Restoration of three indigenous forest types in Tauranga City, New Zealand

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Abstract

This research examined the current state and developmental trajectory of forest restoration projects in Tauranga City with the aim of establishing whether they will eventually develop into functioning forest ecosystems similar to their natural counterparts. Three forest types historically present in Tauranga were studied: coastal *Metrosideros excelsa* forest, semi-coastal broadleaved forest, and semi-coastal *Dacrycarpus dacrydioides* swamp forest.

Forty-five variable-area plots were established in thirteen categories comprising at least two planted sites of different ages for each forest type, naturally regenerating sites within the city, and old-growth reference forests outside of the city. Vegetation parameters including tree diameters, numbers of saplings and seedlings, cover abundance and groundcover were measured or recorded. Site characteristics such as aspect and slope were also recorded. Soil samples were taken in each of the thirteen forest categories and microclimate conditions were recorded over a period of eight months using micro data loggers. Data were analysed by comparing species population structures along with diversity and naturalness in each forest category. Non-metric Multidimensional Scaling and Multi-Response Permutation Procedures were used to examine the relationships between restoration sites and reference sites in each forest type and across all three forest types. Environmental data were compared using ANOVA and relationships between physical, environmental, and vegetation characteristics were examined using Spearman rank correlations.

Results from the planted restoration sites were compared with the naturally regenerating forests and the reference forests. Coastal forest restoration sites were found to be developing into *Metrosideros excelsa* forest but recruitment of mid- and late-successional species was failing, probably due to browse from exotic animals and isolation from seed sources. This was the case even in mature *Metrosideros excelsa* forest on Mauao.

Restricted regeneration of canopy species was evident in the semi-coastal broadleaved reference sites but the reason for this was not clear. Naturally regenerating sites were being invaded by *Prunus campanulata* which has the potential to dominate the vegetation. The understorey in the restoration sites was developing through regeneration and colonisation of species that had not been planted, indicating that the vital ecosystem function of seed dispersal has been restored. However, successional canopy species were failing to recruit.

Old-growth *Dacrycarpus dacrydioides* forest at White Pine Bush was found to be on a trajectory towards *Beilschmiedia tawa*-dominated forest. Naturally regenerating swamp forest in Kopurererua Valley was dominated by *Salix cinerea* and had almost no regeneration of native species. Planted restoration sites in Kopurererua Valley and Te Maunga are likely to become *Dacrycarpus*-dominated stands but with lower stem densities than natural stands. The *Dacrycarpus*

dacrydioides in the older restoration sites at Te Maunga were beginning to naturally regenerate but seedlings are only likely to survive where there is sufficient light and reduced competition.

Across all forest types the proportion of exotic species decreased from an average of 50% in the youngest restoration sites to just 1.5% in the reference forests.

Microclimate conditions generally became more similar to reference forest conditions with increasing stand age. While younger sites had similar average temperatures and relative humidity to reference sites, the fluctuations in temperature and humidity significantly decreased with stand age from an average range of 28.6 °C and 76.7% RH in the youngest restoration sites, to an average range of 19.9 °C and 48.9% RH in the reference sites.

Recommendations relevant to the management of existing and future restoration plantings in each of the three forest types are provided.

Acknowledgements

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Chapter One: Introduction

1.1 Summary

This thesis is the result of a study to establish whether extensive restoration and revegetation plantings in the Tauranga City urban area are working. That is, will they eventually become functional forests resembling their natural forest counterparts? This study examined three forest types which would have been present in Tauranga prior to the arrival of humans: The coastal pohutukawa (*Metrosideros excelsa*) forest of the coastal fringe; the semi-coastal mixed broadleaved forest of the hillsides and ridge-tops; and the semi-coastal swamp forest of the valleys and plains. I have been personally involved in the planning and implementation of some of the plantings included in this study as well as many others in the Tauranga area and elsewhere. This study arose out of my interest in knowing whether those restoration projects will succeed.

1.2 Ecological Restoration

Humans have inflicted wide-scale damage to the planet which has significantly reduced ecosystem function and the ability of the planet to provide essential services to the species it supports (Urbanska et al. 1997; Daily 1995). Through human land use over 40% of the earth's surface has a reduced capability to provide the life-sustaining services such as food, clean air, and water which humans need (Daily 1995). In the process we have induced the extinction of many species and caused the decline of many more to critically low levels (Vie et al. 2009). In New Zealand we have lost 32% of indigenous land and freshwater birds, 18% of sea birds, 11 plant species and a number of other animal species in less than 1000 years of human habitation (Department of Conservation & Ministry for the Environment 2000). Traditionally, conservation of habitats has been the approach most commonly adopted to reduce further decline in natural ecosystems and their provision of essential services (Hildebrand et al. 2005). However, the decline has continued and conservation is no longer enough to sustain the demands of an ever increasing human population and to stop the decline in biodiversity (Hildebrand et al. 2005). The practice of restoring natural ecosystems to reinstate the essential services they provide and enhance biodiversity has recently undergone rapid growth (Young 2000), although the concept of ecological restoration has been around since at least 1935 when Aldo Leopold began the restoration of prairie grassland in Wisconsin (Jordan et al. 1987). A range of terms have been used for ecological restoration including reclamation, remediation, and rehabilitation (Hobbs & Norton 1996) but the Society for Ecological Restoration International Science and Policy Working Group defines it as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004).

The field of restoration ecology arose from the need to provide a sound scientific basis to the practice of restoring ecosystems (Urbanska et al. 1997; van Andel & Aronson 2006). Although the practice of ecological restoration is now commonplace there is no set method or recipe for successfully restoring a particular system and there is much still to learn (Sullivan et al. 2009). In fact, one of the criticisms of restoration ecology is that there is no common framework on which to base the research and that most studies are based on descriptions of individual projects with very little in the way of transferable knowledge (Hobbs & Norton 1996; Halle & Fattorini 2004). Nevertheless, by measuring the results of actual real-world projects we can help to develop ecological theory (van Andel & Aronson 2006).

1.2.1 Urban restoration

Urban environments are among those most drastically transformed by people and urbanisation often severely depletes local native species and radically alters local ecosystems (McKinney 2002). In New Zealand and elsewhere urban centres are often situated in the most threatened habitats (Miller & Hobbs 2002; Clarkson et al. 2007) and maintaining and restoring natural ecosystems in urban areas can be important for conserving and enhancing these habitats. While space restrictions in cities often mean that maintaining viable populations of native species is unrealistic, natural habitat within urban areas can help to maintain meta-populations and provide valuable corridors or other linkages with the surrounding peri-urban and rural areas (Rudd et al. 2002; Dearborn & Kark 2010; Doody et al. 2010). Restored or created habitat within cities may also provide valuable ecosystem services such as storm water retention and cleaning, and air purification (Dearborn & Kark 2010). As well as the biodiversity and ecosystem services benefits, there are social aspects to urban restoration. While public views on appropriate levels of wilderness areas in cities and suitable use of public parks vary greatly and are often disparate (Kilvington et al. 1998), natural areas within cities can provide a valuable link with nature and environmental education opportunities for city dwellers (Dearborn & Kark 2010). In New Zealand more than 74% of the population live in urban areas, and as with much of the rest of the world that number is increasing (Statistics New Zealand 2010). New Zealand's cities have on average less than 2% indigenous vegetation cover and some of this country's most threatened land environments are found in or around urban centres (Clarkson et al. 2007). Furthermore, these threatened land environments are poorly represented within the existing protected natural areas system (Clarkson et al. 2007).

While restoration of natural habitats in urban areas is warranted it is also challenging, and brings with it a unique set of problems such as the predominance of exotic weeds. The number of naturalised exotic plants has been shown to increase with proximity to human settlements (Sullivan et al. 2004; Sullivan et al. 2005) because urban environments are often the source of invasion (Lee et al. 2000). The problem of weeds is not likely to go away. In Auckland an average of 4.2 exotic plants naturalise every year (Esler 1988; Lee et al. 2000). Weed species can have a significant impact on natural regeneration (Standish et al. 2001; Smale et al. 2001) and hundreds of thousands of dollars are spent on weed control every year in Tauranga alone. Animal pests such as rats (*Rattus rattus; Rattus norvegicus*), mice (*Mus musculus*), and possums (*Trichosurus vulpecula*) can also have an influence on the restoration of natural habitats in urban areas (Overdyck et al. 2013).

Still other challenges face urban restoration projects. Urban environments are often isolated from natural vegetation in the hinterland and have much lower diversity of native plants and animals (McKinney 2002; Clarkson et al. 2007). This affects the availability of native propagules and colonisers to restorations sites (McKinney 2002; Doody et al. 2010; Overdyck & Clarkson 2012) which can in turn affect community assembly and developmental trajectory (Hobbs & Norton 2004; Sullivan et al. 2009; MacKay et al. 2011). On-going disturbance of restoration plantings by people through day-to-day use, and highly modified soils have been identified as other issues in urban restoration (Sullivan et al. 2009; MacKay et al. 2011).

Social, cultural, and political constraints are also common in urban restoration, and probably more so than for rural areas because of the higher population density. City dwellers use parkland and open space for a broad range of activities and have diverse opinions about what their green space should include which do not necessarily fit with restoration of natural habitats (Kilvington et al. 1998). For example, criminal activity associated with parks, or at least the perception that parks can harbour criminal activity, has lead Tauranga City Council to thin and heavily prune many areas of revegetation planting to reduce the opportunities for undesirables to conceal themselves (Dianne Paton, Tauranga City Council, pers. comm.). Revegetation plantings must also take into account such things as the maintenance of residents' views (Dianne Paton, Tauranga City Council, pers. comm.). On Mauao the presence of archaeological sites from early Maori settlements has reduced the area that can be restored into native vegetation because the recommended management regime for these areas is for them to remain in grazed pasture (Phillips 2003). Political and financial decisions also play a role in restoration (Halle & Fattorini 2004). For example, in times of financial downturn money is more likely to be diverted away from restoration projects, especially those run by government bodies (pers. obs.). In the Kopurererua Valley in Tauranga there is a reluctance to plant large areas in wetland species because of the on-going cost of controlling weeds which will invariably invade them (Craig Fea, Tauranga City Council, pers. comm.). These kinds of decisions are understandable and entirely necessary if restoration projects are to be sustainable in the long term.

Urban restoration is important for maintaining and enhancing biodiversity where people live and work but a wide range of constraints make it a difficult undertaking.

1.3 The process of restoration and measuring restoration success

1.3.1 The process of restoring an ecosystem

Hobbs & Norton (1996) identified seven key processes which should be considered when planning and implementing restoration projects:

1. Identify the processes leading to degradation or decline (i.e. threats or stressors).
2. Develop methods to reverse or ameliorate the degradation or decline.
3. Determine realistic goals for re-establishing species and functional ecosystems, recognising both the ecological limitations on restoration and the social, cultural, and economic barriers.
4. Develop easily observable measures of success.
5. Develop practical techniques for implementing these restoration goals at an appropriate scale.
6. Document and communicate these techniques.
7. Monitor key ecosystem variables, assess progress of restoration relative to the project goals, and adjust procedures as necessary.

These seven steps provide a generic guideline for how to proceed with a restoration project and emphasise the importance of planning in ecological restoration. Of course, ecological restoration also requires an in-depth knowledge of the subject ecosystem if it is to be successful but being able to measure success of a project within the constraints of budget and available resources can be a challenge.

1.3.2 Measuring restoration success

Being able to determine whether an ecological restoration project has been successful is important for a variety of reasons including verification of techniques or strategies, and justification of the time and money spent on the project. To be able to measure the success of a restoration there must first be a set of clear goals against which to measure ecosystem attributes (Hobbs & Norton 1996; Hobbs & Harris 2001). Setting effective and achievable goals or restoration end-points is problematic however, because natural systems are dynamic, ever-changing entities, often with multiple stable states or end-points rather than static or in some state of equilibrium (Hobbs & Norton 2004; Wallington et al. 2005).

Defining the pre-disturbance state on which to base ecosystem goals has been identified as one of the weak points of restoration ecology (Halle & Fattorini 2004). Historical vegetation pattern can be revealed using pollen records (e.g. Giles et al. 1999), or historical descriptions and aerial photographs in the case of more recent disturbance, but the use of reference sites to infer a pre-disturbance state is a well-established method (Ruiz-Jaen & Aide 2005a). Reference sites are used to help plan a restoration project, set restoration goals, and measure success (SER 2004) and are considered by some as an essential component of restoration (Aronson et al. 1995; Ruiz-Jaen & Aide 2005a). They usually comprise relatively un-disturbed vegetation and should be located as close as possible to the restoration sites and have similar environmental and physical characteristics (Hobbs & Norton 1996; Ruiz-Jaen & Aide 2005a). The use of reference sites is not without problems because any one site might represent one of many possible developmental trajectories or states based on stochastic events, site history, and local environmental conditions (SER 2004). Reference sites are also well-developed by definition, unlike sites which are in the process of being restored. This means that comparing restoration sites to reference sites is not a straight-forward process but requires some interpretation and inference (SER 2004). The SER Primer on Ecological Restoration (SER 2004) recommends using multiple reference sites, along with as much other information as is available from the literature to describe the reference state.

A range of ecosystem attributes that could indicate restoration success are outlined in the SER primer (SER 2004). These include readily measureable characteristics such as species composition, community structure, and diversity but also aspects such as ecosystem function which are less easily measured (SER 2004). Common measures of restoration success include vegetation composition and structure (Reay & Norton 1999; Wilkins et al. 2003), vegetation diversity (Hart & Davis 2011) and invertebrate community attributes (Reay & Norton 1999; Ruiz-Jaen & Aide 2006; Hart & Davis 2011), while less common ones are soil properties (Ruiz-Jaen & Aide 2005b) and trajectory analysis (Matthews & Spyreas 2010). Most authors use more than one measure although many reports of restoration projects do not include measures of success. In a review of the restoration literature Ruiz-Jaen & Aide (2005a) found that of 468 articles only 68 studies had measured restoration success in some way.

In this study single reference forests are used in most cases but the literature is used to supplement these to provide the reference systems. Vegetation structure, composition, and diversity are compared with reference systems as a measure of restoration success. In addition, soil properties and seedling composition and density as a proxy for dispersal are compared as indications of ecosystem processes. Microclimate conditions are also compared as an indication of the extent to which physical properties have been restored.

1.4 Tauranga City

Tauranga City is located in the Bay of Plenty Region of New Zealand's North Island. It is situated on a natural harbour protected from the sea by the low-lying Matakana Island. The city covers some 13,440 hectares and is home to around 111,000 people (Tauranga City Council 2013) while the neighbouring Western Bay of Plenty district has a further 45,000 residents (Statistics New Zealand 2013). The population is older than the national average with 17.4% of residents over the age of 65 (Statistics New Zealand 2013). The local authority is the Tauranga City Council. Three iwi identify Tauranga as being in their ancestral rohe: Ngāti Ranginui, Ngāi Te Rangi, and Ngāti Pūkenga.

The land on which the city is built is generally low-lying comprising coastal plains, shallow valleys, and low ridges. The underlying geology comprises recent sediments around the harbour fringe and in low-lying plains to the east, consolidated dunes along the coast, areas of older pumice and ash-rich alluvium, and poorly consolidated rhyolite ignimbrite which makes up the low hills of the central city and Otumoetai (Leonard et al. 2010).

The climate of Tauranga is warm and heavily influenced by the sea. In 2011 the mean temperature was 15.7 °C with total sunshine of 2271 hours, and annual rainfall of 1698 mm (NIWA 2012). Further climate data were collected during the course of this study (see section 2.2.2.2).

