Table 4.1). The solid line represents the fitted regression line and the dashed lines represent the prediction intervals.

Many of the functional traits measured on these 30 species were correlated. There were significant, positive relationships between SLA and leaf nitrogen ($R^2 = 0.45$, $p < 0.\ 0001$) and significant, negative relationships between SLA and leaf density ($R^2 = 0.31$, $p = 0.\ 0008$), leaf thickness ($R^2 = 0.78$, $p < 0.\ 0001$) and maximum height ($R^2 = 0.14$, $p = 0.\ 0225$) (Figure 4.6). The relationships between SLA and wood density ($R^2 = 0.01$, $p = 0.\ 619$) and seed mass ($R^2 = 0.01$, $p = 0.\ 538$) were not significant.

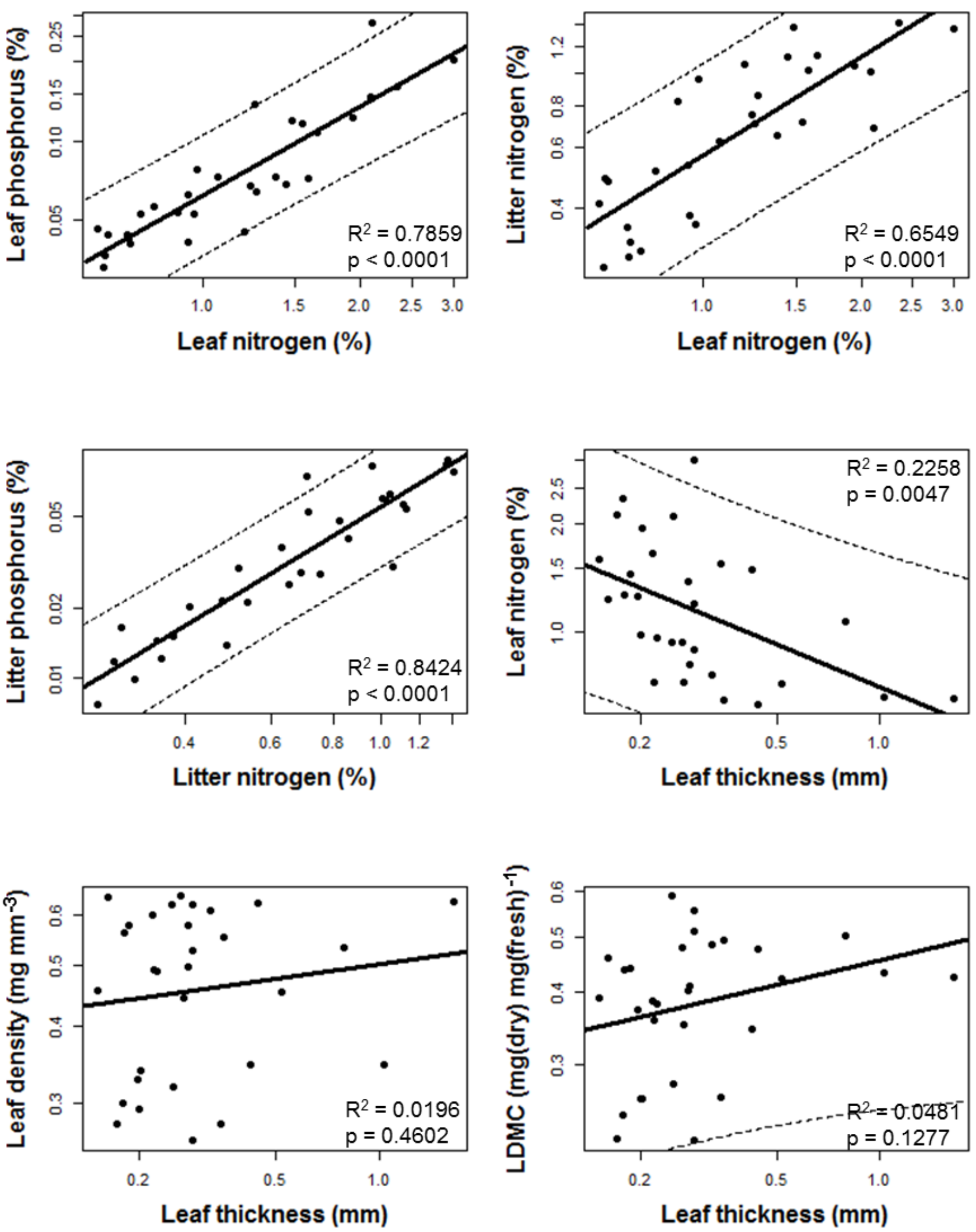

Figure 4.7: Regression of leaf nitrogen (%) and leaf phosphorus (%), litter nitrogen (%) and litter phosphorus (%) and leaf thickness (mm) and leaf nitrogen (%), leaf density (mg mm^{-3}) and leaf dry matter content (mg(dry) mg(fresh)$^{-1}$). Each circle represents the average trait value for one of the 30 species sampled (Refer to Table 4.1). The solid line represents the fitted regression line and the dashed lines represent the prediction intervals.

There were significant, very strong, positive relationships between leaf nitrogen and leaf phosphorus (R^2 = 0.79, p < 0. 0001), litter nitrogen (R^2 = 0.65, p < 0. 0001) and litter phosphorus (R^2 = 0.84, p < 0. 0001) (Figure 4.7). There was a moderately strong, negative relationship between leaf thickness and leaf nitrogen (R^2 = 0.22, p = 0. 0047). The relationships between leaf thickness and leaf density (R^2 = 0.02, p = 0. 4602) and leaf dry matter content (R^2 = 0.05, p = 0. 1277) were not significant.

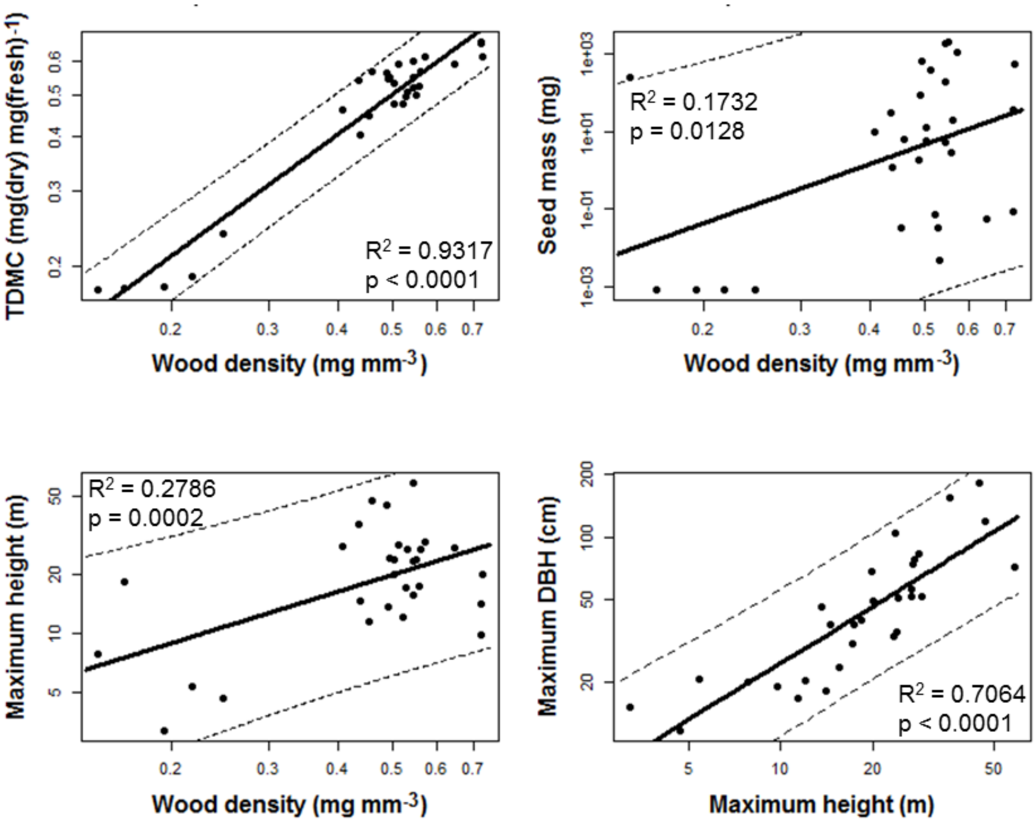

Figure 4.8: Regression of wood density (mg mm^{-3}) and wood dry matter content (mg(dry) mg(fresh)$^{-1}$), seed mass (mg) and maximum height (m) and maximum height (m) and maximum dbh (cm). Each circle represents the average trait value for one of the 30 species sampled (Refer to Table 4.1). The solid line represents the fitted regression line and the dashed lines represent the prediction intervals.

There were significant, positive relationships between wood density and wood dry matter content ($R^2 = 0.93$, $p < 0.\ 0001$), seed mass ($R^2 = 0.17$, $p = 0.\ 0128$) and maximum height ($R^2 = 0.28$, $p = 0.\ 0002$) (Figure 4.8). This figure also shows that there is a significant, very strong, positive relationship between maximum height and maximum dbh ($R^2 = 0.71$, $p < 0.\ 0001$).

4.3 Objective 3: Trait – environment relationships

The leaf, height, seed, wood and environmental gradient relationships presented below are the relationships that are significant in a backwards stepwise multiple linear regression analysis. The main environmental variables that explain how these traits varied along the gradient were the soil C:N ratio, total soil phosphorus and soil pH rather than topography.

4.3.1 Leaf traits – environment relationships

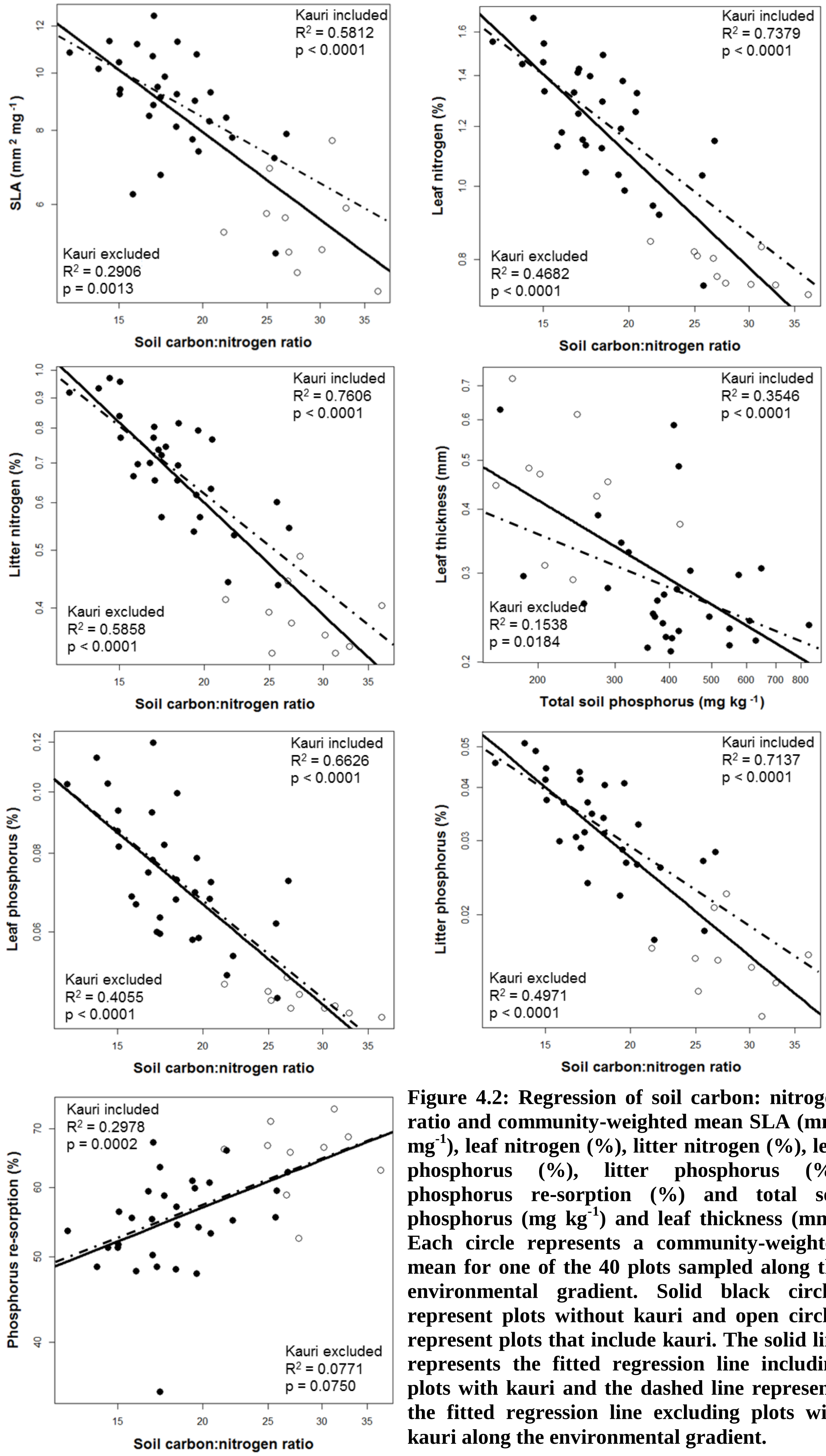

Figure 4.2: Regression of soil carbon: nitrogen ratio and community-weighted mean SLA ($mm^2\ mg^{-1}$), leaf nitrogen (%), litter nitrogen (%), leaf phosphorus (%), litter phosphorus (%), phosphorus re-sorption (%) and total soil phosphorus ($mg\ kg^{-1}$) and leaf thickness (mm). Each circle represents a community-weighted mean for one of the 40 plots sampled along the environmental gradient. Solid black circles represent plots without kauri and open circles represent plots that include kauri. The solid line represents the fitted regression line including plots with kauri and the dashed line represents the fitted regression line excluding plots with kauri along the environmental gradient.

The regression (Figure 4.9) showed that there were significant, negative relationships between soil C:N ratio and SLA ($R^2 = 0.58$, $p < 0.0001$), leaf nitrogen ($R^2 = 0.74$, $p < 0.0001$), litter nitrogen ($R^2 = 0.76$, $p < 0.0001$), leaf phosphorus ($R^2 = 0.66$, $p < 0.0001$), litter phosphorus ($R^2 = 0.71$, $p < 0.0001$) a positive relationship with phosphorus re-sorption ($R^2 = 0.30$, $p = 0.0002$) and a significant, negative relationship between total soil phosphorus and leaf thickness ($R^2 = 0.35$, $p < 0.0001$), for all the plots sampled.

Removing plots that include kauri reduces the overall strength of the relationships between soil C:N ratio and SLA ($R^2 = 0.29$, $p = 0.0013$), leaf nitrogen ($R^2 = 0.47$, $p < 0.0001$), litter nitrogen ($R^2 = 0.59$, $p < 0.0001$), leaf phosphorus ($R^2 = 0.41$, $p < 0.0001$), litter phosphorus ($R^2 = 0.50$, $p < 0.0001$) and total soil phosphorus and leaf thickness ($R^2 = 0.15$, $p = 0.0184$), but these relationships were still significant. Removing plots that include kauri from the soil C:N and phosphorus re-sorption regression significantly reduces the overall strength of this relationship ($R^2 = 0.08$) and as a result, this relationship is no longer significant ($p = 0.0750$).

4.3.2 Height and diameter – environment relationships

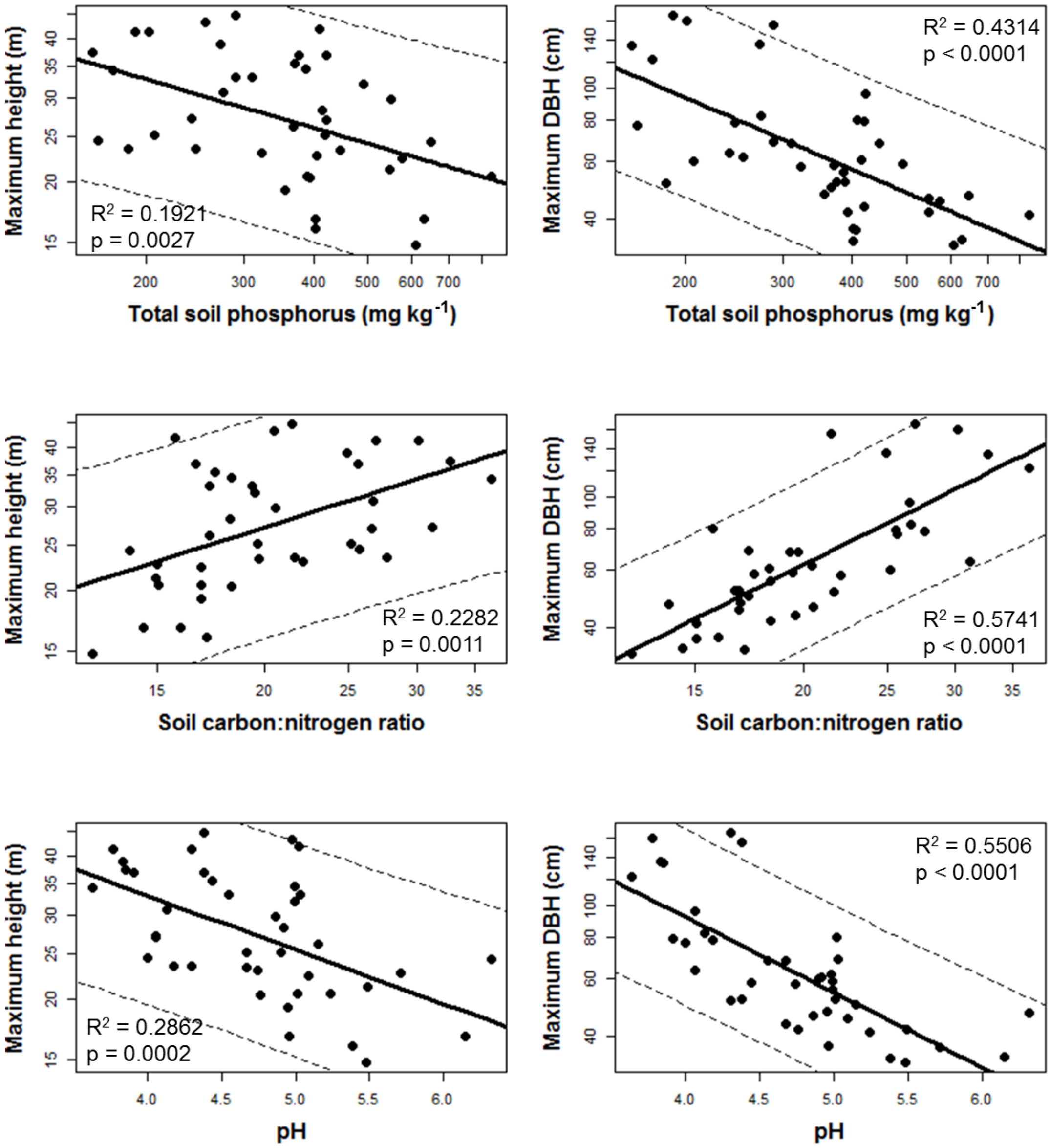

Figure 4.10: Regression of total soil phosphorus (mg kg^{-1}), soil carbon: nitrogen ratio and soil pH with maximum height (m) and maximum dbh (cm). Each circle represents a community-weighted mean for one of the 40 plots sampled along the environmental gradient. The solid line represents the fitted relationship and the dashed lines represent the prediction intervals.

There were significant, negative relationships between total soil phosphorus and maximum height (R^2 = 0.19, p = 0.0027) and maximum dbh (R^2 = 0.43, p < 0.0001), a significant, positive relationship between soil C:N and maximum height (R^2 = 0.23, p = 0.0011) and maximum dbh (R^2 = 0.57, p < 0.0001) and significant, negative relationships between soil pH and maximum height (R^2 = 0.29, p = 0. 0002) and maximum dbh (R^2 = 0.55, p < 0.0001) (Figure 4.10).

4.3.3 Seed size – environment relationships

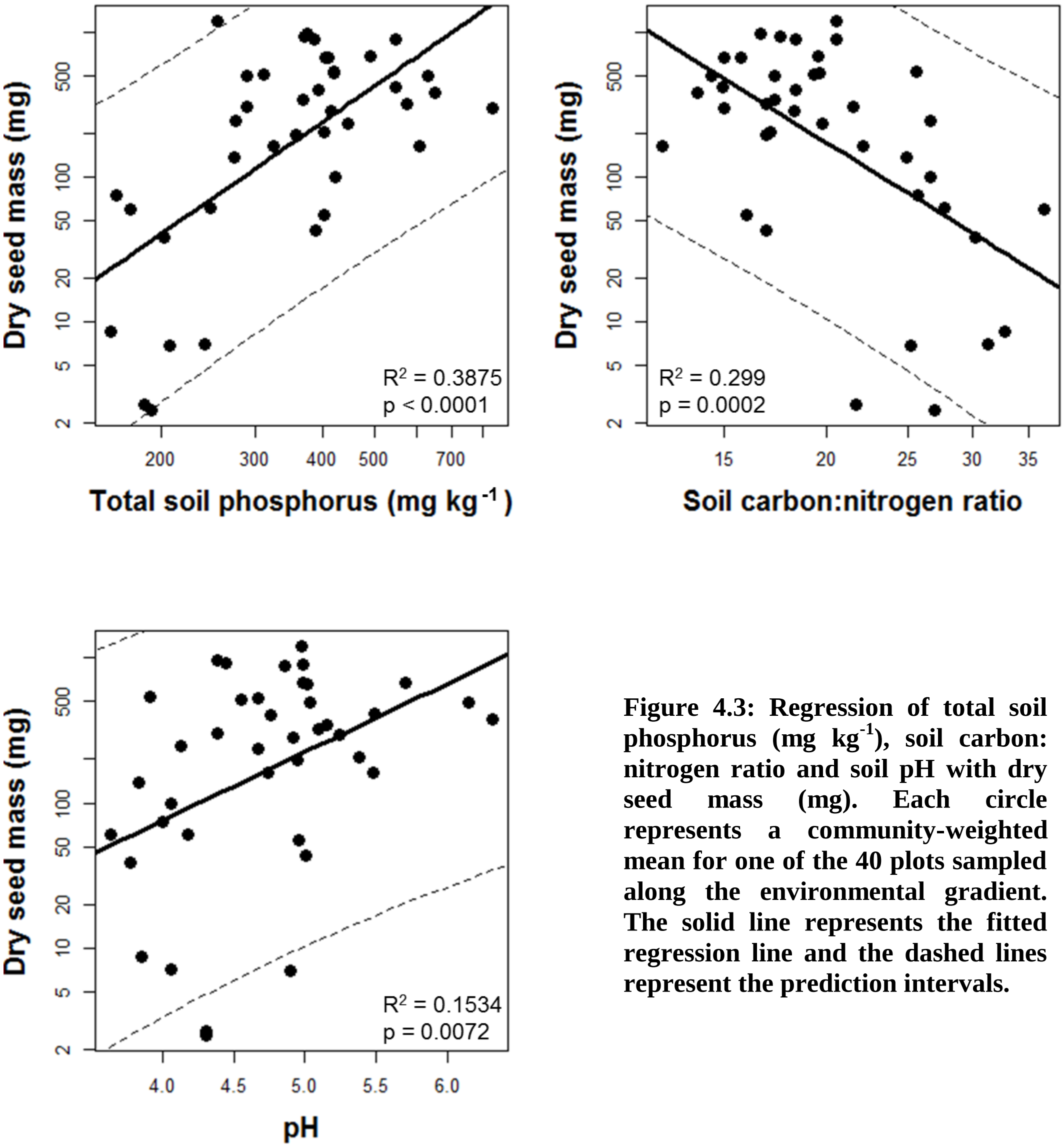

Figure 4.3: Regression of total soil phosphorus (mg kg^{-1}), soil carbon: nitrogen ratio and soil pH with dry seed mass (mg). Each circle represents a community-weighted mean for one of the 40 plots sampled along the environmental gradient. The solid line represents the fitted regression line and the dashed lines represent the prediction intervals.

There were significant, positive relationships between total soil phosphorus and dry seed mass ($R^2 = 0.39$, $p < 0.\ 0001$) and soil pH and dry seed mass ($R^2 = 0.15$, $p = 0.\ 0072$) a moderately strong, negative relationship between soil C:N and dry seed mass ($R^2 = 0.29$, $p = 0.\ 0002$) (Figure 4.11).