1.5 Historical vegetation of the Tauranga area

Tall forest covered as much as 85-90% of New Zealand prior to human settlement (McGlone 1989) and the Tauranga area would have been entirely forested except for areas of wetland, dunes, and coastal scrub. The Tauranga area was one of the first parts of the country to be settled by Polynesians, possibly as much as 1000 years B.P. (Stokes 1980, McGlone 1989). With the establishment of agricultural practices in the area much of the forest was burned and by the time Europeans arrived in the early 19^{th} century the area around Tauranga was either in bracken and scrub or in crops, and the bush-line was as far back as Whakamarama and Oropi (Stokes 1980). Vegetation clearance was continued by European settlers to make room for the development of farms, orchards and the city itself (Stokes 1980). Today there is very little natural vegetation left in the city and this is largely restricted to coastal sand dunes, estuarine wetlands, occasional freshwater wetlands, and secondary vegetation on steep escarpments. No reserves of original forest remain in the city; the closest is at Otanewainuku some 20km to the south and 400m higher in elevation.

Two palynology studies conducted in the area have helped to develop a picture of what the vegetation in the area was once like. Newnham et al. (1995) examined the fossil pollen record from peat taken from mires at Papamoa and Waihi Beach, while Giles et al. (1999) examined palynological evidence from Matakana Island peat. In pre-Polynesian times a mixed conifer-angiosperm forest was dominant in the area with *Dacrydium*, *Dacrycarpus*, *Phyllocladus,* and *Agathis* common, and *Knightia*, *Alectryon* and *Nestegis* also present (Newnham et al. 1995; Giles et al. 1999). *Beilschmiedia* is noticeably absent from either study but this is more likely to be because it is under-represented in the pollen record due to low pollen production (Macphail 1980) rather than indicating that it was not abundant. *Beilschmiedia* is likely to have been at least a component of the semi-coastal forests around Tauranga and, consistent with present day forest in the Bay of Plenty it is probable that it was a major canopy component along with *Vitex lucens*, *Alectryon*, and other broadleaf species and was probably overtopped by large emergent podocarps such as *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*. Variations in forest type would have been found on disturbance-prone sites such as the coastal fringe where *Metrosideros excelsa* would have been dominant as it is today, or on floodplains or the edges of swamps.

1.6 Revegetation in Tauranga City

Efforts to restore vegetation in the city have been on-going since the early 1980s (Tony Murton pers. comm.) and the number of revegetation projects has steadily increased in more recent years. From 2005 until 2009 the Tauranga City Council's parks department installed at least 60,000 native seedlings per year and this number is likely to be less than half of the actual amount when private and commercial developments are considered (pers. obs.). However, many of these projects, while returning native vegetation, have not necessarily been planned or implemented for the purpose of restoring a functioning natural ecosystem. Many of the revegetation plantings resulted in very dense stands of short-lived trees and shrubs with apparently very little in the way of natural regeneration occurring (pers. obs.). Over the last two or three years the council have reduced the number of new plantings, and begun to enhance some of the existing ones (Dianne Paton pers. comm.). This has involved thinning and 'lifting' some stands to open up parkland area especially where there is criminal activity or the perception that these areas pose a risk to users of the parks (Dianne Paton pers. comm.). This opening up of the vegetation has resulted in high-light environments in the understorey (pers. obs.) and there is unlikely to be any regeneration of desirable species in these areas. In other stands larger and longer-lived native tree species are being planted in order to provide a better long-term solution but this has to be balanced with other considerations such as the risk of blocking the views of local residents (Dianne Paton pers. comm.).

The general approach in Tauranga has been active restoration of bare or highly modified sites through planting but then a switch to less active and then passive management: i.e. letting nature take its course. This study was implemented to assess whether this approach works and whether it works in the various vegetation types that are or were present in the city.

In many cases the species that have been used in the city, while being native, are not native to the area or are planted in inappropriate places. Examples of this are harakeke (*Phormium tenax*) being planted *en masse* in non-wetland habitats, and the extensive use of ngaio (*Myoporum laetum*) and akeake (*Dodonea viscosa*), neither of which would have occurred naturally in high numbers in the area. However, using non-native or non-local species may not necessarily be detrimental to the long-term success of a restoration project. In a study of revegetation sites on the Banks Peninsula Reay & Norton (1999) found that sites that had been planted with the non-local fast growing pioneer species *Olearia paniculata* were on a successional trajectory very similar to naturally regenerating sites and were functioning as natural ecosystems. Nevertheless the use of local species can help to conserve genetic diversity which is part of biodiversity as a whole (Convention on Biological Diversity 1992) and is an important aspect of ecological restoration (Falk et al. 2006).

Many of the restoration planting projects in Tauranga City have not been specifically designed to achieve ecological restoration goals but Tauranga City Council policies promote the protection and enhancement of biodiversity (Tauranga City Council 2006a, 2006b) and restoring functional ecosystems within the city is in the best interests of the city and its residents. In many reserves implementing large restoration projects is not practical because of the considerations already mentioned (views, criminal activity etc.) but plantings in some city reserves have been implemented at least in part to protect and restore native biodiversity and it is these projects that are the focus of this study.

1.7 Research objective and hypothesis

This objective of this study is to document the current state of planted restoration sites in Tauranga City and examine the likely developmental trajectory of the vegetation at those sites. Factors likely to affect the success of restoration plantings will be examined with the aim of making recommendations for future management. In this study I aim to:

1. Document the current state of the restoration plantings in the city in terms of vegetation structure and composition, and physical and environmental characteristics;
2. Establish whether revegetation plantings in Tauranga are on an ecological trajectory similar to naturally regenerating sites;
3. Determine whether these sites are functioning as natural systems; and establish what factors affect the long-term structure, function, and successional trajectory of the sites.
4. Provide management recommendations to restoration practitioners based on quantitative data.

Although no target forest types are explicitly stated by Tauranga City Council for the purposes of this study they are as follows.

1. Restoration sites on Mauao are assumed to for the purpose of restoring *Metrosideros excelsa* forest with similar structure and composition to mature forest elsewhere in the Bay of Plenty.
2. The restoration sites in Johnson Reserve is assumed to be targeted at tall mixed broadleaved forest and;
3. Restoration sites in Kopurererua Valley are assumed to be for the purpose of establishing tall *Dacrycarpus dacrydioides* forest, at least in appropriate sites.

1.7.1 Hypothesis

My working hypothesis was that restoration sites in Tauranga City are not on a trajectory that will see them develop into tall forest similar to natural forest in the area. Lack of natural seed sources and competition from invasive exotics are expected to be the main factors restricting natural succession at the sites. Environmental conditions (temperature and humidity) are expected to become more similar to mature reference sites with increasing age. Quantification of the differences with natural succession trajectories will enable development of guidelines for revegetation projects to better achieve ecological restoration goals.

1.8 Study sites

This study focusses on three forest types that would once have occurred within the bounds of present day Tauranga City. This section includes descriptions of the study sites that were utilised during the survey. The location of each of these sites is displayed in Figure 1.3.

1.8.1 Coastal pohutukawa forest

Mauao and Tuhua (Mayor Island) were used to study coastal pohutukawa (*Metrosideros excelsa*) forest. Details of site selection are included in section 2.1.

1.8.1.1 Mauao

Mauao is a significant and unmistakeable landmark of Tauranga City rising above the low duneland of Mt Maunganui and Matakana Island. Mauao is what remains of a rhyolite lava dome (Briggs et al. 2005) and is 231 m tall. The loam soils are classified as acidic orthic allophanic soils derived from tephra (S-MAP 2013).

Prior to human settlement it is likely that Mauao was covered in forest dominated by *Metrosideros excelsa* with *Vitex lucens, Corynocarpus laevigatus,* and various associated shrubs (Bibby et al. 1999). *Dacrydium cupressinum, Beilschmiedia tawa, Litsea calicaris,* and *Weinmannia racemosa* may also have been components of the vegetation (Bibby et al. 1999). However, Mauao has a long history of human inhabitancy and disturbance dating back several centuries to when Maori first settled the area (Stokes 1980; Cunningham & Musgrave 1989). Mauao was an important pa and had extensive fortifications and terraces (Cunningham & Musgrave 1989). This long history of human disturbance has drastically altered the vegetation which would have been cleared very early on. Fires have affected large areas of Mauao throughout its recorded history and appear to have played a significant role in shaping the current vegetation pattern (Bibby et al. 1999). Cunningham & Musgrave 1989 reported a large fire in 1842 and analysis of aerial photography by Bibby et al. (1999) indicate regular fires at least since 1943. The most recent blazes in 1997 and 2003 destroyed large areas of vegetation on the northern slopes. Since Europeans arrived the vegetation has been relatively sparse (see Figure 1.1) but efforts to restore the vegetation have been occurring for many years.

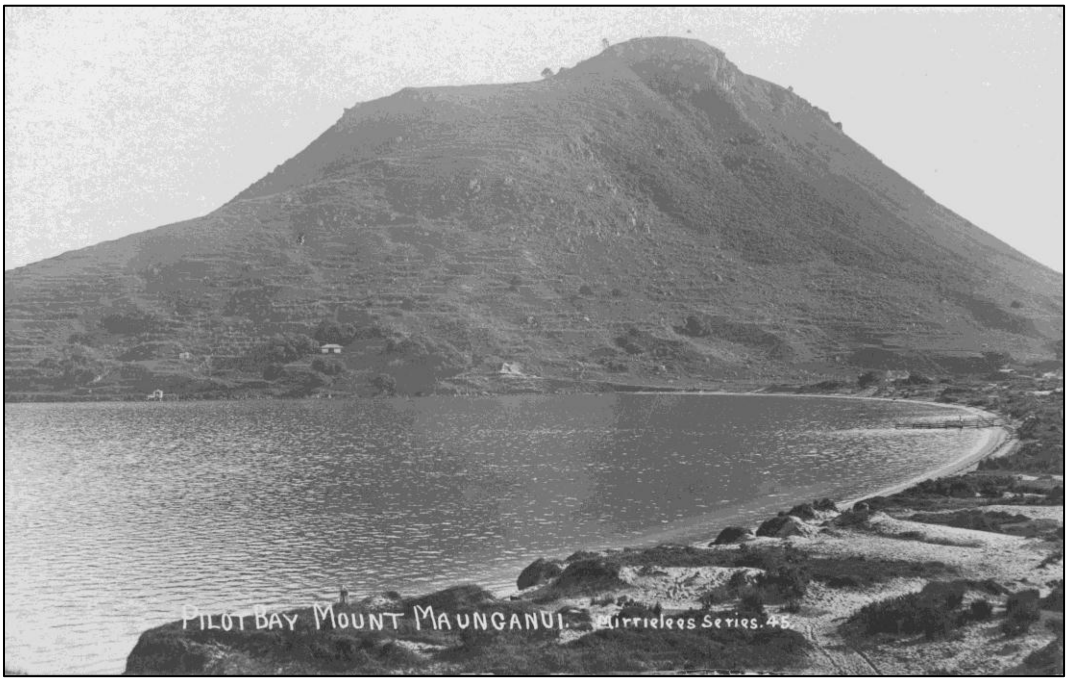

Figure 1.1: Mauao and pilot bay from the eastern side of Tauranga Harbour in 1915. Vegetation is very sparse with only a low cover of what could be fern around the summit and some larger trees at the base. Photo and information supplied by Tauranga City Libraries. Ref: 99-20.

Figure 1.2: The northwest face of Mauao after the fire in 2003.

John Adams, a builder who arrived in 1876 put considerable effort into planting trees on Mauao and was reported to have taken a group of Scouts to the summit and asked them to shoot karaka (*Corynocarpus laevigatus*) berries off the top with catapults in an attempt to spread their seed (Cunningham & Musgrave 1989).

Currently about 60% of Mauao is covered in scrub, forest, and restoration plantings while the remaining 40% is grazed pasture. A fringe of *Metrosideros excelsa* forest around the base of the mountain on the western side is the oldest vegetation. Below the summit on the western slopes and half way down the southern and eastern sides there is mixed forest and scrub which appears to have developed naturally although some planting has obviously been done in this area. The lower slopes on the southern and eastern sides are predominantly in pasture. The fires in 1997 and 2003 destroyed large areas of vegetation on the northern slopes (see Figure 1.2) which prompted Tauranga City Council to implement extensive restoration plantings. These plantings cover approximately 14 ha and are included in the present study.

Mauao was gazetted as a reserve in 1889 and has been a public park ever since (Cunningham & Musgrave 1989). Ownership was recently returned to the Tauranga iwi and it is currently managed by the Tauranga City Council with the Mauao Trust.

Mauao receives up to 1 million visitors each year, most of whom walk the base track (Mark Ray, Tauranga City Council, pers. comm.). This high level of use has implications for restoration management and factors like access and maintenance of views must be considered.

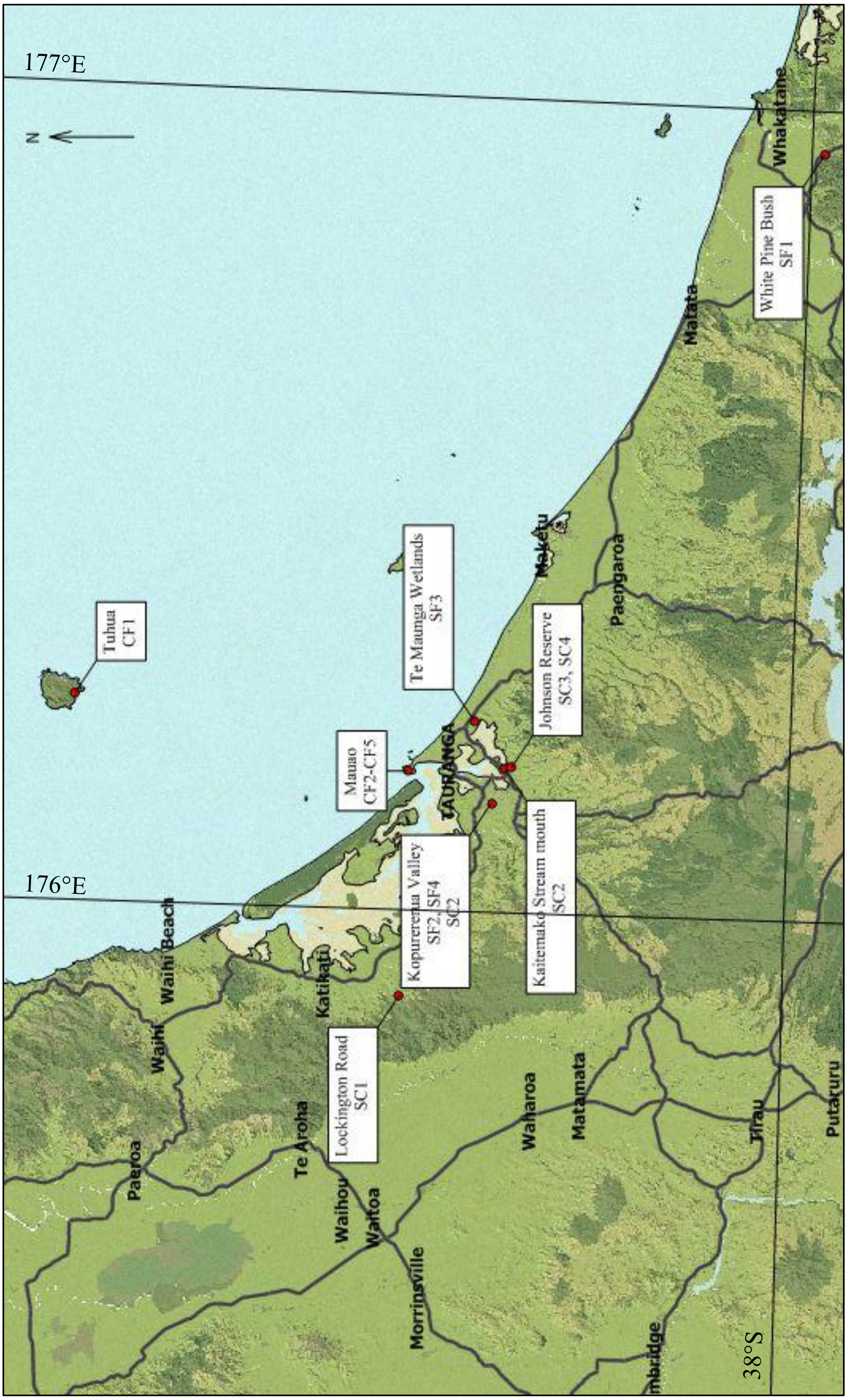

Figure 1.3: Location of study sites in the Bay of Plenty Region. Labels include site names and forest category code: CF = Coastal Forest, SC = Semi-coastal broadleaved forest and SF = Swamp forest. Land-cover map courtesy of Geographx Ltd, Topographic data Crown Copyright Reserved.