4.3.4 Wood – environment relationships

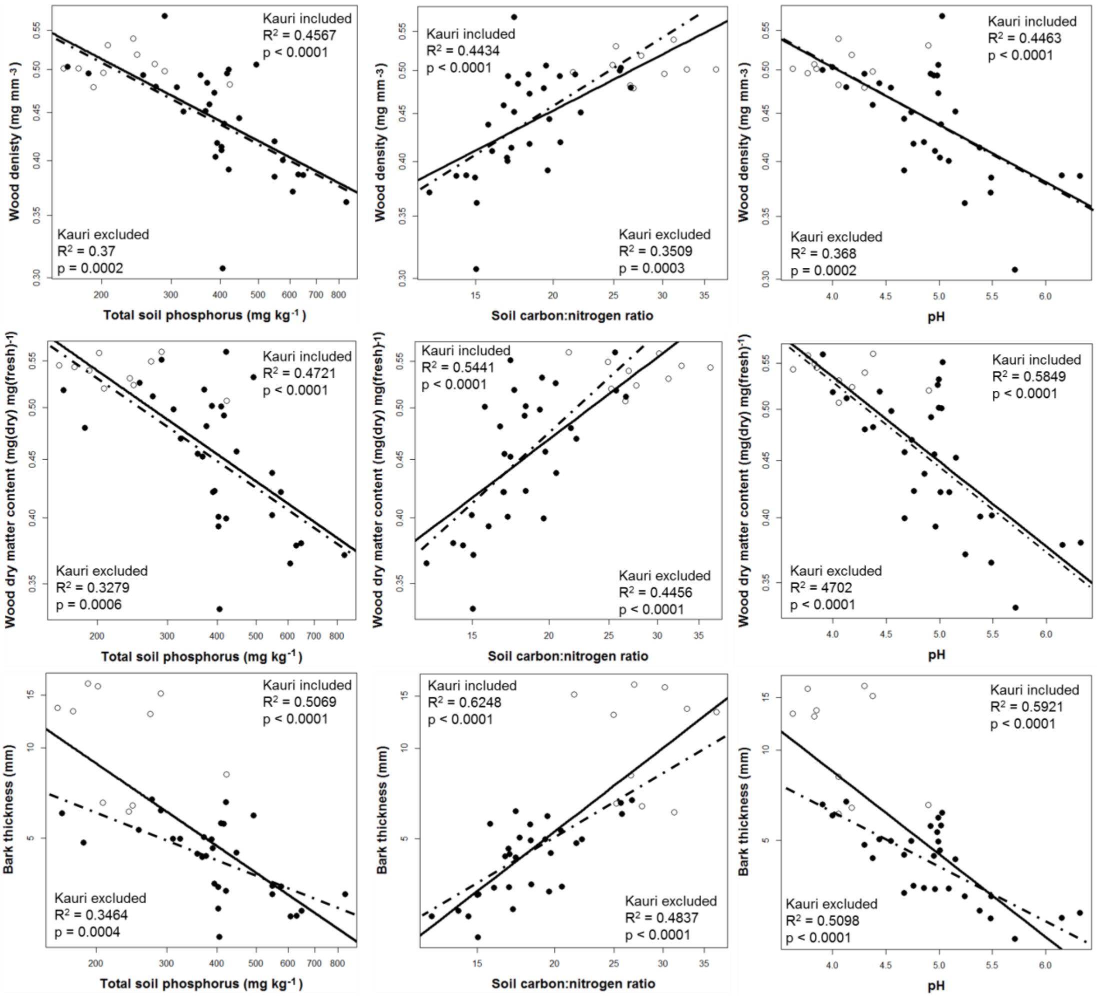

Figure 4.4: Regression of total soil phosphorus (mg kg^{-1}), soil carbon: nitrogen ratio and soil pH with wood density (mg mm^{-3}), wood dry matter content (mg(dry) mg(fresh)$^{-1}$) and bark thickness (mm). Each circle represents a community-weighted mean for one of the 40 plots sampled along the environmental gradient. Solid black circles represent plots without kauri and open circles represent plots that include kauri. The solid line represents the fitted regression line including plots with kauri and the dashed line represents the fitted regression line excluding plots with kauri along the environmental gradient.

The regression (Figure 4.12) shows that there were significant, negative relationships between total soil phosphorus and wood density ($R^2 = 0.46$, $p < 0.0001$), wood dry matter content ($R^2 = 0.47$, $p < 0.0001$) and bark thickness ($R^2 = 0.51$, $p < 0.0001$). There were significant, positive relationships between soil C:N and wood density ($R^2 = 0.44$, $p < 0.0001$), wood dry matter content ($R^2 = 0.54$, $p < 0.0001$) and bark thickness ($R^2 = 0.62$, $p < 0.0001$). This regression also shows that there were significant, negative relationships between soil pH and wood density ($R^2 = 0.44$, $p < 0.0001$), wood dry matter content ($R^2 = 0.58$, $p < 0.0001$) and bark thickness ($R^2 = 0.59$, $p < 0.0001$) for all plots sampled (kauri included and excluded).

Removing plots that include kauri reduces the overall strength of the relationships between total soil phosphorus and wood density ($R^2 = 0.37$, $p = 0.0002$), wood dry matter content ($R^2 = 0.33$, $p = 0.0006$) and bark thickness ($R^2 = 0.35$, $p = 0.0004$), soil C:N and wood density ($R^2 = 0.35$, $p = 0.0003$), wood dry matter content ($R^2 = 0.45$, $p < 0.0001$) and bark thickness ($R^2 = 0.48$, $p < 0.0001$) and soil pH and wood density ($R^2 = 0.37$, $p = 0.0002$), wood dry matter content ($R^2 = 0.47$, $p < 0.0001$) and bark thickness ($R^2 = 0.51$, $p < 0.0001$) but these relationships were all still significant.

4.3.5 Individual level functional traits along the environmental gradient

The figures presented below illustrate traits that have been measured on individual trees across 30 plots along a soil fertility gradient. The circles do not represent a community-weighted mean, but rather individual trees.

These figures show that there was a turnover in species along the soil fertility gradient. This was shown by the coloured lines, which represent the distribution of an individual species along the gradient. These figures also show environmental filtering, with the strength of the filter being the strongest in soils with low nutrient availability (high soil C:N and low total soil phosphorus) where trait convergence is occurring and weaker in soils with high nutrient availability (low soil C:N and high total soil phosphorus).

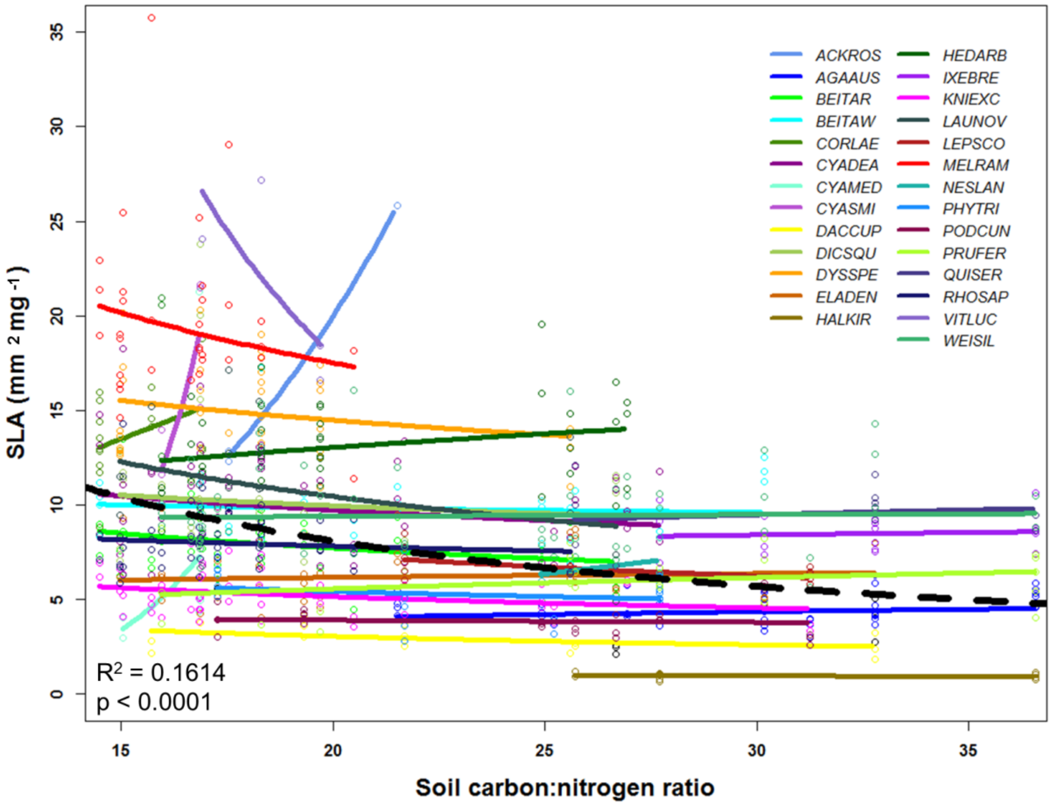

Figure 4.13: Relationship between soil carbon: nitrogen ratio and SLA (mm^2 mg^{-1}). Each coloured circle represents the SLA measured on an individual plant. It does not represent a community-weighted mean. The black dashed line represents the fitted regression line for the given soil carbon: nitrogen ratio gradient. Refer to Table 4.1 for species names.

The mean and variance of SLA (Figure 4.13) decreases with increasing soil C:N ratio ($R^2 = 0.16$, $p < 0.0001$). SLA varies greatly among species with values ranging from 0.69 mm^2 mg^{-1} to 35.77 mm^2 mg^{-1}, however, SLA varied little within an individual species as 81 % of these individual regression relationships were not significant. There is a continuous turnover in the distribution of species along the soil C:N gradient. Species that are more generalist and associated with slope habitats such as *Weinmannia silvicola* were found over a wide range of the soil C:N gradient. Although the turnover of species is continuous, there is little overlap in species associated with high fertility environments such as *Melicytus ramiflorus*, *Laurelia novae-zelandiae*, *Corynocarpus laevigatus* and *Rhopalostylis sapida* and species associated with low fertility environments for example *Agathis australis*, *Halocarpus kirkii* and *Ixerba brexioides* (Table 4.1), which is consistent with the community composition ordination (Figure 4.1).

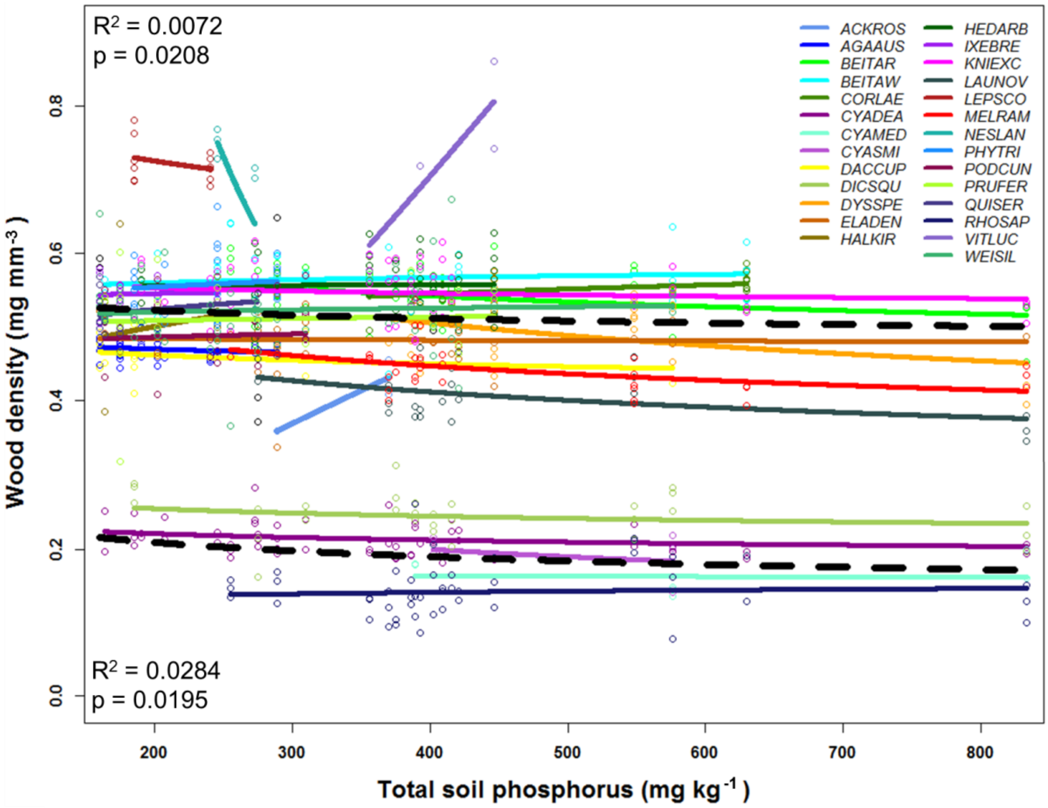

Figure 4.14: Relationship between total soil phosphorus (mg kg^{-1}) and wood density (mg mm^{-3}). Each coloured circle represents the wood density measured on an individual plant. It does not represent a community-weighted mean. The upper black dashed line represents the fitted wood density regression line for the angiosperms and gymnosperms and the lower black dashed line represents the fitted wood density regression line for the ferns and palm species along the total soil phosphorus gradient. Refer to Table 4.1 for species names.

The mean and variance of wood density (Figure 4.14) decreases with increasing total soil phosphorus ($R^2 < 0.01$, $p = 0.0208$ and $R^2 < 0.03$, $p = 0.0195$). Although these relationships were significant the R^2 values were very low, therefore there is only weak evidence for environmental filtering in this relationship. Wood density varies among species with a range of values from 0.08 mg mm^{-3} to 0.86 mg mm^{-3} however, wood density varied little within an individual species along the soil fertility gradient as 89 % of these individual regression relationships were not significant. There are two distinct groupings of wood densities in this figure. The lower stem densities consist mainly of stipe densities from fern species such as *Dicksonia squarrosa*, *Cyathea dealbata*, *Cyathea smithii*, *Cyathea medullaris* and the stem density of the single palm species *Rhopalostylis sapida* (Refer to Table 4.1 for species codes). The upper group consists of all the remaining species, including the angiosperms and gymnosperms that were sampled in this study.

This relationship indicates that wood density is being weakly filtered along the soil fertility gradient. This is shown by a subtle shift in the mean wood density from a slightly higher wood density in the less fertile, low total phosphorus soils to a slightly lower wood density in the more fertile, higher total phosphorus environments.