1.8.1.2 Tuhua

Tuhua, or Mayor Island, lies approximately 40 km off the coast of Tauranga to the north. It is a volcanic island and features a caldera approximately 3km across surrounded by high crater walls reaching up to 355m above sea level. The island covers an area of just over 1,310 hectares and is entirely covered in *Metrosideros excelsa*-dominated forest, except on the steepest cliffs and in the floor of the crater where there are two lakes and associated wetlands. The vegetation is a mosaic of various ages of *Metrosideros excelsa* forest which is the result of a history of volcanic and anthropogenic disturbance (Atkinson & Percy 1955; Empson et al. 2002). Prior to human habitation about 450 years ago Tuhua had a more diverse forest cover which included *Agathis australis, Dacrydium cupressinum,* other podocarps and possibly *Nothofagus spp.* (Empson et al. 2002). The current vegetation appears to still be developing as Atkinson & Percy (1955) mapped a number of areas of grass and *Leptospermum* which have now developed into *Metrosideros* forest.

Tuhua is a pest-free wildlife reserve and is managed by the Department of Conservation in conjunction with the Tuhua Trust who own the land.

1.8.2 Semi-coastal broadleaved forest

Five separate sites were used to study semi-coastal broadleaved forest and a brief description of each is included here. The study focussed on restoration plantings at Johnson Reserve but also utilised regenerating vegetation within the city and two separate reference sites.

1.8.2.1 Johnson Reserve

Johnson Reserve is a 14ha Green space Reserve in the suburb of Welcome Bay and is owned and managed by Tauranga City Council. The reserve is centred on the shallow valley of an un-named stream which enters the Tauranga Harbour just across Welcome Bay Road from the reserve’s northern boundary. The valley floor contains a mix of exotic and native vegetation and is currently being restored by Tauranga City Council and a local care group (Dianne Paton, Tauranga City Council, pers. comm.). The valley sides are forested in planted native species which were mostly planted between ten and 25 years ago and are the subject of this study (see Figure 1.4). At its highest point the reserve is 40 m above sea level.

Pre-human vegetation at this site would have been tall podocarp-broadleaved forest as already described in section 1.5 but this is likely to have been cleared by Maori prior to the arrival of Europeans (Stokes 1980). Urbanisation of Welcome Bay occurred in the early 1970s, prior to which it was farmland (Stokes 1980). The planting at Johnson Reserve began in the early 1980s (Tony Murton, pers. comm.) and plantings of various ages are present in the reserve.

Johnson Reserve's primary purpose is to provide open green space to the neighbourhood (Tauranga City Council 2002), but planting and restoration have been a particular focus of this reserve and on-going management and enhancement of the vegetation is being undertaken by both the Council and a community group (Dianne Paton, Tauranga City Council, pers. comm.).

The soils at Johnson Reserve are loam or sandy loam and belong to the Katikati hill soils, and Te Puke sandy loam groups (S-MAP 2013). They are classified as typic orthic allophanic soils (S-MAP 2013).

Figure 1.4: Restoration plantings >25 years old at Johnson Reserve

1.8.2.2 Hammond Street Reserve and Kopurererua Valley Escarpments

Two sites containing regenerating native vegetation were used in the study of semi-coastal broadleaved forest. Hammond Street Reserve is located in Welcome Bay and is part of the Harbour Reserves network (Tauranga City Council 2007). The Kopurererua Valley is discussed further in section 1.8.3. Vegetation at both sites appears to be relatively young and is dominated by the tree fern *Cyathea medullaris* and contains a range of native and exotic species such as *Geniostoma rupestre* var. *ligustrifolium*, *Melicytus ramiflorus*, *Cyathea dealbata*, and *Prunus campanulata*. Both areas have apparently been allowed to regenerate after previously being cleared because the sites are steep and unsuitable for building or other development. Hammond Street Reserve is subject to the specific management statements in the Harbour Reserves Management Plan (2007). Specifically, it is managed to enhance native vegetation “to recognise and protect the riparian/harbour, wildlife, natural character, and cultural heritage values” (Harbour Reserves Management Plan 2007). The Kopurererua Valley Reserves Management Plan includes the goal to “protect and enhance the landscape character and ecological values of the reserve” (Tauranga City Council 2000).

1.8.2.3 Blaymires

Two mature forest sites were used to describe a reference forest ecosystem for the study. One was located west of Tauranga on Lockington Road while the other was located on the property of Gael and Cedric Blaymires to the west of Te Puke. The Blaymires site comprises a narrow remnant of *Beilschmiedia tawa-Dysoxylum spectabile* forest in a steep gully at around 160m elevation. The soils belong to the Te Puke hill soils and are loam over clay and are classified as typic orthic allophanic derived from tephras (S-MAP 2013). This patch of forest was grazed by livestock until the mid-1980s when stock were excluded (Neil Blaymires, pers. comm.). In the subsequent 25 years without livestock grazing pressure the understorey has developed and is now relatively dense. Rats have been controlled in this forest patch since the mid-1990s but control has been inconsistent (Neil Blaymires, pers. comm.).

1.8.2.4 Amani

The other site used to make up the reference community for the semi-coastal broadleaved forest type is owned by Bruce Parsons and is known as Amani. This site is situated on hillslopes on the northern side of the Tuapo Stream and is at around 140m elevation. The soil at this site is Katikati sandy loam and is derived from tephra (S-Map 2013). The forest at Amani appears to be original although large podocarps were probably removed in the early part of the 20th century. The canopy comprises *Beilschmiedia tawa* with *Vitex lucens, Knightia excelsa, Dysoxylum spectabile, Elaeocarpus dentatus,* and occasional *Dacrydium cupressinum, Prumnopitys ferruginea,* and emergent *Metrosideros robusta*. The understorey is well developed in most areas and includes species such as *Hedycarya arborea, Melicytus ramiflorus, Geniostoma rupestre* var. *ligustrifolium*, *Rhopalostylis sapida*, and *Cyathea dealbata* (see Figure 1.5). This forest patch was fenced to exclude stock at least 30 years ago (Bruce Parsons, pers. comm.) and the control of pests is restricted to the occasional shooting of possums.

Figure 1.5: Semi-coastal broadleaved forest at Amani which was used as a reference ecosystem.

1.8.3 Semi-coastal swamp forest

Three separate sites were used in the study of swamp forest (refer Figure 1.3). Kopurererua Valley was the focus of this forest category and included relatively new plantings and regenerating vegetation. Older plantings at Te Maunga wetlands were included as well as mature forest at White Pine Bush.

1.8.3.1 Kopurererua Valley Reserve

The Kopurererua Valley Reserve comprises some 350ha of alluvial plain and swamp between the suburbs of Greerton and Gate Pa on the east, and Judea, Westridge, and Cambridge Road on the west. The valley has a long history of habitation and includes a number of pa sites and other archaeological features (Phillips & Bowers 2003).

The Kopurererua Stream drains form the Mamaku Plateau to the south enters the harbour at Judea. Work to straighten the stream and drain the wetlands in the valley began as early as 1908 (Phillips & Bowers 2003) and analysis of aerial photography shows that the stream was arrow-straight by 1943. As part of the reserve development the stream was realigned again in 2008/2009 (Fea 2008) to something approximating a previous natural course. The soils in the valley include Te Matai silt loam, Wairi silt loam, and Muriwai sand which are all classified as gley soils (S-Map 2013).

The history of the vegetation in pre-European times can only be guessed at but an early account from a missionary who canoed up the stream in 1835 swamp land and low scrub as well as small kahikatea further up the valley (Phillips & Bowers 2003) which suggest that kahikatea (*Dacrycarpus dacrydioides*) may have been regenerating after some previous clearance. It is likely that tall *Dacrycarpus dacrydioides* forest would have occurred at least in part of the valley in a natural mosaic with lower stature swamp vegetation such as *Phormium tenax*, *Coprosma tenuicaulis*, *Machaerina spp.* and *Carex spp.*. The drainage and realignment of the river allowed the valley to be farmed (see Figure 1.6) and the land on the western side of the stream is still periodically grazed. Much of the land on the eastern side of the stream is very wet, with a water level often of 50 cm deep or more in some places. While the western side remained in pasture and *Juncus* rushes the eastern side was apparently left and there are large areas of *Salix cinerea* forest, particularly in the wetter areas.

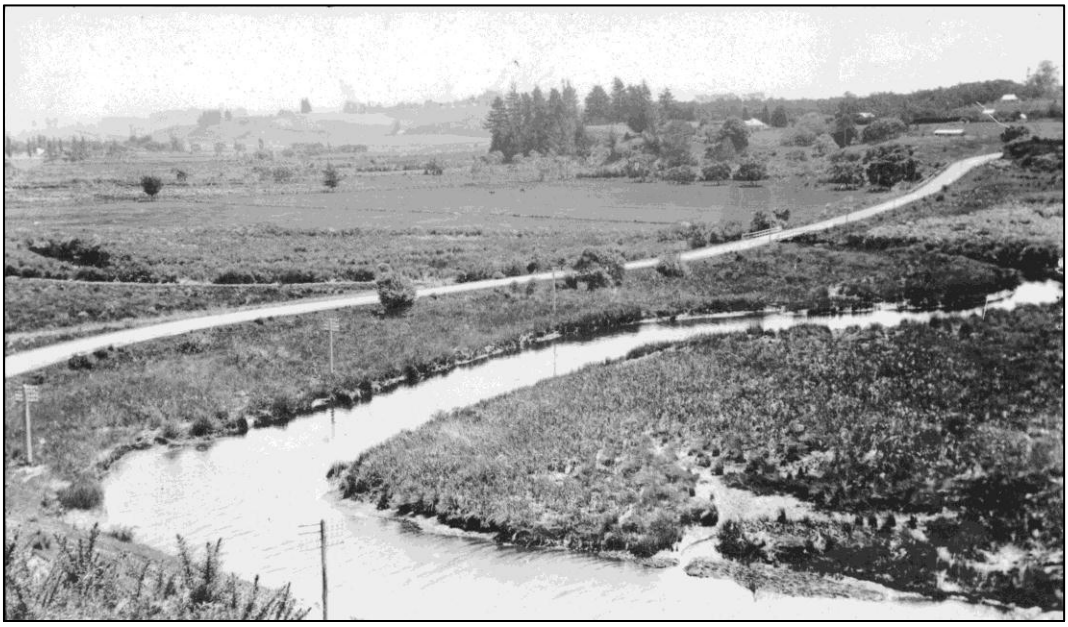

Figure 1.6: Kopurererua Stream taken about 1920 from the top of 12th Avenue. The gravel road is Waihi Road, crossed by the Judea Bridge in top right-hand third of the photo. The current restoration site is in the top left of the photo and appears to be mostly low-growing sedges and rank grasses, as well as some taller shrubs or trees. Photo and information supplied by Tauranga City Libraries. Ref: 02-356.

The land was bought by Tauranga City Council in order to build the Route-K expressway (Fea 2008) which was completed in 2003. Since about 2005 extensive clearance of exotic weeds and *Salix cinerea* forest has been undertaken and hundreds of thousands of native plants have been planted in an effort to restore the native vegetation. As noted in section 1.8.2.2 above restoration of the natural character of the valley is an express goal of the management of the reserve (Tauranga City Council 2000).

1.8.3.2 *Te Maunga Wetlands*

The Te Maunga wetlands include natural estuarine vegetation on the edge of the Tauranga harbour as well as extensive plantings on the grounds of the Te Maunga Wastewater Treatment Plant. The soil at the site is mapped as Ohineanganga silt loam, a typic acid gley soil (S-MAP 2013) but it is likely that a mix of anthropic soils are also present because of the history of earthworks at the site.

The historical vegetation at the site would have reflected the transition from saltmarsh to freshwater wetland and would likely have included areas of *Apodasmia similis-Juncus kraussii* var. *australiensis* as it does today, grading into *Phormium tenax, Coprosma propinqua, Coprosma tenuicaulis,* and *Cordyline australis* and then possibly into tall *Dacrycarpus dacrydioides* or podocarp-broadleaved forest further inland. The current vegetation around the oxidation ponds was planted in around 1996 when the Te Maunga Wastewater Treatment Plant was upgraded (Richard Hart, pers. comm.; Tauranga City Council 2004). It comprises a mixed forest and scrub including *Cordyline australis, Dacrycarpus dacrydioides, Phormium tenax* and *Leptospermum scoparium.*

1.8.3.3 White Pine Bush

White Pine Bush, a remnant of alluvial *Dacrycarpus dacrydioides* forest located 5 km southwest of Whakatane was used to define the reference swamp forest community. The reserve is approximately 4.9 hectares in size and is situated on a river terrace on the south-western side of the Waioho Stream at approximately 10-15 m elevation. The soils at the site are Rangitaiki sand, a typic fluvial recent soil (S-MAP 2013).

The vegetation at the site has been described by Smale (1984) and comprises emergent *Dacrycarpus dacrydioides* over a canopy of *Beilschmiedia tawa* and *Laurelia novae-zelandiae*. The *Dacrycarpus* are up to 40m tall and 1.9m in diameter (Smale 1984). The understorey is well established and includes *Melicytus ramiflorus, Hedycarya arborea,* and abundant *Rhopalostylis sapida*. In places there is a dense groundcover of *Blechnum filiforme* and *Uncinia uncinata* and *Freycinetia banksii* are common.

1.9 Thesis outline

This thesis is structured following the traditional layout of Introduction, Methods, Results, and Discussion. Details of each chapter are included below.

Chapter One: Introduction

This chapter introduces the study and provides background information about restoration ecology, the process of ecological restoration and the importance of measuring success. The research objectives and hypothesis are detailed and information about the Tauranga area and the specific study sites is supplied.

Chapter Two: Methodology

This chapter outlines the sampling design and how sites and plot locations were selected. It then goes on to outline the methods used to collect and analyse the data.

Chapter Three: Results

The results chapter includes vegetation composition and structure data collected from the vegetation survey as well as environmental and soil data associated with each forest category. Vegetation and environmental data are also combined in ordination and correlation analyses.

Chapter Four: Discussion and Recommendations

The final chapter includes interpretation of the results of the study and a discussion of the application of succession and assembly theory. It explores the possible influences on the success of restoration in Tauranga City and provides recommendations for current and future projects.

Chapter Two: Methodology

This chapter outlines how study sites were selected and how plot locations within sites were found and then goes on to detail the methods used to collect vegetation and environmental data at each of the sites. Methods used to analyse the resulting data are also detailed.

2.1 Sampling design

Three forest types were selected for survey based on their historic presence in the Tauranga City urban area and the availability of restoration projects situated in the historic extent of these forest types. Planted and natural sites of various ages in each forest type were surveyed. Coastal pohutukawa forest was surveyed on Mauao; semi-coastal broadleaved forest was surveyed primarily at Johnson Reserve; and swamp forest was surveyed at both the Kopurererua Reserve and the Te Maunga wetlands. Old-growth reference sites for each forest type were also surveyed but these were located away from the city. In selecting reference sites four main factors were considered: (1) Likely similarity to the target ecosystem of the corresponding restoration site; (2) similarity of environmental factors including elevation, soil type, and bio-climatic zone, (3) proximity to the city, and (4) low level of disturbance.