4.4 Objective 4: Functional diversity

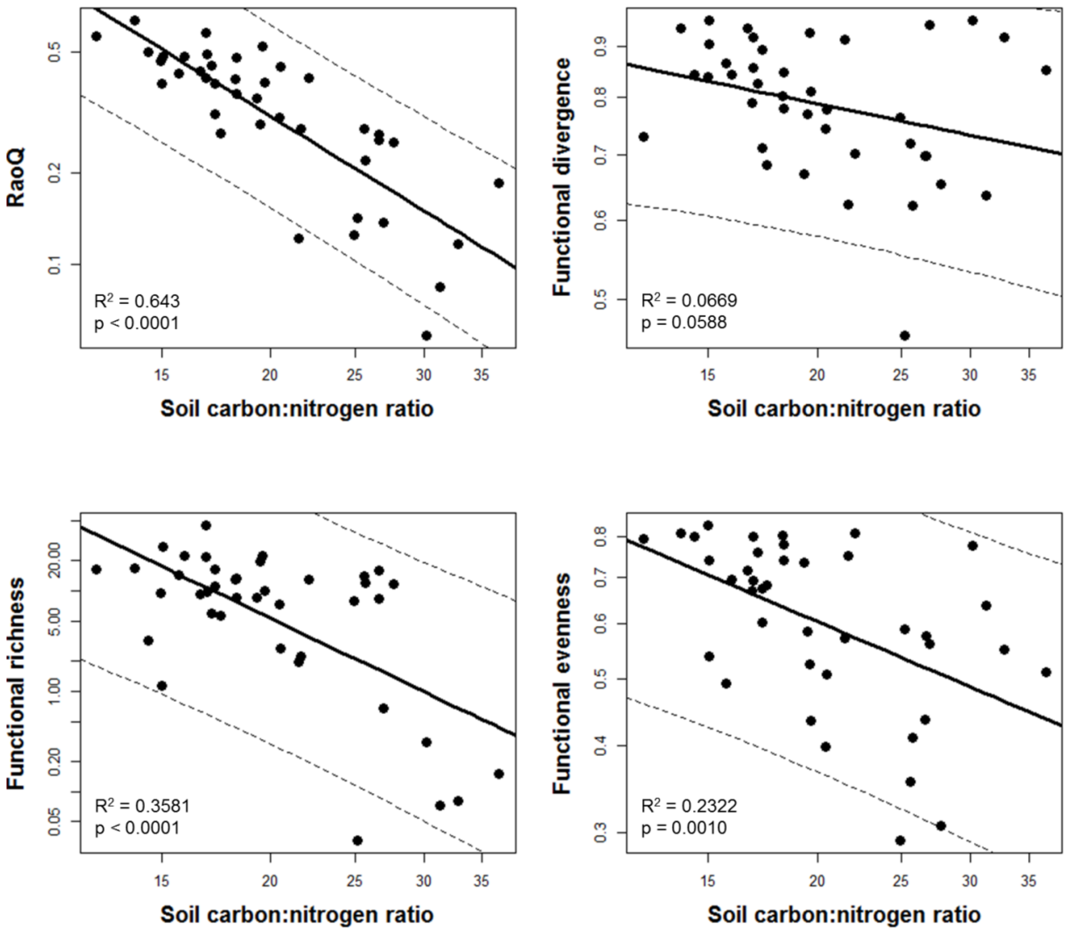

Figure 4.15: Relationship between soil carbon: nitrogen ratio and Rao's quadratic entropy (RaoQ), functional divergence, functional richness and functional evenness. All variables have been calculated using relative abundance. Each circle represents one of the 40 plots sampled along the environmental gradient. The solid line represents the fitted regression line and the dashed lines represent the prediction intervals along the soil carbon: nitrogen ratio gradient.

Functional diversity indices calculated for the 40 plots show that there were negative correlations along the environmental gradient (Figure 4.15). There were very strong, relationships between soil C:N ratio and the RaoQ index of functional diversity ($R^2 = 0.64$, $p < 0.\ 0001$). This figure also shows that there were moderately strong relationships between soil C:N ratio and functional richness ($R^2 = 0.36$, $p < 0.\ 0001$) and functional evenness ($R^2 = 0.23$, $p = 0.\ 0010$). The relationship between soil C:N ratio and functional divergence was not significant ($R^2 = 0.07$, $p = 0.\ 0588$).

Chapter Five: Discussion

5.1 Community composition

The first objective was to determine how the community composition of Puketī Forest changes along the environmental gradients and how soil variables and topography relate to each other. The changes in community composition have been found to be related to the strong gradient in environmental factors (Figure 4.1). The variables that are the most significant in explaining the variation in the distribution of species are soil variables such as carbon: nitrogen ratio (C:N), pH and total phosphorus, rather than topographical variables. However, soil fertility and topographical variables are related (Figure 4.3) and therefore this study further explains (through trait based mechanisms) why Burns and Leathwick (1996) found a change in forest composition along a topographical gradient. The change in community composition along an environmental gradient is therefore due to the link between soil fertility, soil moisture and topography (Oliveira-Filho et al. 1994, Laurance et al. 2010).

Soils that are found on ridge tops are generally less fertile than soils found further downslope and in gullies (Burns and Leathwick 1996). Soils that are found on ridge tops are typically subjected to leaching due to runoff, but the presence of acidic kauri litter in Puketī also causes further leaching and slows down the decomposition and nutrient cycling rates, resulting in lower pH and less fertile soils (lower phosphorus concentrations, lower base saturation and higher C:N ratios), than less leached downslope and gully areas (Wyse et al. 2013). Gully soils have a higher pH and fertility due to the ongoing accumulation of nutrients from upslope, but also faster litter decomposition rates, due to the less acidic litter and faster internal nutrient cycling (Enright and Ogden 1987, Barbier et al. 2008, Wyse et al. 2013).

The main forest types in Puketī are kauri stands, podocarp – hardwood stands and hardwood stands. Kauri stands occur in various sizes with average kauri densities of 120 ± 40 stems ha^{-1}. These trees are mainly present on ridges, where they form a tall canopy, with a sub-canopy of *Ixerba brexioides* (183 ± 30 stems ha^{-1}), *Halocarpus kirkii* (217 ± 30 stems ha^{-1}), *Quintinia serrata* (100 ± 67 stems ha^{-1}) and *Weinmannia silvicola* (154 ± 26 stems ha^{-1}) with scattered *Dacrydium cupressinum* (31 ± 4 stems ha^{-1}) and *Prumnopitys ferruginea* (33 ± 6 stems ha^{-1})

(Powlesland 1987, Best and Bellingham 1991, Burns and Leathwick 1996) This combination of species (excluding scattered trees and *Weinmannia silvicola*, which is a generalist) forms a distinct grouping in the low fertility soil type (Figure 4.1). This grouping of species commonly associated with kauri stands is distinct from the other forest types due to the influence of kauri on soil pH, nutrient cycling and the formation of thick litter layers. As a result of these plant-soil interactions only a few species can tolerate these unfavourable conditions (Wyse 2012).

The most extensive forest type in Puketī is the podocarp – hardwood forest. This forest type represents a transition from the hardwood (gully) forest type to the kauri stands. The canopy consists of a mixture of hardwoods such as *Beilschmiedia tarairi* (134 ± 22 stems ha^{-1}), *Beilschmiedia tawa* (56 ± 10 stems ha^{-1}), *Weinmannia silvicola, Knightia excelsa* (63 ± 8 stems ha^{-1}) and *Dysoxylum spectabile* (123 ± 19 stems ha^{-1}), with *Agathis australis*, *Dacrydium cupressinum, Phyllocladus trichomanoides* (110 ± 47 stems ha^{-1}) and *Podocarpus cunninghamii* (61 ± 10 stems ha^{-1}) occurring as emergent trees. This assemblage of species is not easily recognisable in the ordination plot due to the intermediate fertility of the soils and overlap in generalist species that are typically associated with this transitional forest type and also the gully or ridge habitats (Powlesland 1987, Best and Bellingham 1991, Burns and Leathwick 1996).

The last major forest type is the hardwood stands, which are found in the gully areas that have soils with a higher pH and fertility due to ongoing accumulation of leached material from upslope. The major species which define this forest type are *Laurelia novae-zelandiae* (34 ± 7 stems ha^{-1}), *Melicytus ramiflorus* (85 ± 17 stems ha^{-1}), *Corynocarpus laevigatus* (30 ± 5 stems ha^{-1}), *Vitex lucens* (56 ± 12 stems ha^{-1}) *and Rhopalostylis sapida* (258 ± 55 stems ha^{-1}). Hardwood forests have an overlap in species distribution with podocarp – hardwood stands such as *Weinmannia silvicola*, *Beilschmiedia tarairi* and *Dysoxylum spectabile.* Therefore due to the continuous change in community composition along this environmental gradient, these two forest types are not distinguishable on the ordination.

The outcomes of this section show that we are able to determine how species distributions and forest types change along the environmental gradient and conclude that soil C:N, total soil phosphorus and soil pH are important in influencing species distributions. This section also shows that there are significant relationships between topography and soil variables, therefore the changes in community composition along an environmental gradient are due to the links between soil fertility, soil moisture and topography.

5.2 Trait relationships among species

The second objective was to determine the trait relationships among species (Figure 4.5) and between leaf, height, seed and wood traits (Figure 4.6, Figure 4.7 and Figure 4.8). There are a wide variety of functional traits that can be measured on an individual plant, however many of them are redundant due to the correlation that traits can have. Therefore it is important to measure a variety of traits in order to maximise the number of independent traits that can be used to determine the functional variation among and between species. The trait – species ordination (Figure 4.5) shows the relationship between leaf, height, seed and wood traits and how these traits relate to each other, the species sampled and that the traits measured are not all independent of each other. As a result of the correlations between traits there are three separate groups of species with distinctive sets of traits.

The first notable group of species is the assemblage of *Cyathea dealbata*, *Cyathea medullaris*, *Cyathea smithii*, *Dicksonia squarrosa* and *Rhopalostylis sapida*, which are tree ferns and the single palm species. These species group together due to the low stem density (0.15 – 0.25 mg mm^{-3}), low seed mass (0.0008 – 239.62 mg) and low nutrient re-sorption efficiency. However this group still has relatively high SLA (7.37 – 15.68 mm^2 mg^{-1}) thin leaves (0.15 – 0.42 mm) and high leaf (1.27 – 1.65 %) and litter nitrogen and phosphorus, similar to the second group of species discussed further on. In New Zealand, ferns (75 – 286 stems ha^{-1}) and *Rhopalostylis sapida* (258 ± 55 stems ha^{-1}) are typically found at the highest densities in moist environments that have a high total soil phosphorus level and high light levels, such as gullies and alluvial terraces (Enright and Watson 1992, Mehltreter et al. 2010).

The second group of species includes: *Ackama rosaefolia*, *Melicytus ramiflorus*, *Dysoxylum spectabile*, *Hedycarya arborea*, *Corynocarpus laevigatus* and *Laurelia novae-zelandiae* which are grouped together due to their high SLA (11.59 – 19.73 mm^2 mg^{-1}), low leaf thickness (0.18 – 0.34 mm), low leaf density, high leaf nitrogen (1.25 – 3.00 %) and phosphorus, high litter nitrogen and phosphorus, high seed mass (0.03 – 1980.00 mg) and higher wood density (0.41 –

0.55 mg mm^{-3}) than the tree fern and palm group. These two groups of species are representative of the fertile gully, terrace and lower slope environments, where this suite of traits reflects a fast growing, resource-acquiring strategy (Westoby et al. 2002, Mason et al. 2012). This strategy allows plants growing in fertile environmental conditions to capitalise on available resources by having a quick rate of return on investments such as nutrients in leaves through low construction costs, which can result in an increase in light interception and therefore photosynthetic and growth rates (Wright et al. 2004, Osnas et al. 2013).

The last group of species includes gymnosperms such as *Agathis australis*, *Halocarpus kirkii, Phyllocladus trichomanoides* and *Dacrydium cupressinum* and angiosperms such as *Knightia excelsa, Ixerba brexioides, Weinmannia silvicola* and *Elaeocarpus dentatus* which have associations and trait overlap with these gymnosperms. These species are grouped together due to their low SLA (0.99 – 9.67 mm^2 mg^{-1}), high leaf thickness (0.22 – 1.64 mm), high leaf density, low leaf nitrogen (0.64 – 0.96 %) and phosphorus, low litter nitrogen and phosphorus, low seed mass (0.005 – 656.32 mg) and high wood density (0.46 – 0.56 mg mm^{-2}). This group of species is representative of a low fertility, slow growing environment where these traits reflect a resource-retaining strategy because they emphasize nutrient retention in a low fertility environment, allowing plants to persist in conditions where resources are not readily available (Wright et al. 2004, Richardson et al. 2005, Mason et al. 2012).

The outcomes of this section are that relationships between leaf, height, seed and wood traits exist, but they are not all independent of each other. As a result of the correlations between these traits there are three distinct groups of species with distinctive sets of traits.

5.3 Trait – environment relationships

The third objective was to determine the relationships between community-weighted means of leaf, height, seed and wood traits and the environmental variables and determine the influence of environmental filtering on community assembly. The availability of soil nutrients is an important factor in determining the species composition of plant communities (Ordonez et al. 2009). The non-random distribution of community-weighted means along the soil fertility gradient of Puketī Forest shows that these traits are filtered along this gradient (Shipley et al. 2006). Understanding the distribution of species and their traits along environmental gradients is important because changes in vegetation composition and plant traits are likely to increase in the future due to changes in climate, land use, environmental factors and species invasions (Eviner 2004).