At each site the vegetation pattern was mapped into broad age classes on a Geographic Information System (GIS) using geo-registered aerial photography and my own knowledge of the sites. The aim was to get at least two planted strata of different ages for each forest type as well as a naturally regenerating stand and an old-growth reference site. The naturally regenerating stands were included so they could provide a natural parallel with the restoration sites.

On Mauao plantings of two broad age classes were identified, as well as two age classes of naturally regenerating vegetation (see Table 2.1). Tuhua (Mayor Island) was used as the reference forest for the coastal forest type.

Plantings of two age classes were identified at Johnson Reserve in the semi-coastal forest category. In addition two naturally regenerating sites of similar age were surveyed in other parts of the city (See Figure 1.3). Two reference sites were used; one near Katikati and one near Te Puke. Neither of these sites was ideal as both were at about 100m elevation, which was significantly higher than any of the Tauranga city sites, the Te Puke forest patch was very narrow and the effects of historic stock grazing were still evident, and the Katikati forest patch, although having livestock excluded for more than 30 years was on a very different soil type to the Tauranga restoration sites.

Only one age class of planting was present at the Kopurererua Reserve swamp forest restoration site, as well as a naturally regenerating area. A second age-class of plantings was surveyed at the Te Maunga wetlands for this forest type. White Pine Bush near Whakatane was used as the reference site for the swamp forest category because it is the only remaining area of old-growth swamp forest on the coastal plains in the western half of the Bay of Plenty.

Within each forest type age category a pre-determined number of plots were randomly placed using the Random Points function in Quantum GIS v1.7.2 (Quantum GIS Development Team 2011). A 10 m internal buffer was first added to each polygon and plots were randomly placed within the remaining area so that no plot was closer than 10m to from the edge of the patch. The number of plots for each stratum was based on the area available to survey. For areas 1-5 ha in size two plots were placed, for areas 5-10 ha three plots were placed, and for anything greater than 10ha four plots were placed. In addition, two extra plot locations were generated for every stratum as backups in case the primary locations were not suitable for some reason.   Plot locations were not generated for Tuhua as data from four plots established by BD Clarkson and one plot established by the Department of Conservation was available to use and no additional plots were required.

Exact plot locations for all study sites are included in Appendix 2.

Table 2.1: Sampling design summary. Category names (CF1, CF2 etc.) are used throughout the text in place of any longer description of the study sites.

Forest Type	**Site**	**Vegetation history**	**Vegetation age**	**Category name**	**Number of plots**
Coastal forest	Tuhua	Natural old-growth	mature (>120yrs)	CF1	5
	Mauao	Natural	mature (>120yr)	CF2	3
		Naturally regenerating	regenerating >75 years	CF3	4
		Planted	10-20 years	CF4	3
		Planted	<10 Years	CF5	4
Swamp forest	White Pine bush	Natural old-growth	>100 years	SF1	2
	Kopurererua Valley	Naturally regenerating	Estimated 50 years	SF2	4
	Te Maunga	Planted	>10 years	SF3	3
	Kopurererua Valley	Planted	<10 years	SF4	3
Semi-coastal broadleaf forest	Lockington Rd	Natural old growth	Estimated >200 years	SC1	2
	Looking Glass Gardens	Natural old growth	Estimated >150 years	SC1	2
	K-Valley	Naturally regenerating	At least 70 years	SC2	2
	Hammond Street Reserve	Naturally regenerating	At least 35 years but probably older	SC2	2
	Johnson Reserve	Planted	> 25 years	SC3	3
		Planted	>10 years	SC4	3
Total					**45**

2.2 Data collection

All plots were measured between the 8th of February and the 30th of March 2012 except plots 43 and 44 which were measured on the 29th of May 2012. The data from Tuhua was collected in 2009 except plot 4 which was collected in 2004 by Department of Conservation staff.

The random plot locations were uploaded into a Garmin 60csx GPS unit which was then used to navigate to the plot. Any plots which fell too close to the edge of the forest patch were moved directly away from the edge so that the centre point was at least 20 m from the edge. Similarly, any plot which fell closer than 50m from another plot was moved directly away from the first plot until 50m was reached. If plot locations were found to occur in any vegetation type other than the one intended or had <50% canopy cover they were discarded and a backup plot location was used.

The centre of each plot was marked with an aluminium peg and a piece of aluminium ‘permolat’ (re-cycled venetian blind) with the plot number etched into it (Figure 2.1). These were left in place after measuring the plot to allow future re-measurement.

Figure 2.1: Aluminium pegs were used to permanently mark plot centres

2.2.1 Vegetation Data

Data collection at each plot followed two main published methods, each yielding different data types. Variable area plots following Batcheler & Craib (1985) were established around the centre peg. All stems >2.5 cm diameter at breast height (DBH) were measured until a total of 30 individuals was reached. The distance from the centre of the plot to the 30th individual was measured and became the stem plot radius. Similarly, all saplings <2.5 cm DBH and >1.35 m tall were counted until a total of 30 individuals was reached and again the distance from the centre peg to the 30th individual was measured and became the understorey plot radius. In cases where 30 trees had not been reached within 15 m of the plot centre measurement stopped at 15 m. Similarly, a maximum radius of 10 m was set for the understorey plots. In some cases it was difficult to identify whether two stems belonged to the same tree, particularly in grey willow (*Salix cinerea*) stands. It was therefore decided that any stems that were not joined above ground level would be considered as separate trees unless it was obvious that they were joined.

A Recce plot was also measured following the methods outlined in Hurst & Allen (2007). This method involves recording vegetation cover in seven tiers using a modified Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974). The Recce description was carried out on a 10 m x 10 m square plot centred on the plot centre peg and marked out with two crossed measuring tapes oriented North-South and East-West. This method requires all vascular plants in the plot to be recorded and assigned a cover class in each of seven defined tiers: <0.3 m, 0.3-2 m, 2-5 m, 5-12 m, 12-25 m, >25 m and epiphytes.

Four seedling plots were also established; one at each end of the two crossed measuring tapes used to mark out the Recce plot. Seedling plots were circular with a radius of 49cm which was measured with a string attached to a temporary centre peg. This gave a total seedling sample area of approximately 3m^2 per plot. Seedlings were counted in each of five height tiers (<15 cm, 16-45 cm, 46-75 cm, 76-105 cm, 106-135 cm). Any non-woody species were recorded as present in each of the five tiers.

Ground cover was recorded using a point intercept method every meter along the crossed measuring tapes. Ground cover was recorded as soil, leaf litter, dead wood, root, rock, non-vascular plant, or the species name of any vascular plant <30 cm tall.

Average canopy height was measured using either a builders steel measuring tape or an inclinometer. Unless the age of the stand was already known a core from the stem of one of the oldest trees in or near the plot was taken to assess stand age.

2.2.2 Plot physical data

Plot altitude, slope, and aspect were recorded for each plot. Physiography was recorded as one of four categories; face, ridge, gully, or terrace.

2.2.2.1 Soil sampling

Soil samples were taken for each vegetation category but not at every plot. In most cases sub-samples of soil were taken from at least two plots in the category and pooled to make one sample. Soil samples were sent chilled to Hill Laboratory in Hamilton for testing. Soil parameters tested were pH, Olsen P, Available N, organic matter (OM), total carbon (TC), total nitrogen (TN), carbon : nitrogen ration (C/N), Pottasium (K), Calcium (Ca), Magnesium (Mg), Sodium (Na), cation exchange capacity (CEC), and total base saturation. The following description of soil testing methods is taken from information supplied by the laboratory (Hill Laboratories 2013) and is in some cases verbatim from that document. Soil samples were dried at 35 °C in an oven and a 10 mL sample was mixed with 20 mL of water and the pH was measured (Hill Laboratories 2013). Phosphorus was measured using the method outlined by Olsen et al. (1954) and the extracted phosphorus measured colourimetrically using a molybdenum blue procedure (Hill Laboratories 2013). Cations were extracted using ammonium acetate and determined using ICP-OES (Inductively Coupled Plasma Optical Emission Spectroscopy), and cation levels were converted to concentrations in the soil based on weight (Hill Laboratories 2013). Cation Exchange Capacity (CEC) was determined by summing the extractable cations and the extractable acidity which was "determined from the decrease in pH of the buffered ammonium acetate cation extract" (Hill Laboratories 2013).

Organic matter was measured using the Dumas method of combustion: Samples were combusted to produce CH_4 and CO gas which was then oxidised to CO_2. The CO_2 was then measured using a thermal conductivity meter and the total carbon measured was converted to organic matter using the Van Bremmelen factor (Hills Laboratories 2013).

For available nitrogen samples were incubated at 40 °C for seven days and ammonium-N was extracted with potassium chloride. Ammonium-N was then determined colourmetrically (Hills Laboratories 2013).

2.2.2.2 Temperature and Humidity

Temperature and relative humidity (RH) were recorded hourly in one plot in each of the 13 vegetation categories using DS1923 Hygrochron iButton® data loggers

(Maxim Integrated, San Jose California). The plots in which the data loggers were installed were selected subjectively for their apparent representativeness of the category as a whole and for their accessibility, as logger data had to be downloaded approximately every 10 weeks. Data loggers were left in place from March 2012 until October 2012.

Relative humidity values recorded by the DS1923 loggers are prone to saturation drift. When humidity is over 70% for any period of time the humidity values recorded become higher than the true value so that eventually values much higher than 100% are recorded (Maxim Integrated 2011). To correct for this a formula, supplied by the manufacturer, was applied prior to any analysis (Maxim Integrated 2011). Daily mean, minimum, and maximum humidity and temperature were calculated for each forest category and these data were analysed with one-way ANOVA and post-hoc Tukey HSD comparisons using Statistica 10 software (StatSoft Inc 2002). All environmental data approximated the normal distribution but in some cases the assumption of homogeneity of variances was violated. Welch's F-tests were used instead of normal ANOVA in these cases. Results were considered statistically significant at the $\alpha = 0.05$ level.

2.3 Data Analysis

Analysis of vegetation data focussed on key species within each of the three forest types. Key species were selected based on the literature, the composition of the reference forests, and personal knowledge of these forests. They were canopy or understorey species that were either major or defining components of the reference forest or important successional species. Introduced species were included where they appeared to have a significant influence on successional trajectory and species that dominated the vegetation in particular categories were also included in the analysis of population structures.

Vegetation data were tabulated and basal area and density were calculated for each species in each plot from diameter and count data. Seedlings <15 cm high were excluded from density data as this height class included large numbers of ephemeral seedlings which distorted the data somewhat. The density of individuals in each of seven DBH size classes was calculated. For multi-stemmed trees a single DBH value was calculated by finding the square-root of the sum of the squares of the individual stem diameters: $DBH_{total} = \sqrt{\sum_{i=1}^{n} dbh_i^{\,2}}$.

A formal name for the vegetation in each category was constructed using the cover data from Recce descriptions and the conventions detailed by Atkinson (1985). Recce cover data were also used to show the structure of each forest category.

Indigenous and introduced vascular species richness were calculated for each vegetation category and species lists for the naturally regenerating and planted sites were compared with the reference sites for each forest type. Simpson's Diversity Index was calculated for each plot and each vegetation category. Count data were first converted to individuals per 100 m^2 to correct for different plot sizes. This index is based on the probability that any two randomly sampled individuals are of the same species (Kent 2012) and can be presented in at least three different forms. The form used here (1-D) is one of the most commonly used (Kent 2012) and results in values between zero and one; one being infinitely diverse and zero having no diversity.

Aspect and slope were transformed into heat load using the equations published by McCune & Keon (2002) and the adaptation to southern hemisphere using the online supplement (McCune 2004). Heat load is an estimation of potential annual direct incident radiation (McCune & Keon 2002) which gives an indication of the temperature at the site.

Apparent associations between vegetation characteristics and physical or environmental data were tested using Spearman rank R in Statistica 10 (StatSoft Inc. 2002). Correlation calculations were based on environmental and soil data collected at the category level (CF1, CF2, etc.) and averaged vegetation and physical data collected at the plot level. Associations were considered significant when $p < 0.05$.

2.3.1 Non-nonmetric Multidimensional Scaling

Basal area data were used to analyse the variation and relationships in and amongst the categories within each forest type.

An ordination using Non-metric Multidimensional Scaling (NMS) was performed on the basal area data for plots in each forest type and for each category using PC-ORD 6.0 (McCune & Mefford 2011). Basal area can be used as an indication of biomass (Mueller-Dombois & Ellenberg 1974) and productivity. NMS was chosen because it is well suited to vegetation data as it does not assume linear relationships between species, any distance measure can be used, and is not adversely affected by 'zero-rich' data sets (McCune & Grace 2002; Kent 2012). Ordination of vegetation data can provide an indication of the progress of restoration sites towards a reference state by a reduction in ordination distance over time (Matthews & Spyreas 2010), although in this case different aged sites were used in a 'space for time' approach.

Data were not relativized because relativization adds weight to rarer species and can hide important differences between plots. Sorenson distance was used as the similarity measure. The Autopilot Mode in PC-Ord was used and set to medium which uses a random starting position and carries out 50 runs with the real data as well as 50 runs on randomised data to execute a Monte Carlo test for statistical significance (McCune & Mefford 2011). The number of dimensions is selected automatically by the programme by comparing the final stress on the best run from each dimensionality (McCune & Mefford 2011). The stability of the solution was assessed automatically by PC-Ord but was checked using a scree-plot of stress vs. number of iterations. Environmental data were overlaid as vectors and the resulting NMS plot was rotated to align with the environmental variable with which the data were most strongly correlated.

2.3.2 Multi-response Permutation Procedures (MRPP)

Multi-response Permutation Procedures (MRPP) was performed using PC-ORD on the same basal area data used in the NMS, to ascertain whether the pre-defined categories within each forest type were significantly different from one-another. MRPP is a non-parametric method which uses distance measures to compare pre-assigned groups of sample units and test the hypothesis of no difference between groups (Mielke et al. 1981; McCune & Grace 2002). Unlike multivariate analysis of variance (MANOVA) there are no assumptions of normal distribution of data (McCune & Grace 2002). Sorensen distance was used in the analysis along with the standard weighting formula recommended by McCune & Grace (2002): $C_i =$

$\frac{n_i}{\sum n_i}$. The distance matrix was rank-transformed so that the results would more closely correspond to the Nonmetric Multidimensional Scaling (NMS) ordinations which similarly manipulate the distance matrix (McCune & Grace 2002). The option to undertake pair-wise analysis was also selected so that each category was compared to all others. Pair-wise comparisons involve testing multiple hypotheses simultaneously and are therefore subject to the problems of family-wise Type 1 error whereby the probability of making a Type 1 error increases with the number of tests (McCune & Grace 2002; Quinn & Keough 2002). To control the family-wise Type 1 error the Holm-Bonferroni correction was applied (Holm 1979) and significance was tested at the $\alpha=0.1$ level. The old-growth swamp forest site (SF1) was omitted from the pair-wise comparisons because there were only two plots in that category. MRPP cannot run with groups with only two members because there is only one within-group distance (Bruce McCune pers. comm.).

Chapter Three: Results

Results in this chapter are presented in three sections; one each for coastal forest, semi-coastal forest, and swamp forest. Each section includes vegetation composition, structure and diversity data, formal names for each vegetation type, environmental data and ordinations, and each section is presented in the same order.

The 45 plots included in the survey covered approximately 11,500 m^2. In total 214 plant species were recorded during the study comprising 127 indigenous vascular species and 85 exotic vascular species. A full species list is presented in Appendix 1. Canopy height ranged from just 1.8 m in CF5 and SF4 to 26 m in CF1 (Tuhua) and SC1. Details of individual plots, including location, size, slope, aspect, altitude, canopy height, and measurement date are included in Appendix 2.

A summary of the physical and environmental characteristics of each of the 13 forest categories is included in Appendix 3. Average temperatures ranged from 10.2 °C at White Pine Bush (SF1) to 14.3 °C in CF5 on Mauao. The minimum temperature recorded was -2.4 °C in Kopurererua Valley (SF4) while the maximum temperature of 31.5 °C was recorded in CF5 on Mauao. Average daily humidity (RH) ranged from 76.2% in CF5 to 91.4% at White Pine Bush (SF1). The lowest overall RH of 29.6% was recorded in CF5 while all sites except SF3 and SC2 reached 100% humidity.

3.1 Coastal Forest

All of the results for the coastal forest categories are presented in this section.

3.1.1 Abundance of key coastal forest species

The key species chosen to represent the coastal forest vegetation included species identified by Atkinson (2004) as common components of coastal forest and species that are commonly planted in coastal restoration projects. The canopy species chosen were *Corynocarpus laevigatus, Dysoxylum spectabile, Knightia excelsa Kunzea ericoides, Leptospermum scoparium, Metrosideros excelsa,* and *Vitex lucens,* and the understorey species were *Coprosma robusta, Geniostoma* *rupestre* var. *ligustrifolium, Macropiper excelsum, Melicytus ramiflorus, Myrsine australis, Pittosporum crassifolium,* and *Pseudopanax arboreus*.

There was a general trend of increasing basal area from the youngest restoration site to the old growth forest sites although basal area was higher on Mauao than on Tuhua (Table 3.1). There was no obvious trend in overall density. *Metrosideros excelsa* (hereafter *Metrosideros*), the dominant canopy species in the reference forest, was most dense in the 10-20 year old planted site (CF4) and the <10 year old planted site (CF5), and was completely absent from the naturally regenerating forest on Mauao (CF3). *Metrosideros* basal area was largest in the natural forest on Mauao (CF2) and smallest in the planted CF5 category. *Litsea calicaris* (hereafter *Litsea*) was present only in the oldest site at Tuhua (CF1) and although the stem density was very high the basal area was low, indicating many small individuals.

Table 3.1: Mean basal area (BA, m^2ha^{-1}) and density (D, individuals ha^{-1}) comparison of key coastal forest species. The total basal area and density of all species recorded in each class (i.e. not just the key species listed) are also included.

	CF1 Tuhua		**CF2 Mauao**		**CF3 Mauao**		**CF4 Mauao**		**CF5 Mauao**	
Canopy trees	BA	D	BA	D	BA	D	BA	D	BA	D
Corynocarpus laevigatus	0.0	10.0	0.0	0.0	0.0	0.0	0.2	32.7	0.0	0.0
Dysoxylum spectabile	0.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Knightia excelsa	3.3	35.0	0.0	0.0	1.6	72.0	0.0	0.0	0.0	0.0
Kunzea ericoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	96.0
Leptospermum scoparium	0.0	0.0	0.0	0.0	0.0	0.0	0.6	224.5	0.2	1710.9
Litsea calicaris	1.2	33158.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metrosideros excelsa	75.2	265.0	191.5	145.5	0.0	0.0	15.3	583.9	0.1	358.8
Vitex lucens	0.02	20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sub-canopy trees & shrubs										
Coprosma robusta	0.0	0.0	0.7	547.2	4.7	1437.9	0.8	226.5	0.0	0.0
Geniostoma rupestre var. ligustrifolium	0.0	195.0	0.8	647.0	2.6	8488.5	0.0	0.0	0.0	0.0
Macropiper excelsum	0.6	11066.1	0.7	1061.1	0.7	4785.3	0.9	2489.3	0.0	0.0
Melicytus ramiflorus	4.7	775.5	3.7	954.2	4.0	10395.9	1.7	297.4	0.1	5.3
Myrsine australis	2.5	8075.8	0.0	12.5	0.0	0.0	0.0	12.0	0.0	0.0
Pittosporum crassifolium	0.0	55.0	0.1	37.8	0.0	0.0	1.0	247.5	0.0	0.0
Pseudopanax arboreus	0.0	205.0	0.0	37.8	0.0	36.0	0.0	0.0	0.0	0.0
Total (all species)	**89.1**	**65606.8**	**201.6**	**3992.8**	**32.1**	**28701.8**	**28.0**	**5360.3**	**0.91**	**5461.7**

Knightia excelsa (hereafter *Knightia*) was present in both the CF1 and CF3 categories. The density of *Knightia* in CF1 was less than half of the density in

CF3, while the basal area was more than twice as much, indicating fewer but much larger trees in the CF1 category. *Kunzea ericoides* was present in only the youngest category (CF5) and *Leptospermum scoparium* was present only the planted categories (CF4, CF5). *Dysoxylum spectabile* (hereafter *Dysoxylum*) and *Corynocarpus laevigatus* were present in low densities on Tuhua and the lack of basal area data indicates that only saplings or seedlings were recorded. *Corynocarpus laevigatus* was also present in CF4.

In the sub-canopy layers *Coprosma robusta* was present in the highest density in the naturally regenerating forest on Mauao (CF3) and was completely absent from Tuhua (CF1) and the youngest of the planted sites (CF5). *Geniostoma rupestre* var. *ligustrifolium* was present only in the non-planted sites and was most dense in the youngest of these (CF3) and least dense in the oldest site (CF1). The density of *Macropiper excelsum* was highest at the oldest site (CF1) but its basal area was highest in CF4 indicating fewer but larger trees in that category. It was completely absent from CF5. *Melicytus ramiflorus* was present at all of the sites and was most dense in CF3, although CF1 had the highest basal area which indicates larger trees. *Myrsine australis* was most dense and had the highest basal area in the old growth forest of CF1. It was also present in CF2 and CF4 as seedlings or saplings but there were no measurable trees. *Pseudopanax arboreus* was present in the three natural sites only and was only recorded in the seedling and sapling count data.

3.1.2 Population structure of key coastal forest species

Population structure data shows a trend from high densities of small early successional species in the recently planted restoration sites to low densities of large trees with high density sub-canopy trees and shrubs in the old-growth sites (refer Figure 3.1 to Figure 3.5).

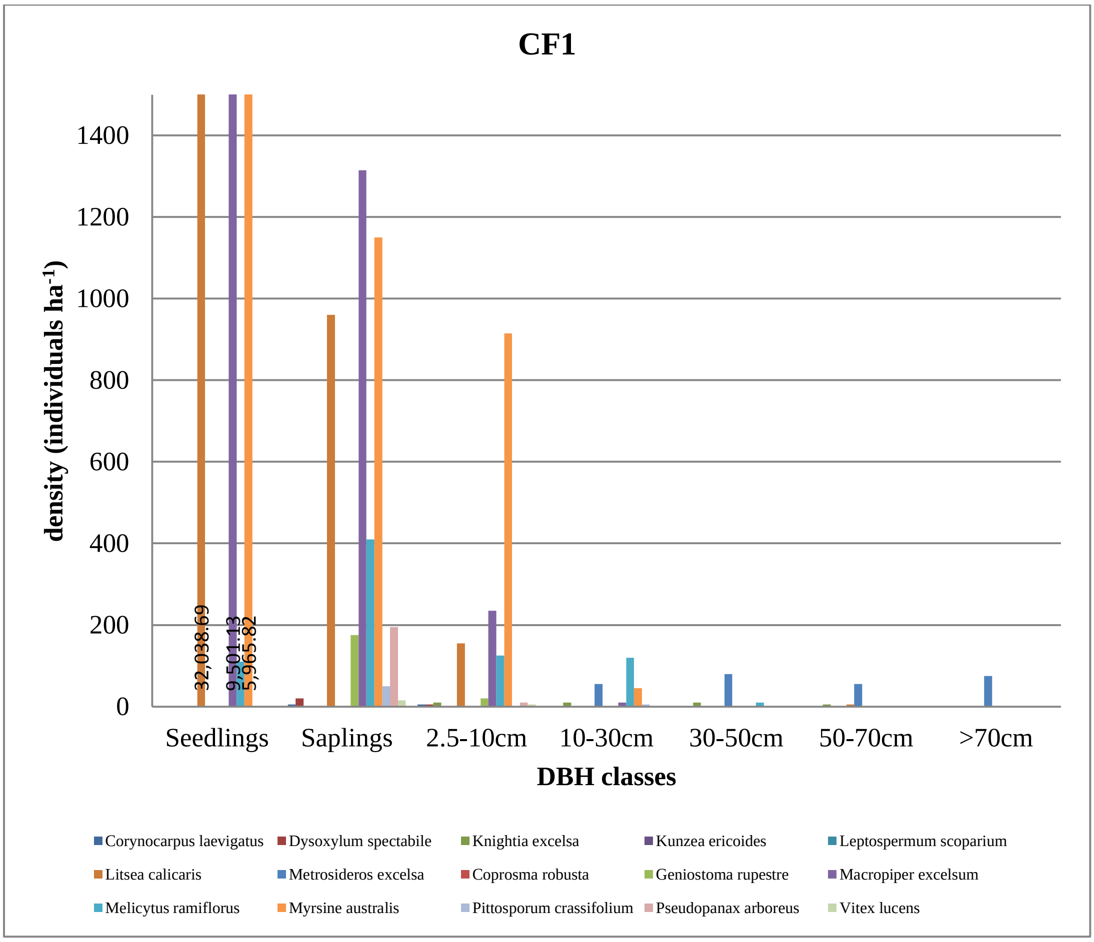

Figure 3.1: Density of individuals in seven size classes in category CF1. Saplings are >135cm tall and <2.5cm DBH while seedlings are >15cm and <1.35m tall. Seedling data has been truncated and actual values are shown at the base of the truncated bars.

Metrosideros excelsa was present only as trees larger than 10cm DBH and had densities ranging from 55 ha^{-1} to 80 ha^{-1} in each of the four size categories in which it occurred (Figure 3.1). *Metrosideros* were the largest trees present in CF1. *Knightia excelsa* was also present as large trees in the 50-70 cm DBH class although the density was relatively low (5 individuals ha^{-1}). *Knightia* was also present in the three smaller tree classes at low densities but no saplings or seedlings were recorded. *Dysoxylum spectabile* was recorded in only the sapling and 2.5-10 cm DBH size classes where it had densities of 20 ha^{-1} and 5 ha^{-1} respectively while *Vitex lucens* was recorded in the same two classes and also at low density. Very high densities of *Litsea* were recorded in the seedling class (32,038.69 ha^{-1}). *Litsea* density was successively lower over the subsequent two size classes and it was present at very low density (5 ha^{-1}) in the 50-70 cm size class.

In the understorey, *Myrsine australis* and *Macropiper excelsum* showed a similar pattern to *Litsea* with very high density in the seedlings tailing off to low density in the 10-30 cm class.

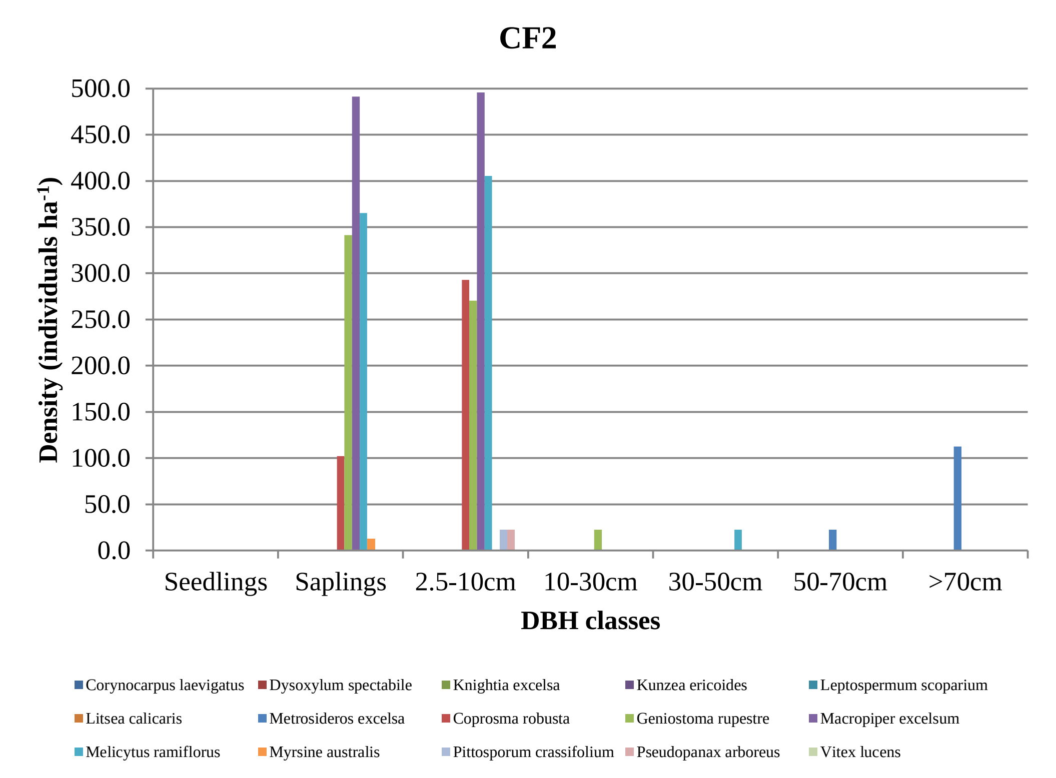

Figure 3.2: Density of individuals in seven size classes in category CF2. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

In the natural coastal forest on Mauao (CF2, Figure 3.2) *Metrosideros excelsa* was only present as large trees >50 cm DBH. No seedlings between 15 cm and 135 cm tall were recorded for any of the key species. *Geniostoma rupestre* var. *ligustrifolium*, *Coprosma robusta*, *Macropiper excelsum*, *and Melicytus ramiflorus* were all recorded at relatively high density in the sapling and 2.5-10 cm classes but only *Melicytus* was recorded in the 30-50 cm class and then only at low density (22.5 ha^{-1}). No *Vitex lucens*, *Dysoxylum spectabile*, or *Litsea calicaris* were recorded.

Metrosideros excelsa was not present at all in the naturally regenerating forest on Mauao (CF3, Figure 3.3) and no species >30 cm DBH were present. High densities of *Macropiper excelsum* and *Geniostoma rupestre* var. *ligustrifolium* were recorded in the seedling class (3314.3 ha^{-1} and 4971.5 ha^{-1} respectively) and *Melicytus ramiflorus* was present at very high density (7457.3 ha^{-1}). The density of all three species reduced over the subsequent size classes.