5.3.1 Leaf traits

The availability of soil nutrients is an important factor in determining plant communities, however, it is necessary to recognise that plants can have a feed-back effect on the environment and nutrient availability (Facelli and Pickett 1991, Casper and Castelli 2007). This is because plants growing in nutrient-rich, fertile environments, such as the gully habitats of Puketī, generally produce nutrient rich litter, as shown by the high litter nitrogen and litter phosphorus in the low soil C:N ratio environment (Figure 4.9). This in turn releases a large proportion of these nutrients back into the soil during decomposition and as a result sustains the high level of soil nutrients. In nutrient-poor environments, plants conserve nutrients in long lived leaves and have high re-sorption efficiencies (Figure 4.9), therefore reinforcing the infertility of these soils (Facelli and Pickett 1991, Hobbie 1992). The presence of kauri in Puketī amplifies this infertility, as the acidic litter of kauri reduces the pH of the soil which increases leaching and slows down decomposition and nutrient cycling. It is therefore important to note that there are feedback responses of plants to the environmental conditions and nutrient availability and that soil fertility alone cannot be considered the only driver of the change in plant traits and species distributions (Wyse et al. 2013).

The amplification of the soil infertility caused by the acidic litter of kauri does not significantly affect the leaf trait – environment relationships in Puketī (Figure 4.9). Kauri trees and plots were removed from this analysis to determine if kauri trees were driving the regression relationships to be significant. The removal of plots that include kauri from the leaf – environment analyses reduces the overall strength of these relationships, but they are still significant. This shows that the leaf – environment relationships are driven by other processes and the feedback effects of kauri on the soil could impose another environmental filter and is one of the many processes shaping these relationships. For example, SLA is significantly, negatively correlated with soil C:N when kauri is both included ($R^2 = 0.58$, $p < 0.0001$) and excluded ($R^2 = 0.29$, $p < 0.0013$) from this relationship. This relationship is consistent with Ordonez et al. (2009) who found soil C:N alone explained 32 – 34 % in the variability in SLA among sites globally. This relationship has also been shown by Cunningham et al. (1999), who investigated leaf structure along a soil fertility gradient in New South Wales, Australia. They showed that species found on low-nutrient soils have leaves with a lower SLA than those found on more fertile soils. These two studies are consistent with the relationship of SLA and soil fertility in Puketī.

Mason et al. (2012) investigated foliar traits such as leaf nitrogen, leaf phosphorus, leaf thickness and tissue density, along a soil chronosequence where strong gradients in soil nutrient availability occur. The decline in leaf nitrogen and leaf phosphorus, and increase in leaf thickness and density, with decreasing soil fertility are consistent with this study (Figure 4.9). A similar study by Ordonez et al. (2009) also showed that there was a shift from species with low SLA, leaf nitrogen and leaf phosphorus on low soil fertility sites to species with high SLA, leaf nitrogen and leaf phosphorus on high soil fertility sites.

The leaf traits discussed above (SLA, leaf thickness, leaf nitrogen and leaf phosphorus) reflect the growth and resource conservation strategy where thicker, more conservative leaves on are found on less fertile soils and thinner, less conservative leaves are found on more fertile soils (Hobbie 1992, Mason et al. 2012). This is because faster growing species from nutrient rich habitats have a combination of high SLA, low leaf thickness, high nutrient tissue concentration, and short lived leaves. At the other end of this fertility gradient the characteristics of plants in low nutrient environments which help a plant to maximise the use of the limiting resources are longer lived leaves that have low SLA, are thicker, have low leaf nutrient concentrations and high re-sorption of nutrients from the senescing leaves (Aerts and Chapin 1999, Liu et al. 2012). These strategies are evident in Puketī due to the strong relationships and variation in leaf traits along the soil fertility gradient.

The leaf economics spectrum (Wright et al. 2004) has transformed the way ecologists quantify plant ecological trade-offs (Funk and Cornwell 2013). The leaf economics spectrum and this study show that there are relationships between key traits across a broad range of species. For example leaf photosynthetic rates are positively correlated with SLA, because a higher leaf area displayed per unit mass invested leads to more efficient light capture and shorter transport distances of carbon dioxide (Wright et al. 2004, Funk and Cornwell 2013). However the trade-off of having a high photosynthetic rate is that the leaves have a short lifespan.

Plants with low SLA have a longer leaf lifespan which allows for carbon gain over a much longer period of time than leaves with a shorter lifespan (Reich et al. 2003). These strategies are co-occurring in Puketī, because there is a range of SLA values (0.69 – 35.77 $\mathrm{mm}^2\ \mathrm{mg}^{-1}$) present along the soil fertility gradient.

5.3.2 Tree height

The investment of resources into plant height improves access to important resources such as light (Ackerly 2009), but the position of an individual tree's canopy, in relation to surrounding trees, will influence other environmental factors such as temperature, humidity and wind exposure. By maximising height, this increases light interception and taller trees are able to displace shorter trees, by making resources unavailable to their neighbours. Therefore the advantages and disadvantages of height depends on the surrounding plants and their height strategies (Westoby 1998). However, increased height comes at a cost of investment of resources for support and continuous maintenance costs for the stems and vascular tissues. The increase in height adds the associated risks of cavitation of the xylem when transporting water over longer distances (Falster and Westoby 2003, Niklas 2007, Moles et al. 2009). A study by Falster and Westoby (2003) found plant height to be positively correlated with functional traits such as SLA, which infers that tall trees are found in high fertility environments. In support of this study was the finding by Liu et al. (2012), that maximum height was positively correlated with soil fertility and negatively correlated with soil acidity (pH). My study does not support these results because maximum height was found to be negatively correlated with soil fertility (Figure 4.10). A possible explanation for this is that tall kauri – 40 m (Table 4.5) are causing this moderately weak (R^2 = 0.19) relationship to be significant. The removal of kauri trees from the tree height – environment analysis results in this relationship no longer being significant (results not shown). Without kauri, there is no height - environment relationship, which confirms that that the tall, long lived kauri trees are driving this relationship to be significant.

5.3.3 Seed traits

The variation in seed mass between species is generally understood by ecologists to be the result of a trade-off between seed mass and seed size, where producing fewer larger seeds that have a higher probably of establishing is compared to producing many small seeds that have a low probability of establishing (Westoby et al. 2002, Moles and Westoby 2006). In Puketī Forest, seed mass has been shown to increase with increasing soil fertility (Figure 4.11), therefore it could be inferred that larger seeds are produced in more fertile environments and smaller seeds are produced in less fertile environments. This relationship is consistent with the seed mass of species found in these environmental conditions with a range of seed mass values from 0.005 – 656.32 mg for species found in low fertility environments and the range of seed (and spores) mass values from 0.0008 – 1980.00 mg for species found in high fertility environments. This relationship is consistent with the positive relationship of SLA and seed mass, reported by Diaz et al. (2004), because SLA increases with increasing soil fertility, but not consistent with studies such as Westoby et al. (1996), which found that SLA and seed mass were negatively correlated. The regression of SLA and seed mass from Puketī were not significant, therefore further investigation into why seed mass and soil fertility were correlated and SLA and seed mass were not correlated is necessary to resolve this result.

5.3.4 Wood traits

Ecologists consider wood to be an important functional trait as it is indicative of a plant's life history strategy (Muller-Landau 2004, Swenson and Enquist 2007). Wood has several different, essential functions in plants including the following: support, transfer of nutrients and water, storage of nutrients, carbohydrates, defensive secondary compounds, lipids and water (Chave et al. 2009). In Puketī Forest, wood density ($R^2 = 0.46$, $p < 0.0001$) and wood dry matter content ($R^2 = 0.58$, $p < 0.0001$) have been shown to be strongly, negatively correlated with soil fertility and bark thickness has been shown to be strongly, positively correlated with soil fertility ($R^2 = 0.62$, $p < 0.0001$). This indicates that individuals found in low fertility environments have denser wood and thicker bark than trees found in higher fertility environments. As mentioned previously, kauri has a feed-back effect on environmental conditions as a result of the acidic litter produced, however, these environmental conditions do not significantly affect any of the wood traits measured. This shows that any environmental filtering effects imposed by kauri are not significantly influencing wood traits (Figure 4.12).

The relationships between wood traits and environmental variables presented in this study have also been shown to occur in various other studies including Gourlet-Fleury et al. (2011) who observed how soil type affects species traits, such as wood density, in a moist Central African Republic forest. The results from this study showed that resource-poor soils favoured slower growth rates and dense wooded species, whereas resource-rich soils favoured faster growth rates and lighter wooded species. This relationship is also consistent with the results measured by Muller-Landau (2004) in four Neo-tropical forests in Costa Rica, Panama, Peru and Brazil and a sub-tropical evergreen broad-leaved forest in northern Taiwan by Lasky et al. (2013).

There are numerous trade-offs for wood traits such as wood density, which will influence the competitive ability of a plant, the resistance to stress and conduit efficiency (Chave et al. 2009). Species that have low wood density are typically found in more fertile environments due to the fast-growing, resource-acquiring strategy that the plants have (Quesada et al. 2009, Gourlet-Fleury et al. 2011, Richardson et al. 2013). This is because plants with larger vessels are able to support a larger leaf area per unit sapwood, therefore plants with bigger conduits are able to supply nutrients and water efficiently to a large total leaf area (Chave et al. 2009). However, the trade-off of having large vessels is a lower wood density, which makes plants less resistant to disturbance and drought induced cavitation (Quesada et al. 2009). The need for a fast growth rate and the ability to compete for available resources, such as light, can result in a lower level of investment in structures such as wood (Swenson and Enquist 2007). Trees that have a slower growth rate and low species turnover, such as in low fertility soils, need to have a higher investment in long term structures in order to support tall, long term canopies. Slow growing species have a higher mechanical strength, which allows them to be more resistant to disturbances and drought induced cavitation (Swenson and Enquist 2007, Curran et al. 2008). The conflicting demands on wood structure depend upon the environmental conditions, therefore a wide range of wood densities are found along an environmental gradient.

The outcomes of this section advance our knowledge and understanding of community assembly because we are able to determine how species traits relate to environmental variables and how they change along the gradient. This section also shows that traits are filtered along the gradient. Species that have high SLA, low leaf thickness, high leaf and litter nitrogen, high seed mass and low wood density are found on soils with higher nutrient availability and species with low SLA, high leaf thickness, low leaf and litter nitrogen, low seed mass and high wood density are found on soils with lower nutrient availability. The change in functional traits along the soil fertility gradient is strong evidence for environmental filtering.

5.4 Functional diversity

Community assembly along environmental gradients is driven by two antagonistic processes that select functional traits in opposing directions (Laughlin et al. 2012). These are environmental filtering and limiting similarity. This study aimed to determine the influence of environmental filtering, which selects individuals with functional traits that yield the highest fitness and performance for the given environmental conditions. This process increases functional similarity of species within a community, resulting in trait convergence. The effect of environmental filtering is that it results in a clustered community structure, where species with similar traits occur together more often than could be expected by chance (Laughlin et al. 2012). Examples of environmental filters include climate, topography, soil and disturbances (Freschet et al. 2011).

From this study it is evident that environmental filtering of both leaf and wood traits is occurring in Puketī Forest. This is because there is a change in community-weighted means, species distributions and trait values along the soil fertility gradient. The change in trait values at each plot along the soil fertility gradient is evidence for environmental filtering, because only certain traits will exist at a site due to being filtered out by the environmental conditions. As a result of the trait selection through environmental filters, the community-weighted mean will vary along the gradient, because the relative abundances of species will change due to the size and strength of the environmental filter, but also the ability of a species to be competitive along the environmental gradient (Gourlet-Fleury et al. 2011, Laughlin et al. 2012, Lasky et al. 2013).

An example of a leaf trait that is filtered along the soil fertility gradient is SLA (Figure 4.6 and Figure 4.13). This is because there is a continuous turnover of species and their distribution along the gradient, which will result in a change in the community-weighted mean of SLA. The strength of soil fertility as a filter on SLA is strongest in the low fertility soils and weakest in the more fertile soils. This is because trait convergence (small variation) is occurring in the less fertile soils. Studies such as Wright et al. (2004), Ackerly and Cornwell (2007), Laughlin et al. (2011) and Dwyer et al. (2013) also show that is SLA is filtered along environmental gradients.

Wood traits, such as wood density, are also filtered along the soil fertility gradient in Puketī Forest. However, the influence of soil fertility as a filter on wood density is not as pronounced as on leaf traits. This is shown in Figure 4.14, where there is only a subtle decrease in the mean wood density from low soil fertility to high soil fertility. Wood density has been shown to be filtered along environmental gradients in studies by Chave et al. (2006), Preston et al. (2006), Gourlet-Fleury et al. (2011) and Laughlin et al. (2011).

Functional diversity indices such as functional richness, functional evenness, functional divergence and Rao's quadratic entropy (RaoQ) are useful in determining changes in community assembly and determining the influence of processes such as environmental filtering along environmental gradients (Mason et al. 2013). Functional richness indices aim to measure how much of the niche space available is occupied by the species present within a community (Mason et al. 2005, Schleuter et al. 2010). The indices of functional richness in Puketī are correlated with soil fertility (Figure 4.15). Plots that were measured in more fertile environments were calculated to have a higher functional richness index than plots that were measured in less fertile environments. However, it is important to measure multiple functional indices because functional richness can increase without any change to assembly processes due to change in species richness (Mason et al. 2005).

Functional evenness indices measure the distribution of species traits within the occupied niche space (Mason et al. 2005, Schleuter et al. 2010). The indices of functional evenness in Puketī are correlated with soil fertility (Figure 4.15) and plots that were measured in more fertile environments have a higher functional evenness index, indicating that there is regular distribution of species traits. Plots that were measured in less fertile environments have a lower functional evenness index and therefore a less regular distribution of species traits (Villéger et al. 2008, Schleuter et al. 2010).

RaoQ is an index that combines both functional richness and functional divergence. This index incorporates both the distribution of species and their traits in trait space as well as the volume of functional trait space occupied (Mason et al. 2012). RaoQ is significantly correlated with soil fertility in Puketī (Figure 4.15).

Higher RaoQ indices were calculated for plots measured in more fertile soils, which suggests that functional divergence is positively correlated with soil fertility. Functional divergence measures the degree to which the distribution of species abundances of a community is distributed towards the extremities of occupied trait space (Mason et al. 2005, Schleuter et al. 2010). However when these indices are plotted against the soil fertility gradient of Puketī it is not strictly significant (Figure 4.15). Lower RaoQ indices were calculated for plots in low fertility soils, which indicate that the dominant species in these environmental conditions converge on similar trait values (Villéger et al. 2008, Mason et al. 2012). This is consistent with traits such as SLA (Figure 4.13), which shows trait convergence in low fertility soils.

A recent study by Mason et al. (2012) showed that functional divergence, functional evenness and RaoQ decreased with decreasing soil fertility, which are the same functional diversity indices relationships to those calculated in Puketī. These indices show that trait variability varies along the soil fertility gradient and that there are different community assembly processes driving the assemblage of traits and therefore the species that are present. In low fertility soils, environmental filtering results in convergence towards traits where the outcome is a resource-retaining strategy. This strategy is essential because for a species to be dominant in these low fertility environmental conditions efficient nutrient retention and nutrient scavenging is important. Environmental filters are weaker in the more fertile soils, resulting in co-occurring species having a broader range of functional trait values (Mason et al. 2012).

Chapter Six: Synthesis

6.1 Conclusions

The overall objective of this thesis research was to test the importance of traits in mediating the relationship between topography, soils and community composition. Previous kauri forest research (Burns and Leathwick 1996) showed that community composition was driven by topography. This thesis shows that those observations were driven by environmental filtering of functional traits along a topographically-driven soil fertility gradient. The main environmental variables that are influencing species distributions are soil C:N, total soil phosphorus and soil pH. Puketī is considered to have a number of different forest types, however, due to the continuous distribution and turnover of species along the gradient, there are few abrupt changes in forest types that occur, with the exception of kauri-dominant stands. Kauri stands and associated species form a unique forest type, due to the presence of low fertility, highly acidic soils, which are reinforced by the acidic kauri litter that results in slow decomposition and nutrient cycling (Wyse et al. 2013).

It has been widely shown throughout the literature that there are relationships among leaf, height, seed and wood traits and that not all traits are independent of each other. As a result of these relationships, there are three distinct groupings of species in Puketī. The first group includes gymnosperms such as *Agathis australis*, *Halocarpus kirkii*, *Dacrydium cupressinum* and *Podocarpus cunninghamii* and angiosperms such as *Elaeocarpus dentatus*, *Knightia excelsa* and *Beilschmiedia tawa*, which have associations and trait overlap with these species. The second group is made up of species that are typically associated with gully habitats such as *Vitex lucens*, *Corynocarpus laevigatus*, *Laurelia novae-zelandiae*, *Melicytus ramiflorus* and *Dysoxylum spectabile*. The last group includes tree ferns such as *Dicksonia squarrosa*, *Cyathea dealbata*, *Cyathea smithii*, *Cyathea medullaris* and the single palm species (*Rhopalostylis sapida*). These groupings of species are the result of different life history strategies, ranging from resource-retaining to resource-acquiring strategies (Laurance et al. 2010, Mason et al. 2012).

This study has shown the influence of environmental filtering on traits and community composition, because there is a change in community-weighted means, species distributions and trait values along the soil fertility gradient (Shipley et al.

2006). Removing kauri from this analysis, for both leaf and wood traits, the strength of the relationships decreased, but all but one relationship were still significant. From this study it is evident that environmental filtering of both leaf and wood traits is occurring in Puketī Forest.

Changes in functional diversity indices indicate that the strength of environmental filtering changes along the soil fertility gradient (Mason et al. 2013). These indices show that trait variability does vary along the soil fertility gradient and that there are different community assembly processes driving the assemblage of traits and therefore the species that are present. In low fertility soils, environmental filtering results in convergence towards traits that result in a resource-retaining strategy. Environmental filters are weaker in more fertile soils, resulting in co-occurring species having a broader range of trait values.

6.2 Applications

This study helps to increase the understanding of forest dynamics, as it links community assembly with traits and environmental variables. By understanding how environmental variables determine the traits that are present, which influences the species that are present, it will give a better indication on how to restore forest ecosystems. If we can determine the suite of traits that are, or should be, present within a forest, based on environmental variables such as soil or topography, then the forest can be managed appropriately, rather than trying to introduce species that do not have traits that would make a species competitive or able to tolerate the given environmental conditions (Funk et al. 2008).

Understanding the distribution of traits and species along an environmental gradient can also be used to help manage forests where herbivores are present. This is because more palatable leaves (higher SLA and high nitrogen content) will be found in the more fertile environments (gullies). Herbivory by ungulates has the potential to alter the functional composition and diversity of plant communities through their selection of palatable plants with high leaf nutrient concentrations and low resource allocation to structural or chemical defences (Lloyd et al. 2010, Mason et al. 2010).

This research can also be used to assess the impacts of global change on species and communities. Having a detailed record of the species that are present within a forest through the use of permanent plots will show how species abundances, distributions and growth rates change over time. This will allow for the effects of climate change such as variations in temperature, precipitation and atmospheric carbon dioxide levels, to be documented.

6.3 Recommendations for future research

In order to gain a greater understanding of the processes and relationships that are occurring in Puketī Forest it would be beneficial to investigate the differences in above and below ground (root) strategies that plants have and how these change along this fertility gradient. Roots are the organs of plants that are in direct contact with the soil and therefore root traits will determine the ability of a plant to acquire essential resources. Studying root traits will help to further understand species distributions along an environmental gradient.

This study occurs only along a soil fertility gradient in a single forest. These findings should be compared with other studies in New Zealand along a broader range of environmental gradients, such as precipitation and temperature and in different forest types, such as beech and other mixed podocarp – broadleaf forests that do not include kauri.

Quantifying mechanisms that determine spatial variation, species abundance and community composition is a central goal in ecology. This study indicates that environmental filtering drives community assembly in Puketī. The Traitspace model, proposed by Laughlin et al. (2012) could incorporate this data to predict species abundances and then compare them with actual species abundances measured in this study. This modelling exercise will help improve ecological models and further our knowledge and understanding of trait-based community and species distributions.

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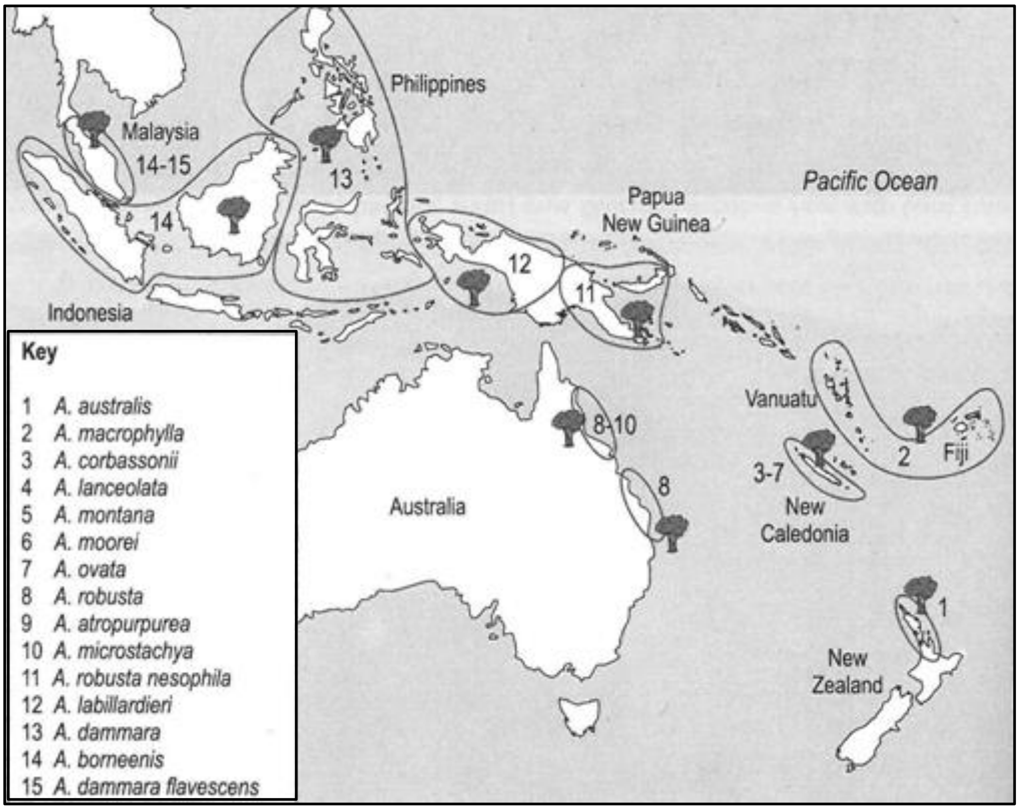
Appendix: The ecology and history of New Zealand's kauri (*Agathis australis*)

This appendix provides an overview of the morphology, distribution, species interactions, regeneration and succession of kauri forests. Also outlined are the human influences on kauri, in particular the significance to Māori, early European settlers and logging and the most recent threat to these forests – kauri dieback. There is a continuous compositional change along the environmental gradient in Puketī Forest and consequently there are few visually abrupt changes that occur between forest types. The one exception to this is kauri dominant stands, where there is an abrupt boundary change from broadleaved-dominant forest to kauri-dominant forest. The distinct and abrupt change to a kauri stand is due to the influence that kauri have on soil processes beneath the canopy such as reducing soil pH, slowing down of nutrient cycling processes and the formation of thick, acidic litter layers. Kauri trees are one of the dominant species in Puketī and because of this, their ecology and history are important components in understanding community assembly in Puketī Forest.

Introduction

New Zealand has four families of indigenous conifers. These are Araucariaceae, Cupressaceae, Podocarpaceae and Phyllocladaceae. Araucariaceae is an ancient family that is largely restricted to the tropics and subtropics of the Southern Hemisphere, excluding southern Africa. This family was widespread in both hemispheres throughout the Mesozoic era, but disappeared from the Northern Hemisphere at the time of the extinction of the dinosaurs, during the Cretaceous period. There are three genera (*Araucaria*, *Agathis* and *Wollemia*) in this family. The genus *Agathis* contains 21 species, which are distributed throughout Sumatra, Malaysia, Borneo, Philippines, New Guinea, Australia (Queensland only), Solomon Islands (Santa Cruz only), Vanuatu, New Caledonia, Fiji and northern New Zealand (Appendix Figure 1.1). This review will focus on a single species in this genus, *Agathis australis* (D. Don) Lindl. ex Loudon, (henceforth kauri) which is endemic to New Zealand (Ecroyd 1982, McKenzie et al. 2002, Dawson and Lucas 2011).



Appendix Figure 1.1: Distribution of *Agathis* species (figure taken from Orwin (2004)).

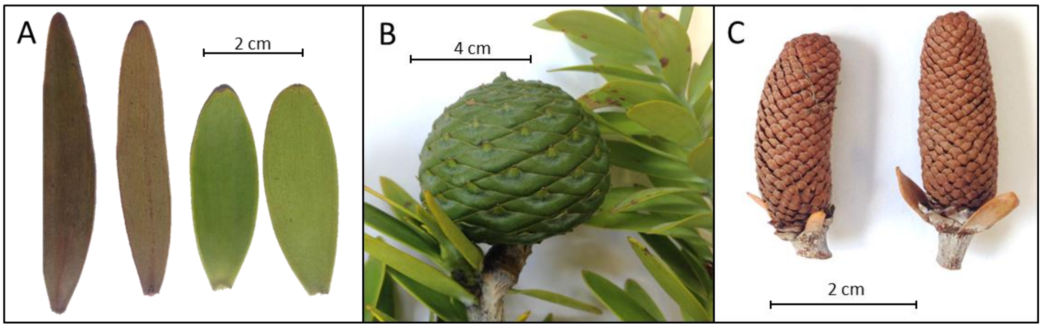
Kauri morphology

Kauri are monoecious trees that reach heights of 30 – 50 m in the emergent layer of a forest and have trunks that are 100 – 400 cm in diameter (Allan 1961, Dawson and Lucas 2011). This is the largest species of the genus *Agathis*, with giant individuals exceeding 1000 years in age. Tāne Mahuta “God of the Forest” (dbh 4.4 m, height 51.5 m and stem volume 248 m^3) and Te Matua Ngahere “Father of the Forest” (dbh 5.9 m, height 29.9 m and stem volume 210 m^3) are the two largest living kauri in New Zealand and are located in Waipoua Forest, Northland. The largest kauri tree in Puketī Forest is Te Tangi o Te Tui, which is the fourth largest living kauri tree (Orwin 2004, Beever et al. 2007, Boswijk 2010).