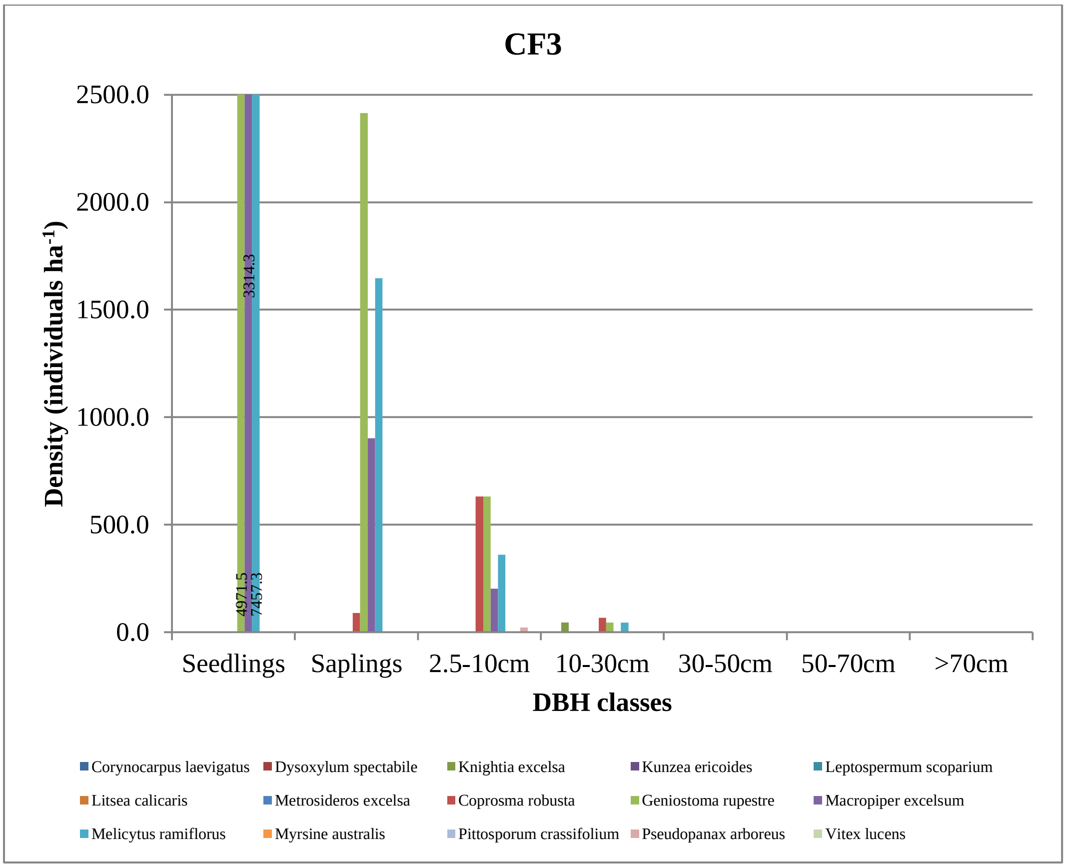

Figure 3.3: Density of individuals in seven size classes in category CF3. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall. Seedling values have truncated and actual values are shown at the base of truncated bars.

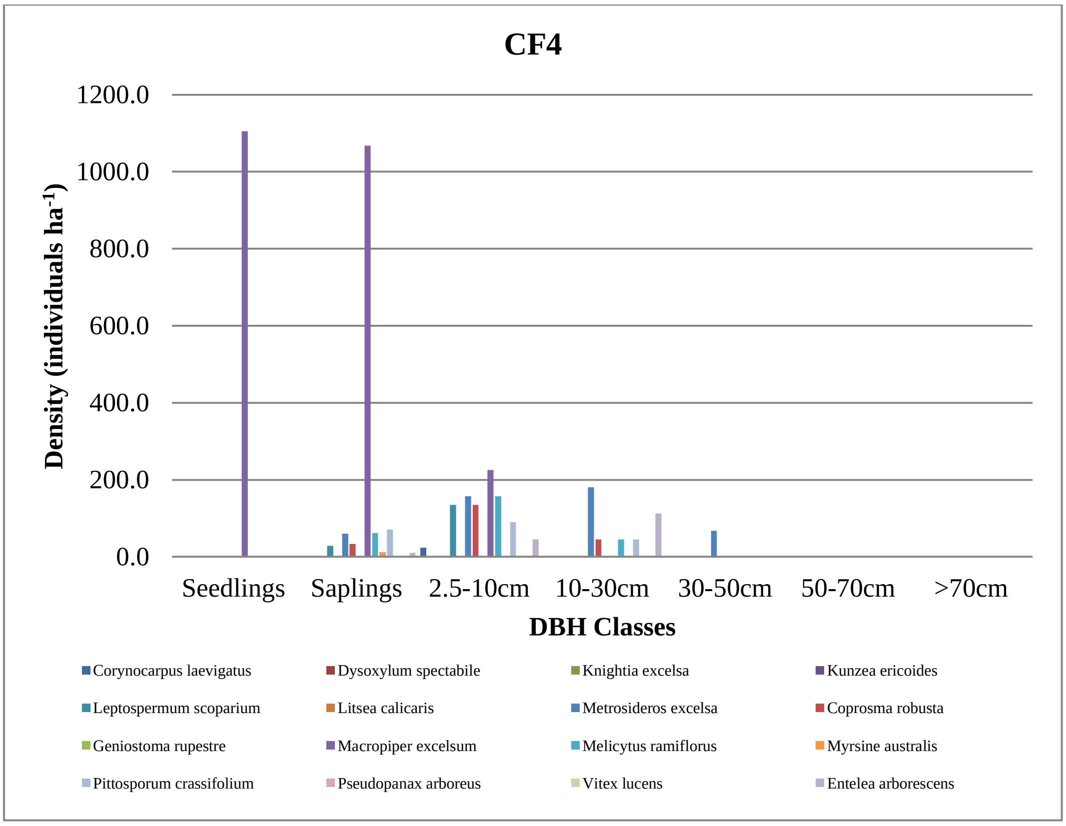

Figure 3.4: Density of individuals in seven size classes in category CF4. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

In the 10-20 year old planted sites on Mauao (category CF4, Figure 3.4) *Metrosideros excelsa* was present in four size classes and had the highest density in the 10-30 cm size class (180.2 ha^{-1}). *Macropiper excelsum* was present at high density in the seedling and sapling size classes and much lower density in the 2.5-10 cm class. *Melicytus ramiflorus*, *Coprosma robusta*, *Pittosporum crassifolium*, and *Leptospermum scoparium* all peaked in the 2.5-10 cm size class.

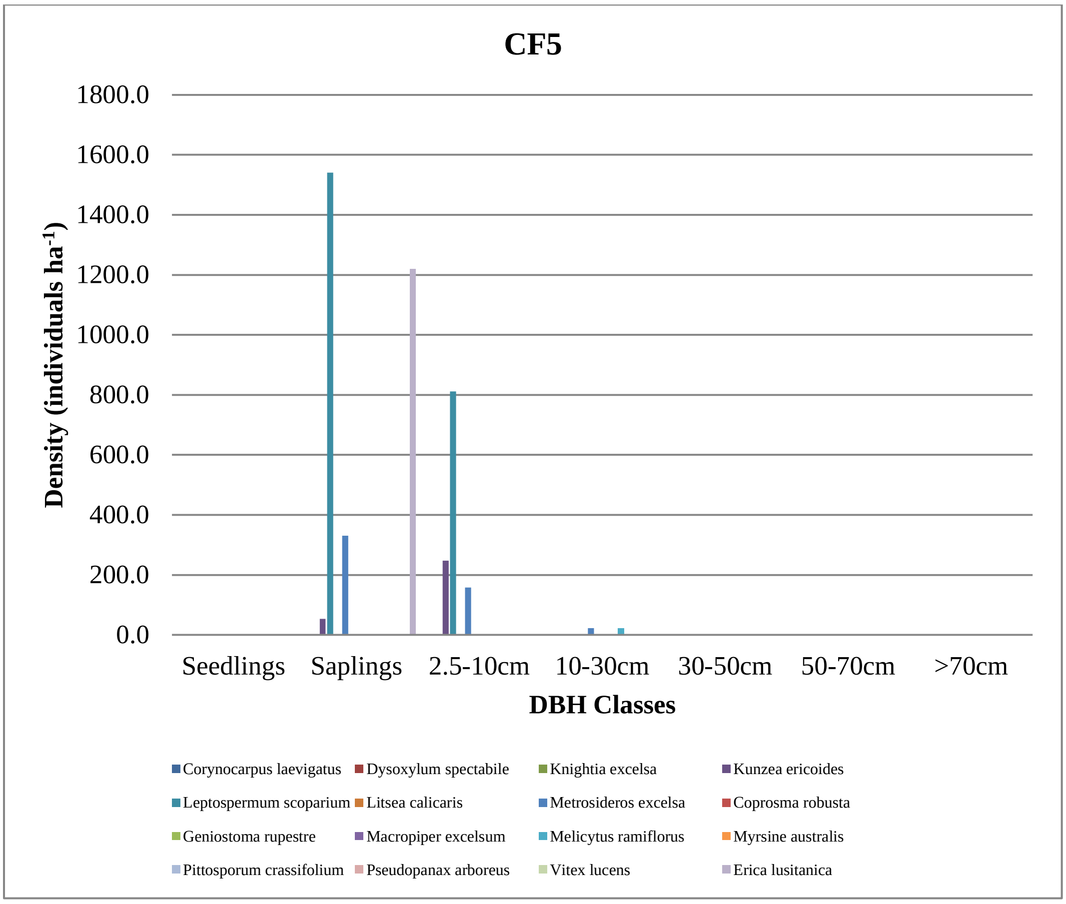

Figure 3.5: Density of individuals in seven size classes in category CF5. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

Of the key coastal forest species only *Metrosideros excelsa*, *Leptospermum scoparium*, and *Kunzea ericoides* were present in the <10 year old planted sites on Mauao (CF5) and none of these were larger than 30 cm DBH (Figure 3.5). *Leptospermum* was the most abundant of the three with densities in the sapling and 2.5-10 cm classes of 1,540.2 ha^{-1} and 811 ha^{-1} respectively. *Metrosideros* was most abundant in the sapling size class (330.6 ha^{-1}) and had lower values in the two next largest size classes.

3.1.3 Formal vegetation name

Formal vegetation type names for the five coastal forest categories show significant variation in the vegetation (Table 3.2).

Table 3.2: Vegetation names for each of the five coastal forest categories. Underlined species have a cover of ≥50%, species with no underlining and no brackets have a cover of 20-49%, round brackets indicate cover of 10-19% while square brackets indicate cover of 1-9%. Species in different canopy tiers are separated by a / whereas species within the same tier are separated by a -.

Category	Vegetation name
CF1	<u>*Metrosideros excelsa / (Coprosma macrocarpa) - (Melicytus ramiflorus) - (Myrsine australis) forest*</u>
CF2	<u>*Metrosideros excelsa*</u> */ (Melicytus ramiflorus) - (Cyathea medullaris)* forest
CF3	*[Cyathea medullaris] / (Coprosma robusta) - [Melicytus ramiflorus]* scrub
CF4	*Metrosideros excelsa - [Pittosporum eugenioides] / (Entelia arborescens)* scrub
CF5	*Leptospermum scoparium / [Erica lusitanica] / (Sporobolus africanus) - (Microlaena stipoides)* shrubland

3.1.4 Vegetation Cover

The total cover of indigenous and exotic (non-native) species in six vegetation tiers was calculated from Recce total cover and Recce species cover data for each of the five coastal forest categories (Figure 3.6 below). No exotic plant species were recorded in the old-growth forest on Tuhua but exotic species were present in all of the sites on Mauao. Exotic species were most abundant in the lower three tiers (i.e. below 5m in height) and in the naturally regenerating scrub (CF3) and <10 year old planted sites (CF5) whereas no exotic species were recorded on in CF1.

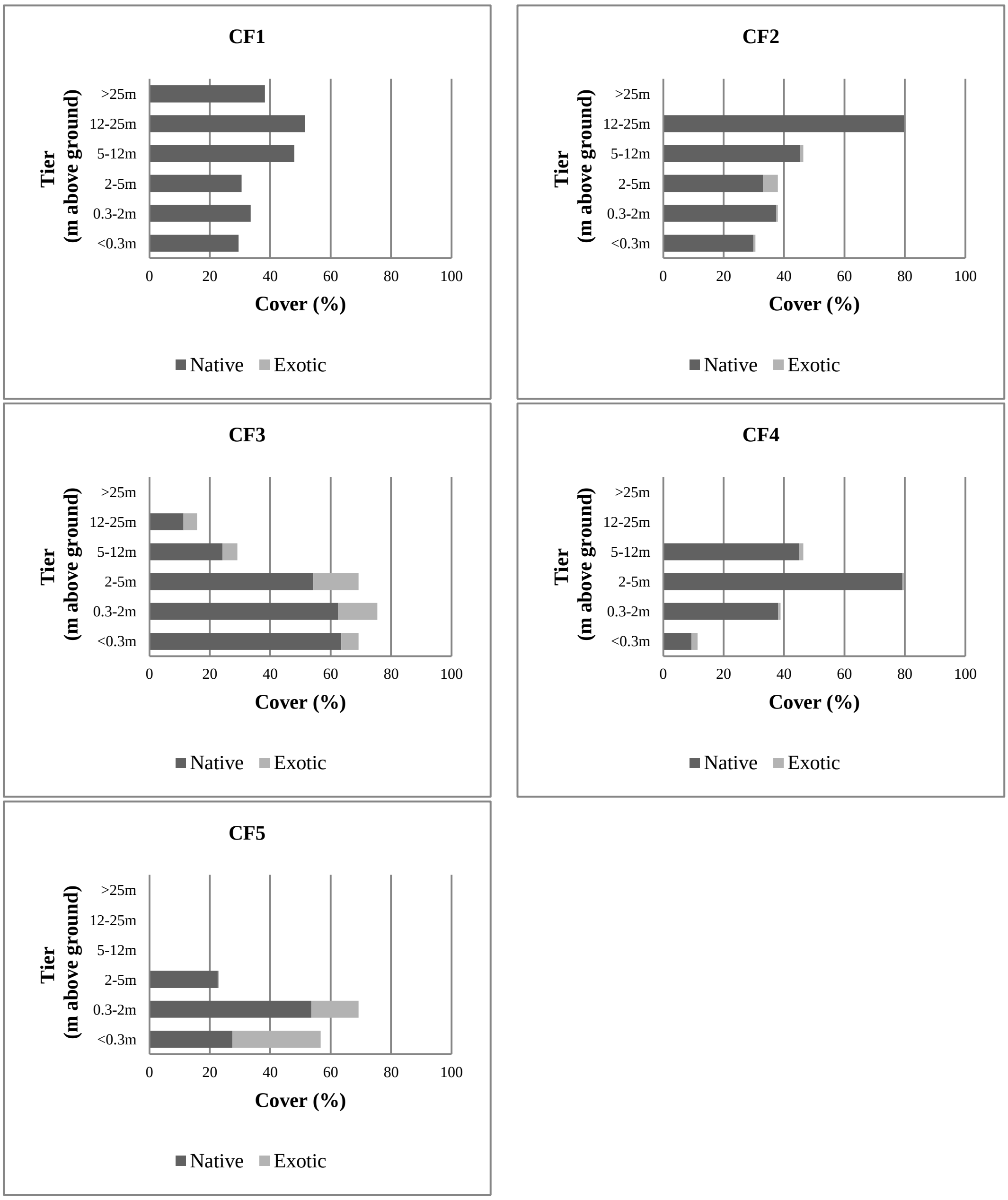

Figure 3.6: Cover of native and exotic species in each of six vegetation tiers each of the five coastal forest categories (CF1 – CF5).

The structure of the vegetation shows considerable variation (Figure 3.6) but there is an obvious trend from low stature vegetation in the restoration sites to high stature vegetation in the mature sites. The forest on Tuhua was the only coastal forest site to exceed 25 m in height and the two oldest categories had high cover values in the tallest tiers. In the regenerating scrub category (CF3) low cover values in the 5-12 m and 12-25 m tiers indicate few tall trees overtopping a lower canopy. The canopy height successively dropped over categories CF4 and CF5 and there was a noticeable increase in groundcover vegetation (<30 cm tall) from the two older forest categories to the younger ones. Category CF4 was the exception with a relatively low groundcover of around 11%.

3.1.5 Ground Cover

The point-intercept groundcover data from plots in the coastal forest category (Figure 3.7) shows higher levels of litter and dead wood in the mature CF1 category compared with the other categories and a clear trend from low litter cover in the newly established vegetation to high litter cover in the old-growth forests. No exotic groundcover plants were recorded in the two oldest sites (CF1, CF2) whereas the youngest site (CF5) had >20% exotic plants in the groundcover. The naturally regenerating site (CF3) had the highest native plant groundcover at 30% and was the only category in which non-vascular species were recorded.