Kauri trees have juvenile and adult stages. Young trees, known as rickers, have narrow conical shaped crowns and short whorled branches around the whole length of the trunk. As the tree grows, the lower branches are shed in a self-pruning process. This juvenile stage can last for 50 years or more. When the rickers reach maturity, the crown branches, forming a flat topped crown that dominates over the rest of the canopy. Crown branches can be more than 1 m in diameter and support an abundance of epiphytes (Ecroyd 1982, Dawson and Lucas 2011).

In most conifers, the trunk is cylindrical and tapers with height. However, the trunk of a kauri is columnar with little or no tapering with height, making them a favourable logging tree, due to the large volume of clear wood contained within their trunk. The bark of these trees is silvery-grey and, in mature trees, large, thick flakes fall off leaving hollows in the trunk (Allan 1961). Kauri exudes resin known as kauri gum, which flows from wounds on the tree, as well as from cones, branchlets and the base of leaves (Dawson and Lucas 2011).

The juvenile and adult foliage of kauri are very different (Appendix Figure 1.2). Juvenile leaves are long, narrow and often bronze coloured, whereas adult leaves are wider, shorter and bright green in colour. Both leaf types are stiff, tough and leathery. They have parallel veins, a smooth margin and are round to pointed at the tip. The leaves of juvenile trees are arranged in opposite pairs, whereas adult leaves are arranged in a spiral around the branchlet (Dawson and Lucas 2011).



Appendix Figure 1.2: Morphological features of kauri. (A) comparison of the long, bronze juvenile foliage and the bright green adult foliage. (B) female cone. (C) male cones.

Fallen leaves, branchlets and bark flakes build up a layer of litter around the trunk, which can be as deep as 3 m. The litter of kauri is very acidic, which promotes leaching of nutrients from the soil (Dawson and Lucas 2011).

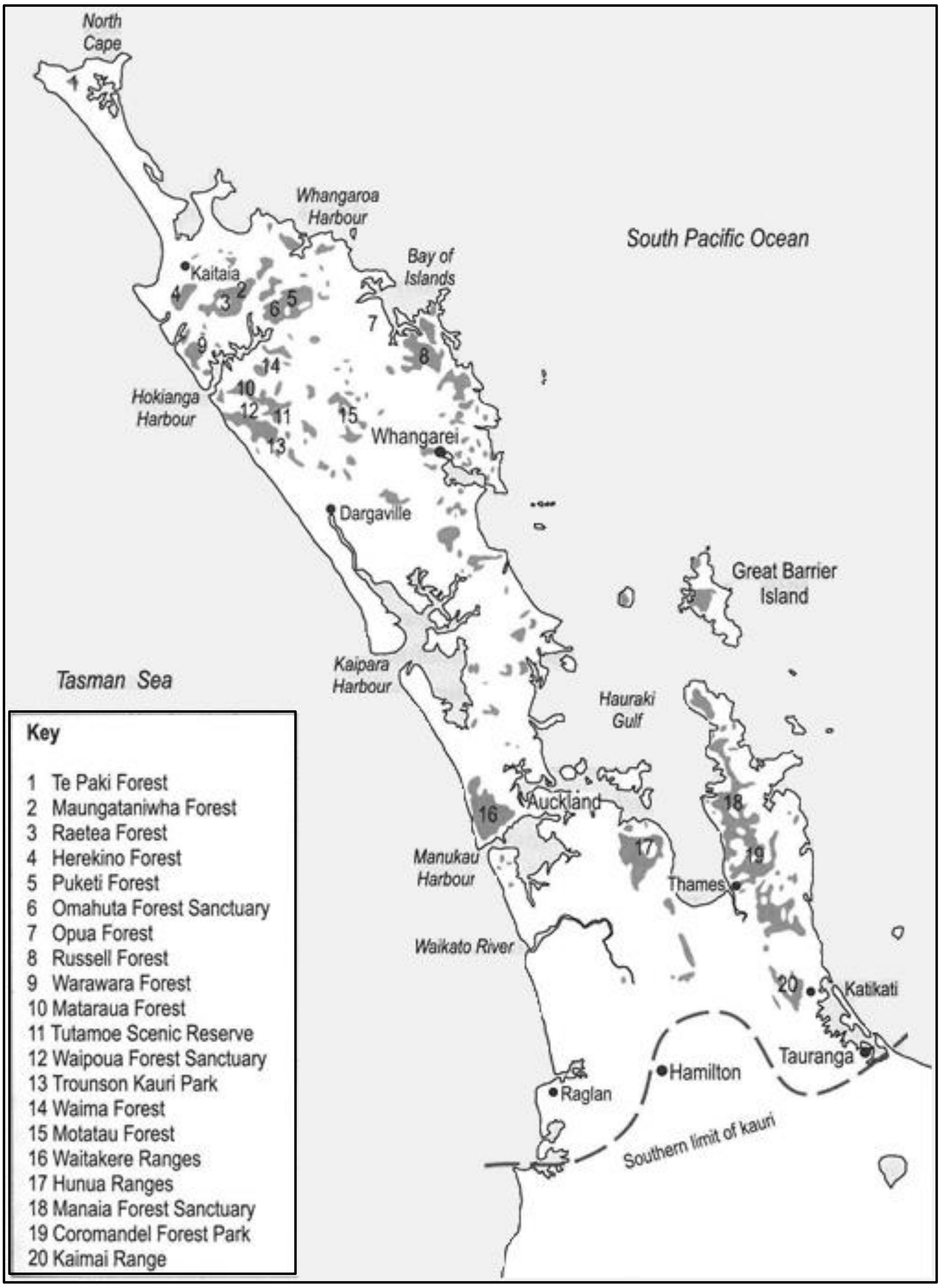
The female cones are green, globulose and have a diameter of 5 – 7 cm. Pollen cones are cylindrical and 2 – 5 cm long (Appendix Figure 1.2). The reproductive cycle of kauri is slow as it takes approximately 19 – 20 months from pollination in October to seed maturity in February or March of the second year following pollination. Trees are generally twenty five years old before they begin to produce fertile seeds (Owens et al. 1997). When the female cone is mature the scales open, releasing single winged seeds, which are carried away by the wind. Seeds remain viable for only a few months, therefore they germinate quickly when they reach the forest floor (Ecroyd 1982, Salmon 1996).

Spatial and temporal distribution

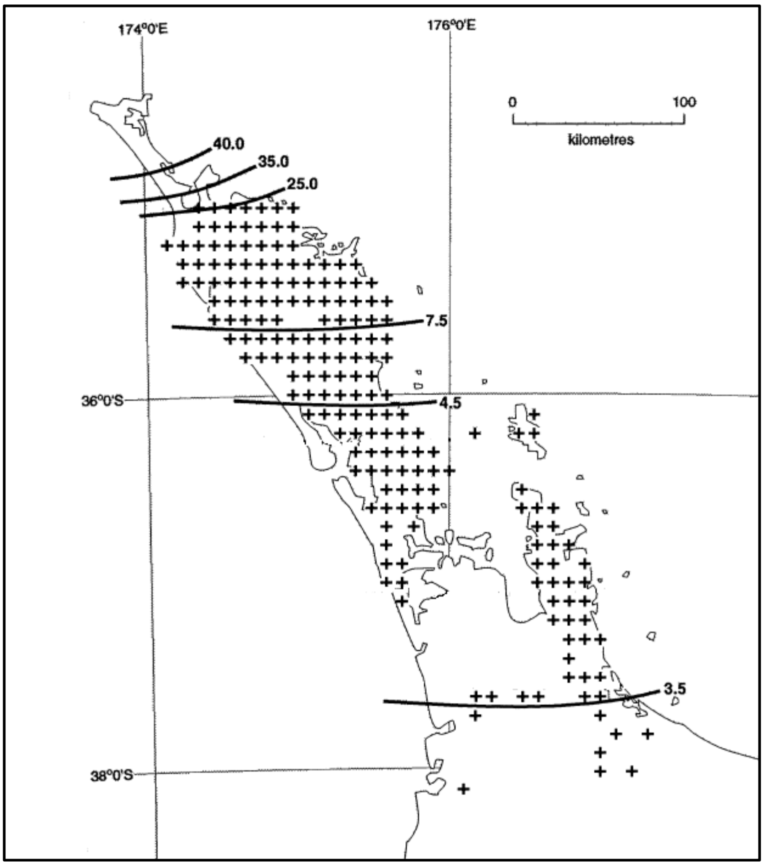
Kauri grows naturally in the warm, northern districts of New Zealand. It has a southern limit of approximately 38^{o} S latitude, which corresponds to a line from Kawhia Harbour through Hamilton and a little south of Tauranga (Appendix Figure 1.3) (Salmon 1996, Orwin 2004). These are mainly lowland plants that grow at elevations of 150 – 400 m, but can be found in stunted forms at 800 m on the Coromandel Peninsula (Dawson and Lucas 2011).

The present and past distribution of a species is determined by a complex interaction between biotic and abiotic factors (Mitchell 1991). At the peak of the last glacial maximum (the late Otiran stadial period) during the Holocene approximately 18,000 – 22,000 years ago, the climate of New Zealand was very different to the present. This resulted in substantial changes to the vegetation of New Zealand and as a consequence forest cover declined dramatically (Ogden et al. 1992, Newnham 1999). It is thought that kauri trees survived this glacial period in a few isolated remnant areas in the far north. This is because radiocarbon dating from wood samples preserved in swamps and pollen records show that forest cover was restricted during this time (Ogden et al. 1992).

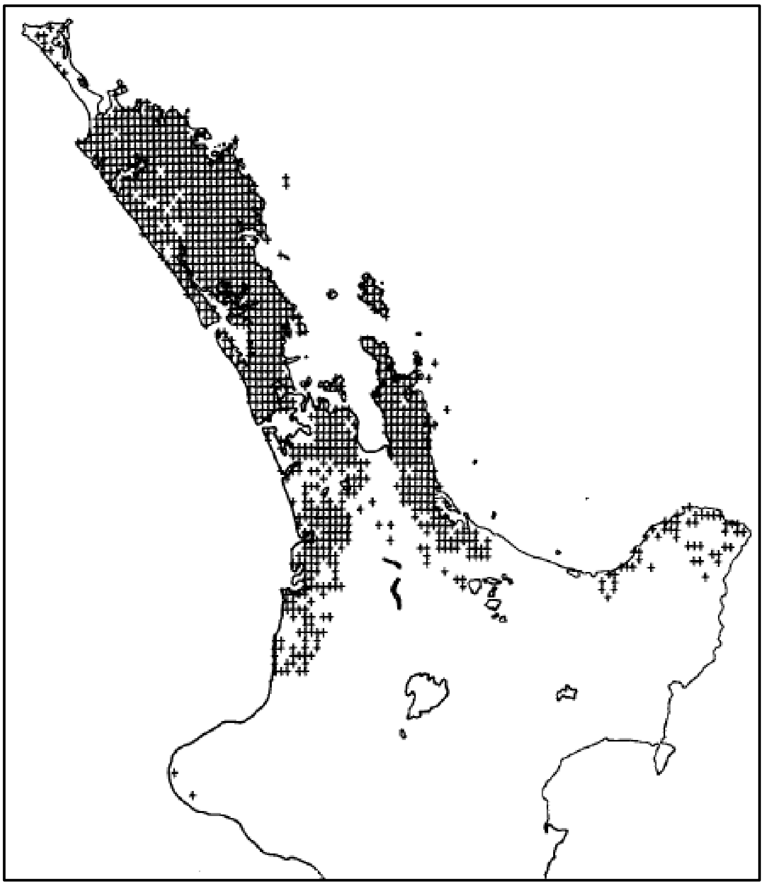
The expansion of kauri southwards occurred during the mid to late Holocene commencing 7,500 years before present and reaching its maximum distribution approximately 3,500 years before present (Appendix Figure 1.4). The late Holocene records show an increase in kauri pollen as well as *Phyllocladus* and *Libocedrus* pollen, indicating that the expansion southwards was of a mixed kauri forest community (Newnham 1999). Kauri trees were present on North Kaipara Head approximately 7,000 years before present, which is the earliest Holocene wood date. Radiocarbon dating of wood shows that kauri was present in Omahuta State Forest approximately 7,400 ± 200 years before present. Holocene dates > 5, 000 years before present are all south of latitude 35^{o} S but north of Auckland. The first date of a wood sample south of Auckland is 4,300 ± 200 years before present. Kauri became abundant in the Waikato from 4,000 to 2,000 years before present. Calculations based on these migration dates show that kauri migration southwards reached speeds of up to 197 m yr^{-1} (Ogden et al. 1992).



Appendix Figure 1.3: Southern limit of kauri and the locations of the main remaining kauri forests in New Zealand (Orwin 2004).



Appendix Figure 1.4: Holocene expansion of *Agathis australis* in thousands of years (modified from Ogden et al. (1992)).



Appendix Figure 1.5: The predicted distribution of kauri based on the climate profile in Mitchell (1991).

The present day distribution of kauri (Appendix Figure 1.3 and Appendix Figure 1.4) is different to the predicted distribution (Appendix Figure 1.5) using climatic conditions which are considered to be suitable for kauri growth. The predicted distribution of kauri extends both further south and further east than the present limits. Mitchell (1991) proposes four possible explanations for the extended distribution. These are: local micro-climates, biological effects, edaphic conditions and accuracy of the algorithm to represent the climatic conditions based on the long and short term records at each site. Local micro-climates is considered to be a possible explanation for the extended distribution because the sites predicted have climate characteristics typical of places further north. However, the predicted sites lying to the south and east of the current range may be too remote or scattered for seeds to disperse to these locations. It is also possible that other site conditions, such as soil type and drainage, could make these predicted sites unsuitable for kauri growth. The present day distribution and correct combination of factors that result in successful establishment of kauri decline with increasing latitude and so does the abundance of kauri, because the probability of establishment becomes lower than the probability of mortality (Mitchell 1991).

Species distribution within a kauri forest

The distribution and composition of species within a forest is not uniform. This is because environmental gradients such as topography, soil moisture and fertility lead to a change in vegetation composition. A study by Burns and Leathwick (1996) of vegetation - environment relationships in Waipoua Forest showed that compositional changes of vegetation within a forest is linked to soil fertility and soil moisture. This is because stable, deeply weathered soils on ridges were less fertile than soils further downslope and in gullies. The large number of species and the wide range of relationships that they form with their environment, results in few abrupt boundaries in forest composition being identified. However, gradual compositional changes are evident along topographical (soil fertility) gradients in this forest from *Rhopalostylis sapida*, *Dysoxylum spectabile*, *Corynocarpus laevigatus* and *Dacrycarpus dacrydioides* at low altitudes (high fertility) to *Beilschmiedia tarairi*, *Rhopalostylis sapida*, *Dysoxylum spectabile* and *Knightia excelsa* at mid altitudes to *Podocarpus totara*, *Quintinia serrata*, *Ixerba brexioides*, *Phyllocladus trichomanoides* and kauri at high altitudes (low fertility).

The one exception to this is kauri dominant stands, where there is an abrupt boundary change from broadleaved dominant forest to kauri dominant forest. The distinct and abrupt change to a kauri stand is due to the influence that kauri have on soil processes beneath the canopy such as reducing soil pH, slowing down of nutrient cycling processes and the formation of thick litter layers (Wyse et al. 2013).

Regeneration and succession

The view that kauri has scarce, natural regeneration in a mature stand is an idea that persists throughout the literature. In a survey of the Waipoua Forest, Cockayne (1908) commented that there were no kauri between seedling size and mature trees. Cheeseman (1914) also noted that young kauri were not commonly found in groves of mature kauri. Cheeseman (1914) and Cockayne (1958) suggested that the reason behind the scarce regeneration in a mature stand, is because the amount of light was not sufficient for the growth of the young trees, due to kauri being a strongly light demanding species as a seedling. Bieleski (1959a) showed that Cheeseman and Cockayne were not correct in their suggestion, as Bieleski’s field and glasshouse experiments show that kauri can survive and grow at light intensities as low as 2% of full sunlight, but they will grow more rapidly in higher light environments. The light compensation point for seedlings grown in glass house conditions is 0.9%, whereas in the field experiment the light compensation point for seedlings is 1.5% of full sunlight. Bieleski suggests that low light alone is not responsible for the low numbers of regenerating kauri and soil temperature, moisture, mycorrhiza and podsolization of the soil by mature kauri, could be factors that hinder establishment and regeneration (Bieleski 1959b).

Kauri is one of many species that considerably influences the properties of the soils beneath them by modifying variables such as soil nutrient availability, pH, and moisture levels. The leaf litter and bark flakes that are shed by individuals, along with slow decomposition rates, leads to the build-up of thick layers of organic material (up to 3 m thick) within a kauri forest. The large quantity of organic material, along with the acidic (pH 4), tannin-rich litter, creates acidic, infertile and highly podsolized soils that leads to the modifying of environmental properties, which can potentially influence the development of understorey vegetation through exclusion of species. This can create a distinct vegetation patch that can enhance biodiversity with a forest fragment (Verkaik et al. 2007, Wyse 2012, Wyse et al. 2013).

Mature kauris are generally accompanied by a predictable and unique group of plant taxa such as *Astelia trinervia*, *Brachyglottis kirkii*, *Dracophyllum latifolium*, *Leionema nudum* and *Leucopogon fasciculatus*. This distinct vegetation assemblage is often surrounded by vegetation that is dominated by different broadleaved angiosperms such as *Beilschmiedia tarairi*. Wyse (2012) investigated the influence of the soil environment beneath mature kauri on the growth of a number of forest species, to assess whether soil could be a factor contributing to the observed vegetation patterns and associations. This study used seedlings of five plant species (*Corokia buddleioides*, *Dacrydium cupressinum*, *Geniostoma ligustrifolium* var. *ligustrifolium*, *Melicytus ramiflorus* and kauri), which are all found in a kauri forest, but with differing degrees of association with the kauri trees. The results showed that the kauri soils had a slightly negative impact on the growth of *Dacrydium cupressinum*, and a very negative impact on *Melicytus ramiflorus* and therefore could be a factor used to explain this species frequent absence in kauri forests. *Corokia buddleioides* (kauri associated species) and *Geniostoma ligustrifolium* var. *ligustrifolium* (kauri independent species) were neither advantaged nor inhibited by the soil conditions produced by mature kauri. The soil conditions created by mature kauri were of no direct advantage to kauri seedlings. A potential explanation for this is that by modifying the soil environment in order to disadvantage competitors, it will benefit kauri seedlings by reducing competition (Wyse 2012).

Mirams (1957) study in the Waitakere Ranges also indicated that there is a lack of naturally regenerating seedlings in a mature kauri forest. However, in other areas of this forest where the mature kauri has been cut down and *Leptospermum* scrubland is present, there is an abundance of regenerating young kauri. Over time, as the *Leptospermum* community develops, the abundance of kauri increases and eventually a ricker community forms and develops into a mature stand. As a consequence of this, there is a decline in the regenerative capacity of kauri in the ricker and mature stands, compared to under the *Leptospermum* community. If a kauri forest is to be considered a climax community, it must be capable of replacing itself. This is because a climax community represents the last stage of succession and in order to prevent the community composition from changing as the older individuals die, they must be replaced by their own seedlings. However, the climax and stable community ideas are no longer viewed favourably as we now have a more dynamic view of forest succession. This is because the processes of growth, death and replacement as well as natural disturbances ensure that ecosystems and communities are dynamic (Pickett and White 1985).

There are numerous ideas about the timing and occurrence of kauri forests in relation to succession and climax communities. Cockayne (1928) proposed the succession theory, which implies that kauri in any one area is temporary because it is one generation, and therefore the location of groves of mature kauri will vary through time, tracing the history of major disturbances. Cockayne (1958) furthers his succession theory by stating that kauri is a seral species on the way to the climax community, which is a forest dominated by *Beilschmiedia tarairi, Beilschmiedia tawa* and *Weinmannia silvicola*. This is because these species are able to successfully establish under stands of kauri. From the previously mentioned studies, kauri would not be considered a climax community. The idea that a kauri forest might not be the climax community could be used to explain the lack of replacement and low numbers of seedlings and saplings in a mature forest.

In contrast to Cockayne’s theory is the climax theory by Latter (1932), who studied kauri in Puketī Forest, before many of the areas were logged. Latter suggested that natural regeneration of kauri occurs in gaps formed by the felling of large trees. Regeneration in these gaps is by a group of small, even aged kauri trees, which eventually will give rise to one or two mature trees. The evidence for this theory was the presence of several patches of evenly aged pole-sized kauri, similar to the area of the crown of a mature tree. This theory suggests that kauri is present before the *Leptospermum* community establishes and that kauri is able to regenerate under their own canopy.

The study by Ogden et al. (1987) in Trounson Kauri Park, located in Kaihu Valley, north of Dargaville, supports a cohort regeneration model in which dense regeneration occurs in successional communities after large-scale disturbances. After a disturbance, even-aged stands develop, which leads to a self-thinning ricker stand, under which seedling recruitment is rare, creating a localised re-generation gap. Continued mortality of kauri within the initial survivors creates new canopy gaps, allowing a second wave of recruitment to occur. However, it is important to note that not all gaps within a kauri forest are recolonised by kauri.

Twenty gaps of various ages in Trounson Kauri Park were investigated and the results showed that only approximately 5 – 15 % of kauri tree falls are recolonised by kauri. The remainder are colonised by shorter lived, hardwood species. The low efficiency of gap capture of kauri is balanced by the longevity (≥ 600 years) of this species. Multiple recruitments of kauri in the same gap allows them to occupy an area for 1500 to 2000 years, which is long enough, that a large-scale natural disturbance in the form of a storm, fire or landslide occurs to reinitiate this process through gap formation.

Human influence on kauri

Significance to Māori

Kauri is an important feature in Māori culture and in the creation of their legends. One of the Māori legends about the creation of Ranginui, the sky father, and Papatūānuku, the earth mother features kauri. The legend states: at the beginning of time it was all darkness, because Ranginui and Papatūānuku clung together, trapping their sons in the darkness between them. Endless time passed before the sons, desperate for light and space, agreed to separate their parents. The strongest child, Tāne Mahuta (the god of the forest), pressed his shoulders against his mother and pushed upwards with his powerful legs, separating his parents and allowing light to enter, bringing life to the world. Northern Māori tribes state that the legs of Tāne Mahuta are the trunks of the kauri trees, because they are described as holding the earth and sky apart (Orwin 2004).

Early Europeans and logging

The early Europeans who arrived in New Zealand from the late 1700’s were impressed with the quality of kauri timber and by the mid 1820’s heavy logging of kauri trees was well underway, with timber merchants, pit sawyers and ship builders setting up stations along the coastal regions of Northland. The increase in European settlements around 1840, created a demand for sawn timber for construction. This demand for timber drove the increased production in steam-driven sawmills along the margins of deep water harbours and waterways, throughout the kauri regions of Northland. Sea-going ships and coastal scows, built from the logged kauri, served the expanding export and timber industry, collecting floating logs from within the harbours. From the 1870’s to the 1910’s, sawmilling was one of the biggest employers of workers in the Auckland and Northland regions (Reed 1964, Mackay 1991, Orwin 2004).

Due to the immense size of kauri, extracting logs from the remote and rugged bush was a physical and dangerous job. Early loggers cut felled trees into manageable lengths and used levers, timber jacks, and blocks and tackle to roll them into stream beds. The logs accumulated in the streams until natural floods floated them downstream and out into harbours, where they could be collected by scows and processed. Some were then exported offshore to destinations such as Australia, the United States, Mauritius, Great Britain, the Pacific Islands and China for furniture, street paving, railway, ship and building construction. However, transporting logs using streams and rivers depended on ample rain and in dry spells sawmills could not be supplied with enough timber and the mill workers were laid off (Reed 1964, Mackay 1991, Dawson and Lucas 2011).

To speed up the transportation of felled logs, skilled bushmen in the 1850’s used the timber they felled to build dams on site, along the streams to simulate natural floods. An estimated 3,000 dams were built throughout the kauri regions, mostly in the steep terrain of the Coromandel Peninsula, but also in the Waitakere Ranges and around Kaeo and Hokianga regions. This was a very efficient way of transporting kauri to the harbours, however many logs were destroyed or lost during transport. In the later years of kauri logging, bullocks, steam haulers and tramways replaced the use of dams (Reed 1964, Mackay 1991).

The intense logging that has occurred within the kauri forests of New Zealand has resulted in the majority of the original kauri being removed and the landscape transformed from forest to farmland. It is estimated that only approximately 4 – 5 percent of the kauri forest existing when the Europeans arrived still remains. The kauri remnants are generally found on sites with poor soils, on spurs, ridges and plateaus, often in steep, broken terrain. These are the areas that were not easily accessible to loggers, or the land was not productive enough for farming. Heavy logging of kauri forests stopped in the mid to late 1900’s, as there was growing concern for the survival of the remaining native forest. However, the high value of kauri and demand for timber for railways meant that the easily accessible forests were still exploited. It was not until the kauri forests were protected as state forests that old growth stands were safe. Examples of remnants of old growth forests (Appendix Figure 1.3) include the Manaia Sanctuary in the Coromandel

Peninsula and Puketī and Waipoua Forest in Northland (Orwin 2004, Stewart 2008).

Kauri dieback

In 2006 a microscopic soil-living, root rot water mould known as *Phytophthora* taxon *Agathis*, which is one of five *Phytophthora* species recorded in soil or kauri forests in New Zealand, was found in a stand of regenerating kauri on the Maungaroa Ridge in the Waitakere Ranges near Auckland City. Infected trees show yellowing of foliage, canopy thinning and bleeding of resin from the lower trunk and the major roots, which can lead to tree death. This disease is spread by soil and water movement, which is enhanced when humans and animals spread infected soil over large areas through feet, fur and boots. Natural spread would be much more localised and much slower. Kauri dieback is serious because it causes trees to weaken and die, and it can kill trees and seedlings of all ages. This disease poses a threat to individual iconic trees, as well as to entire stands and populations of kauri. This will have flow on effects to kauri ecosystems. For example the death of kauri is likely to lead to a shift towards dominance by podocarp tree species, which are present in the affected sites, but appear unaffected by the disease, such as *Dacrydium cupressinum* (Beever et al. 2007, Ducey 2010).