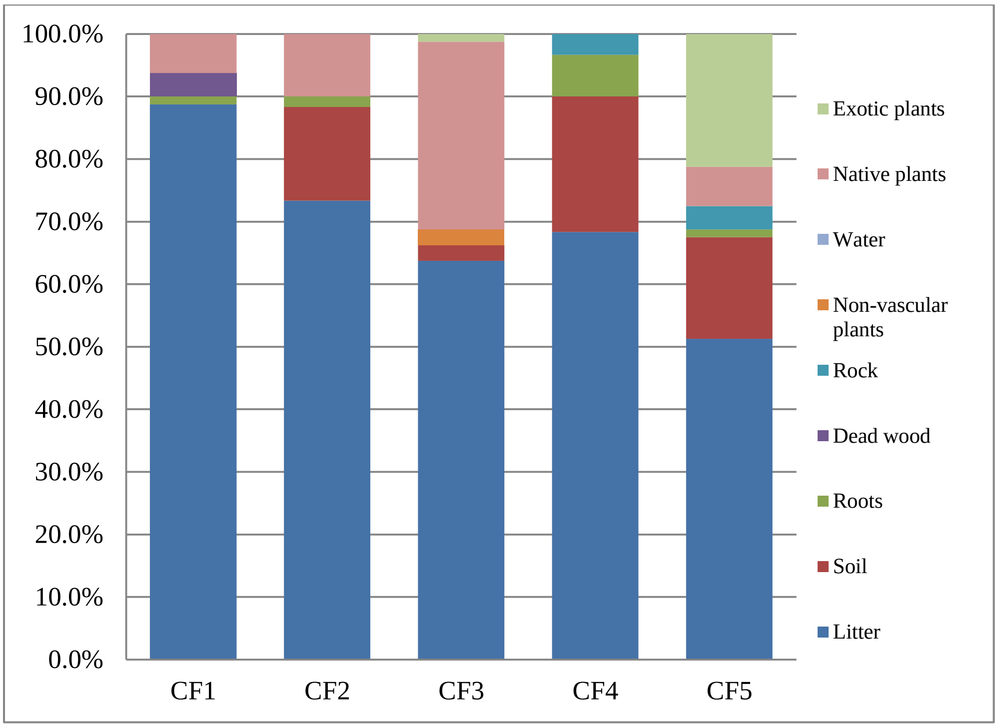

Figure 3.7: Groundcover in each of the five coastal forest categories. Groundcover includes any plants <30 cm tall.

Table 3.3: Species richness, diversity, and a comparison of the regenerating sites with the reference site (CF1) in terms of native species composition. Simpson’s diversity index is based on pooled stem, sapling, and seedling data from all plots in each category, relativized by area, and only includes woody species whereas richness data are based on Recce cover data and includes non-woody species. The species listed are those that occurred in the reference site but not in the category they are listed under.

	CF1	**CF2**	**CF3**	**CF4**	**CF5**
Number of native species	27	28	43	26	17
Number of non-native species	0	4	13	14	19
Total species richness	27	32	56	40	36
Modified Simpson's diversity index (1-D)	0.26	0.59	0.62	0.58	0.83
Number of native species in common with CF1		15	17	6	2
Missing species		12	10	21	25
		Asplenium polyodon *Coprosma grandifolia* *Coprosma lucida* *Coprosma macrocarpa* *Dysoxylum spectabile* *Hedycarya arborea* *Knightia excelsa* *Litsea calicaris* *Pittosporum umbellatum* *Ripogonum scandens* *Schefflera digitata* *Vitex lucens*	*Carex testacea* *Coprosma grandifolia* *Coprosma macrocarpa* *Dysoxylum spectabile* *Hedycarya arborea* *Litsea calicaris* *Pittosporum umbellatum* *Ripogonum scandens* *Schefflera digitata* *Vitex lucens*	*Adiantum cuninghamii* *Asplenium oblongifolium* *Asplenium polyodon* *Astelia banksii* *Carex sp.* *Carex testacea* *Coprosma grandifolia* *Coprosma lucida* *Coprosma macrocarpa* *Cyathea dealbata* *Dysoxylum spectabile* *Geniostoma rupestre var. ligustrifolium* *Hedycarya arborea* *Litsea calicaris* *Microsorum pustulatum* *Pittosporum umbellatum* *Pseudopanax arboreus* *Pseudopanax lessonii* *Ripogonum scandens* *Schefflera digitata* *Vitex lucens*	*Adiantum cuninghamii* *Asplenium oblongifolium* *Asplenium polyodon* *Astelia banksii* *Carex sp.* *Carex testacea* *Coprosma grandifolia* *Coprosma lucida* *Coprosma macrocarpa* *Cyathea dealbata* *Dysoxylum spectabile* *Geniostoma rupestre var. ligustrifolium* *Hedycarya arborea* *Litsea calicaris* *Macropiper excelsum* *Melicytus ramiflorus* *Microsorum pustulatum* *Myrsine australis* *Pittosporum umbellatum* *Polystichum richardii* *Pseudopanax arboreus* *Pseudopanax lessonii* *Ripogonum scandens* *Schefflera digitata* *Vitex lucens*

3.1.6 Species diversity

The reference forest on Tuhua (CF1) had the lowest diversity and lowest overall species richness with just 27 species, while CF3 had the highest number of species at 56, although 13 of those were non-native (Table 3.3). The youngest site CF5 had the highest diversity. Categories CF2 and CF4 had a similar number of native species to CF1 but less than half of the native species in each of those sites were also in CF1. In general the number of missing species (i.e. those that did not occur in the younger categories but were present in the reference forest) increased towards the younger stands, as did the number of exotic species.

3.1.7 NMS and MRPP

The NMS ordination of coastal forest basal area data produced a 2-dimensional plot with final stress of 16.029 after 49 iterations (Figure 3.8). The plot was rotated to align with the heat load variable after which axis 1 accounted for 31.9% of the variation in the community and axis 2 accounted for 28.4%.

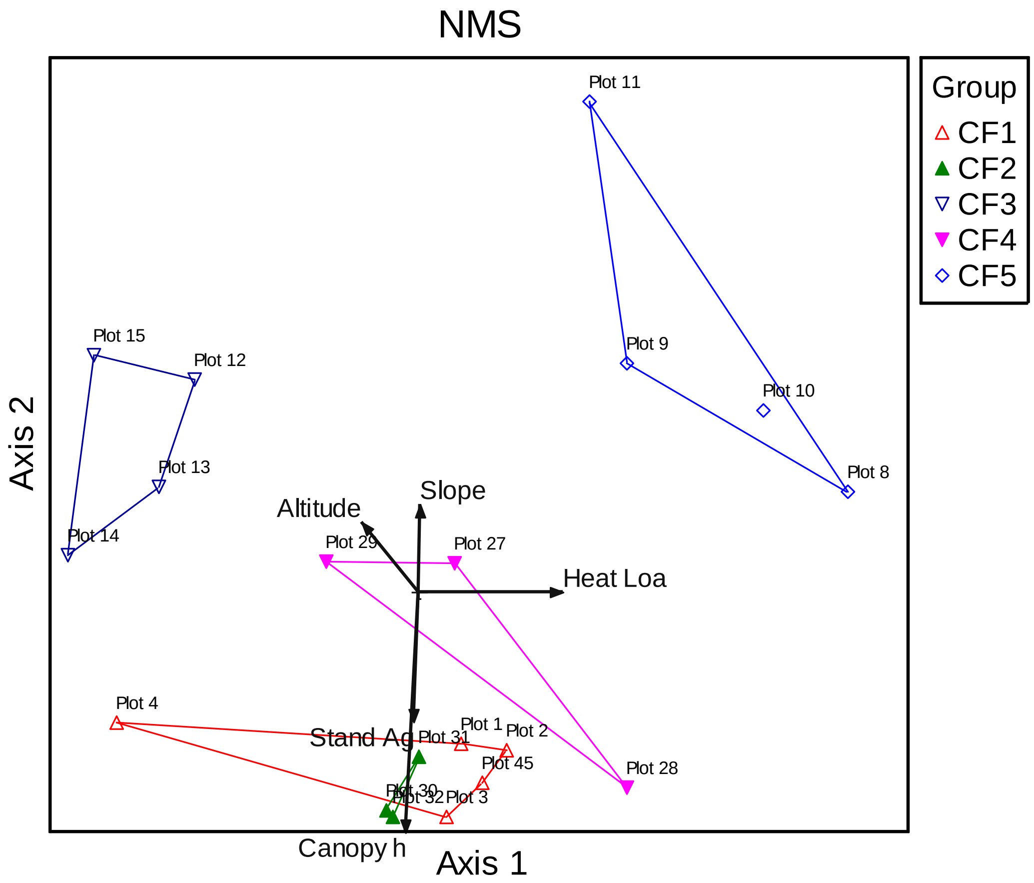

Figure 3.8: NMS ordination plot of 38 species and 19 coastal forest plots based on un-relativized basal area data and eight environmental, biotic, and physical variables. Groups were pre-defined according to the study design.

Forest categories were clearly separated in ordination space except for CF1 and CF2 which overlapped somewhat, indicating similarities in the vegetation and physical conditions. Axis 1 had a weak correlation with heat load (r^2=0.369) and axis 2 had a moderate correlation with canopy height (r^2=0.617) and a weak correlation with stand age (r^2=0.334). The ordination largely captures the developmental sequence from the youngest plots at the top right to the oldest plots at the bottom left which may indicate a progression towards the desired tall forest state.

MRPP analysis of the coastal forest categories showed a significant result (A = 0.501, $p < 0.001$), indicating that the groups are indeed significantly different. The high chance-corrected within group agreement (A) indicates strong similarities within groups.

Pair-wise comparisons showed statistically significant differences between all groups (Table 3.4) at the α = 0.1 level and with the Holm-Bonferroni procedure applied. The strongest differentiation was between CF1 and CF5 while the weakest was between CF1 and CF2. This is consistent with the NMS ordination.

Table 3.4: MRPP pair-wise comparisons for coastal forest categories. The more negative the test statistic (T) becomes the stronger the separation between groups while the larger the within-group agreement (A) becomes the more similarity there is within groups (McCune & Grace 2002).

Compared groups			T	A	p	Holm-Bonferroni correction of α
CF1	vs.	CF5	-4.74271	0.367901	0.00237	0.01
CF5	vs.	CF3	-4.0643	0.391204	0.005226	0.011111111
CF1	vs.	CF3	-3.83054	0.35144	0.005249	0.0125
CF5	vs.	CF2	-3.49536	0.387755	0.008357	0.014285714
CF3	vs.	CF2	-3.25412	0.431973	0.009115	0.016666667
CF5	vs.	CF4	-3.17929	0.329932	0.009468	0.02
CF3	vs.	CF4	-3.15677	0.387755	0.010093	0.025
CF4	vs.	CF2	-2.7412	0.365079	0.023028	0.033333333
CF1	vs.	CF4	-2.19907	0.138889	0.03397	0.05
CF1	vs.	CF2	-1.51646	0.111111	0.081154	0.1

3.1.8 Temperature and Humidity

The vegetation developmental stage is reflected in the temperature and humidity results. The youngest, most open sites were warmer, drier, and had the largest range in both temperature and humidity compared with the older sites. Statistically significant differences between group means were detected for each of the six environmental variables (mean daily temperature: $F(4,1060) = 19.5$ $p < 0.001$; minimum daily temperature: $F(4,1060) = 11.32$ $p < 0.001$; maximum daily temperature: $F(4,1060) = 210.53$ $p < 0.001$; mean daily RH: Welch $F(4,527.5) = 42.8$ $p<0.001$; minimum daily RH: $F(4,1060) = 193.9$ $p < 0.001$; and maximum daily RH: Welch $F(4,524.2) = 11.6$ $p < 0.001$, refer Table 3.5). Data from Tuhua (CF1) showed no significant difference in average daily temperature when compared to the natural forest site on Mauao (CF2, $p = 0.49$) but Tuhua was significantly more humid ($p < 0.001$) and had a smaller range in temperature and humidity with differences in minimum temperature, maximum temperature, minimum RH, and maximum RH all being statistically significant ($p < 0.05$ for all). Site CF3 was significantly cooler than the Tuhua reference forest ($p < 0.001$) and although it was cooler than the mature forest area on Mauao (CF2) this result was not statistically significant ($p = 0.099$). Site CF3 was more humid than any other site on Mauao (all $p < 0.05$) but there was no statistically significant difference in humidity when compared to CF1. The <10 year old planted site (CF5) was significantly warmer and less humid than all other sites ($p < 0.001$ for all) and it had the highest and the lowest temperatures as well as the lowest humidity. CF4, the >10 year old planted site, was significantly less humid than both of the natural forest sites (CF1 $p < 0.001$, CF2 $p < 0.001$) but there was no statistically significant difference in their average temperatures (CF1 $p = 0.997$, CF2 $p = 0.284$).

3.1.9 Soil

Soil pH was near neutral or slightly acidic in all of the five categories although it was most acidic in CF5 with a value of 6.0 (Table 3.5). Olsen P was considerably higher in CF1 than in any other site but Total Nitrogen (TN) was an order of magnitude lower in CF1 than in any other site. Total carbon (TC) was also lowest in CF1 but there were moderate levels of organic matter at all of the sites. Cation Exchange Capacity (CEC) was highest in CF1 and lowest in CF5.

Table 3.5: (a) Average physical and environmental characteristics of each coastal forest category and (b) representative soil characteristics. The values for temperature and relative humidity represent the average of the daily mean temperatures; i.e. means for each day were first calculated using the hourly readings and then these means were averaged across the whole data collection period.

(a)

	Altitude (m asl)				**Slope (°)**				**Heat Load**				**Average daily temperature (°C)**				**Average RH (%)**				**Canopy Height (m)**			
	x̄	Min	Max	s.d.	x̄	Min	Max	s.d.	x̄	Min	Max	s.d.	x̄	Min	Max	s.d.	x̄	Min	Max	s.d.	x̄	Min	Max	s.d.
CF1	59	40	90	22.19	4.8	4	5	0.45	0.94	0.93	0.94	0.00	13.2	6.0	20.4	2.46	87.2	51.0	100.0	7.44	21.60	18.00	26.00	3.65
CF2	60	30	100	36.06	30.0	30	30	0.00	0.95	0.77	1.07	0.16	12.8	3.9	23.1	2.72	83.9	48.8	100.0	7.39	20.33	15.00	24.00	4.73
CF3	128	100	180	37.75	29.3	20	37	8.10	0.79	0.66	0.90	0.10	12.1	3.5	23.1	2.87	86.6	46.5	100.0	7.92	6.00	3.00	13.00	4.76
CF4	50	40	60	10.00	23.3	20	25	2.89	0.95	0.83	1.06	0.12	13.3	4.1	24.8	2.67	82.9	43.8	100.0	9.22	5.73	4.50	7.70	1.72
CF5	86	55	120	26.89	30.0	25	35	4.08	1.04	1.01	1.07	0.03	14.3	2.8	31.5	2.61	76.2	29.6	100.0	11.11	2.15	1.80	2.50	0.40

(b)

	pH	**Olsen P (mg/L)**	**Available N (kg/ha)**	**Organic Matter (%)**	**TC (%)**	**TN (%)**	**C/N Ratio**	**K (me/100g)**	**Ca (me/100g)**	**Mg (me/100g)**	**Na (me/100g)**	**CEC (me/100g)**	**Total Base Saturation (%)**
CF1	6.8	47	97	10.7	6.2	0.37	16.6	1.17	19.2	6.39	1.15	32	86
CF2	6.5	3	142	7.5	13.5	4.3	0.32	0.53	11.5	2.65	0.3	17	90
CF3	6.2	5	188	9.4	11.4	5.4	0.48	1.24	8	3.8	0.38	19	73
CF4	6.8	8	202	9.3	10.4	5.4	0.52	1.73	10.1	4.84	0.28	20	84
CF5	6	3	101	6.7	12.6	3.9	0.31	0.61	4.2	2.19	0.22	13	56

3.2 Semi-coastal broadleaved forest

This section includes all of the results for the semi-coastal broadleaf forest type and is presented in the same order as the previous coastal forest section. Vegetation data for the key forest species as well as total values are presented.

Key canopy species selected for the semi-coastal broadleaved forest were *Alectryon excelsus*, *Beilschmiedia tawa*, *Dysoxylum spectabile*, *Knightia excelsa*, and *Vitex lucens*, while understorey species were *Cyathea dealbata*, *Cyathea medullaris*, *Geniostoma rupestre* var. *ligustrifolium*, *Hedycarya arborea*, *Macropiper excelsum*, and *Melicytus ramiflorus*. These species were selected based on personal knowledge of the vegetation type being studied and the composition of the reference forests.

3.2.1 Abundance of key semi-coastal forest species

Total basal area ranged from 29.6 m^2ha^{-1} in the >20 year old planted site (SC3) up to 39.9 m^2ha^{-1} in the old-growth sites (SC1), while total density increased with stand age from 8,921 stems ha^{-1} in SC5 up to 30,282 stems ha^{-1} in SC1 (Table 3.6). *Beilschmiedia tawa* (hereafter *Beilschmiedia*) had a high basal area but low density in the old-growth SC1 category, indicating widely spaced large trees. *Dysoxylum* had a high density in SC1 as well as a moderate basal area. Both *Dysoxylum* and *Beilschmiedia* were absent from any other category. *Alectryon excelsus* was present in the two planted categories (SC3, SC4) but was absent from the natural forest plots. *Knightia excelsa* was present in high densities in the old-growth SC1 category and very low densities in the >20 year old planted sites (SC3).

In the understorey the tree ferns *Cyathea dealbata* and *C. medullaris* were present in all categories, having low densities in the younger sites and much higher densities in the older sites. *Cyathea medullaris* had a particularly high basal area in the natural regenerating SC2 category. *Geniostoma rupestre* var. *ligustrifolium* had a very high density in SC2 and its corresponding basal area was relatively low. *Geniostoma rupestre* var. *ligustrifolium* was present in all categories. *Hedycarya arborea* was present only in the old-growth SC1 category where it had a high density and relatively low basal area, indicating high numbers of small plants. *Melicytus ramiflorus* showed a clear increase in density from the youngest category (SC4) through to the old-growth forest (SC1) although the basal area was low in all categories.

Table 3.6: Mean basal area (BA, $m^2 ha^{-1}$) and density (D, individuals ha^{-1}) comparison of key semi-coastal forest species.

	SC1		SC2		SC3		SC4	
Canopy trees	BA	D	BA	D	BA	D	BA	D
Alectryon excelsus	0.0	0.0	0.0	0.0	1.2	18.9	4.1	103.4
Beilschmiedia tawa	18.4	118.9	0.0	0.0	0.0	0.0	0.0	0.0
Dysoxylum spectabile	6.2	2827.3	0.0	0.0	0.0	0.0	0.0	0.0
Knightia excelsa	1.8	2511.3	0.0	0.0	1.4	32.7	0.0	0.0
Vitex lucens	2.4	32.0	0.0	0.0	0.0	0.0	0.0	19.4
Sub-canopy trees & shrubs								
Cyathea dealbata	0.7	2410.1	3.1	184.3	0.0	49.7	0.0	21.2
Cyathea medullaris	2.7	907.7	28.1	998.7	1.6	98.4	3.4	84.3
Geniostoma rupestre var. ligustrifolium	0.1	872.1	0.9	7932.0	0.0	0.0	0.1	25.9
Hedycarya arborea	3.8	4606.2	0.0	0.0	0.0	0.0	0.0	0.0
Macropiper excelsum	1.9	6032.3	0.0	1938.4	0.0	93.8	0.2	58.1
Melicytus ramiflorus	1.1	7198.6	1.3	472.4	0.5	222.7	0.8	75.1
Total (all species)	**39.9**	**30282.8**	**36.3**	**21636.4**	**29.6**	**20431.1**	**36.5**	**8921.3**

3.2.1 Population structure of key semi-coastal forest species

The population structures of species in the semi-coastal forest show a trend from cohorts of small early-succession trees in the youngest sites, to large trees and more complex structure in the reference forest (Figure 3.9-Figure 3.12).

In the old growth forest (SC1, Figure 3.9) *Beilschmiedia* was present in all size classes except the seedlings and saplings and reached its highest density of 53.2 individuals ha^{-1} in the 30-50 cm class. *Dysoxylum* was present in all classes except the 50-70 cm class and was most dense in the seedlings and saplings (2485.8 ha^{-1} and 272.6 ha^{-1} respectively) and least dense in the largest category. *Vitex lucens* was present in the 50-70 cm size class in low densities, as well as in the sapling class. The understorey species all had high densities of seedlings but steadily decreased into the larger classes.

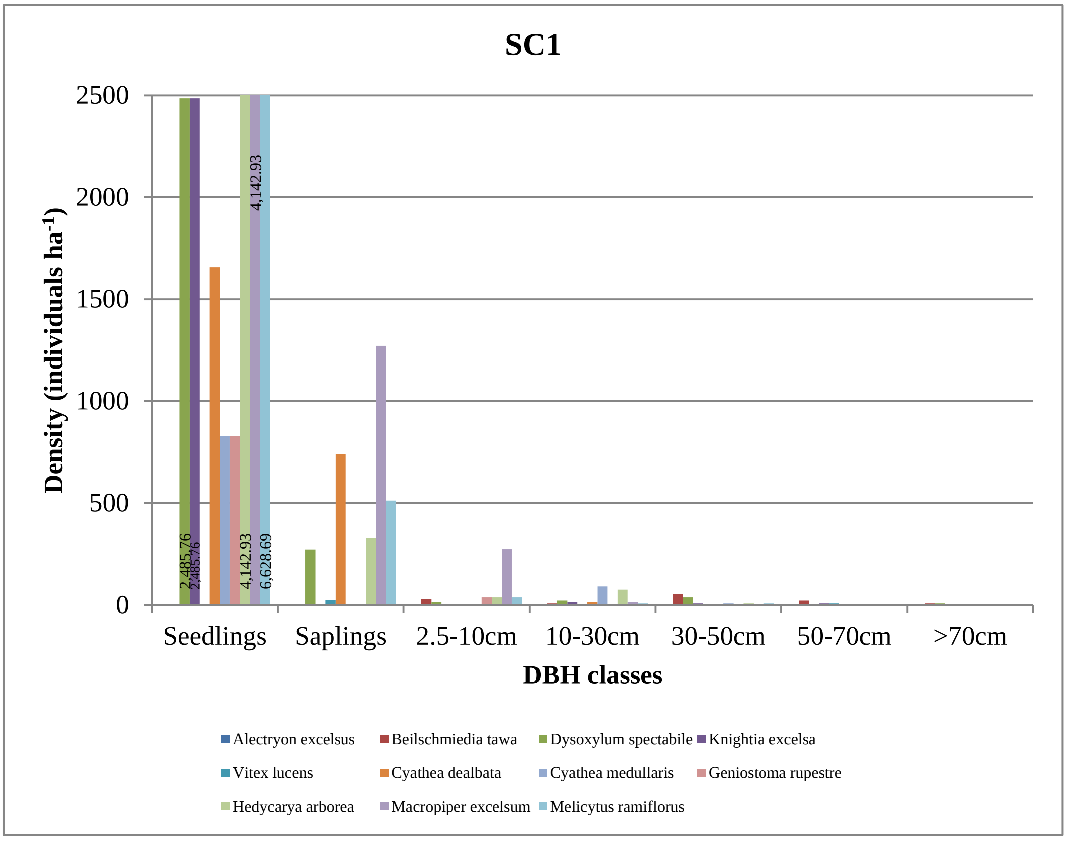

Figure 3.9: Density of individuals in seven size classes in category SC1. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall. Truncated seedling data includes Hedycarya arborea 4143, Macropiper excelsum 4143, and Melicytus ramiflorus 6629.

None of the key semi-coastal canopy species were present in the naturally regenerating sites (SC2, Figure 3.10). Mature *Cyathea medullaris* had the highest density of any species in the 10-30 cm size class and were also present in the 2.5-10 cm and sapling classes. *Melicytus ramiflorus* was present in moderate density in the sapling class and decreased over the two larger classes. *Geniostoma rupestre* var. *ligustrifolium* was very dense in the seedling class and decreased over the two larger classes. *Macropiper excelsum* showed a similar pattern although at lower density. Exotic *Ligustrum sinense* and *Prunus campanulata* were also common in this category.

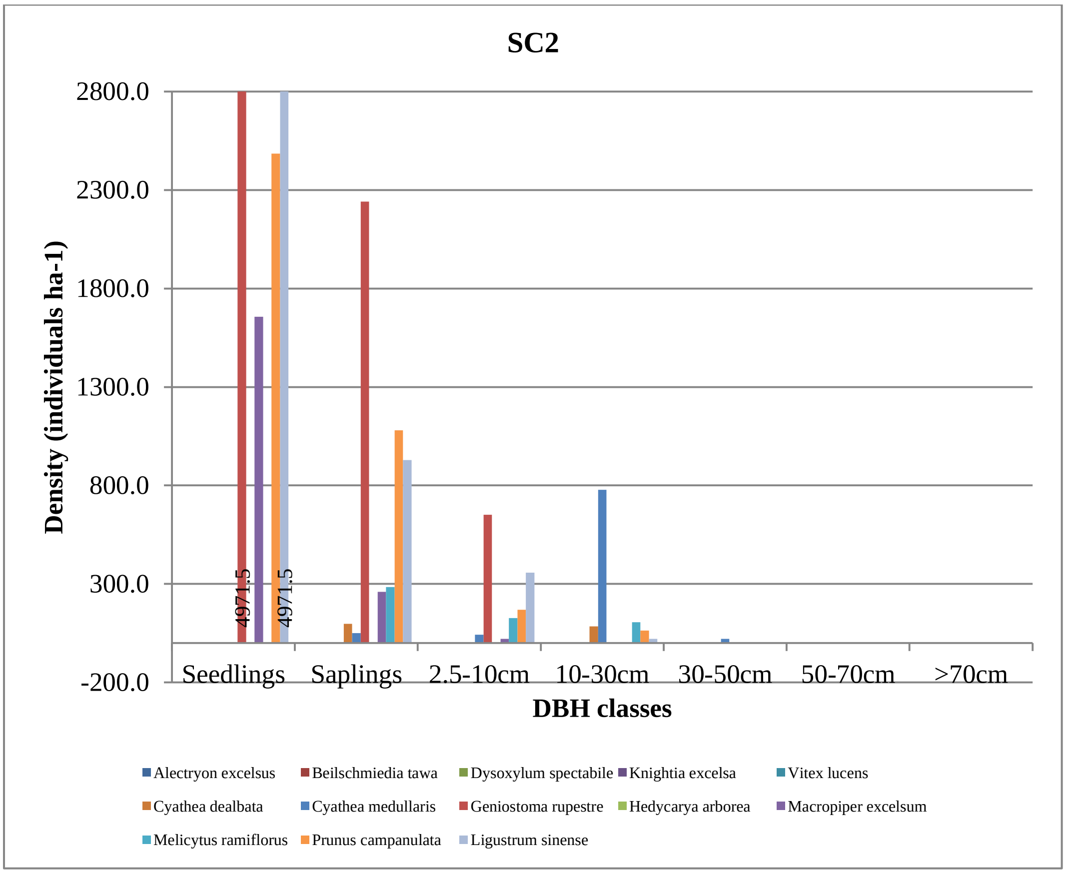

Figure 3.10: Density of individuals in seven size classes in category SC2. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall. The values for the truncated bars are included at the base of the bar.

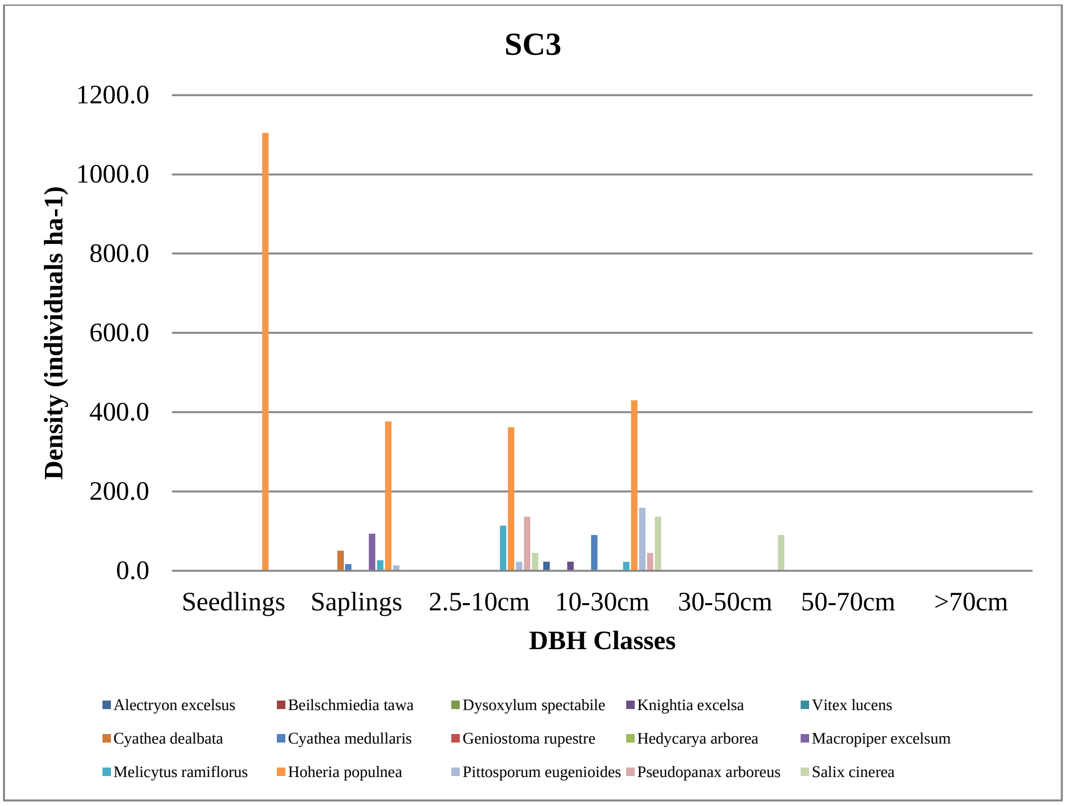

Figure 3.11: Density of individuals in seven size classes in category SC3. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

In the >25 year old planted site (SC3, Figure 3.11) none of the key species are present as seedlings and *Knightia excelsa* and *Alectryon excelsus* are the only large canopy tree species present, both at relatively low densities and only in the 10-30 cm size class. The two tree ferns *Cyathea dealbata* and *C. medullaris* were significant components. *Melicytus ramiflorus* was most dense in the 2.5-10 cm size class (113.2 ha^{-1}) but substantially less dense in the next smallest and next largest classes.

Two key canopy species were present in the 10-20 year old planted sites (SC4, Figure 3.12): *Alectryon excelsus* and *Vitex lucens*. *Vitex* was only recorded in the 2.5-10 cm DBH class at relatively low density while *Alectryon* was present in the 10-30 cm class at moderate density and in the larger 30-50 cm class at low density. The black tree fern *Cyathea medullaris* was relatively abundant in the 10-30 cm size class while *Macropiper excelsum* was the most abundant species in the 2.5-10 cm class. Overall the density in all classes in this category was considerably lower than in other semi-coastal forest classes.

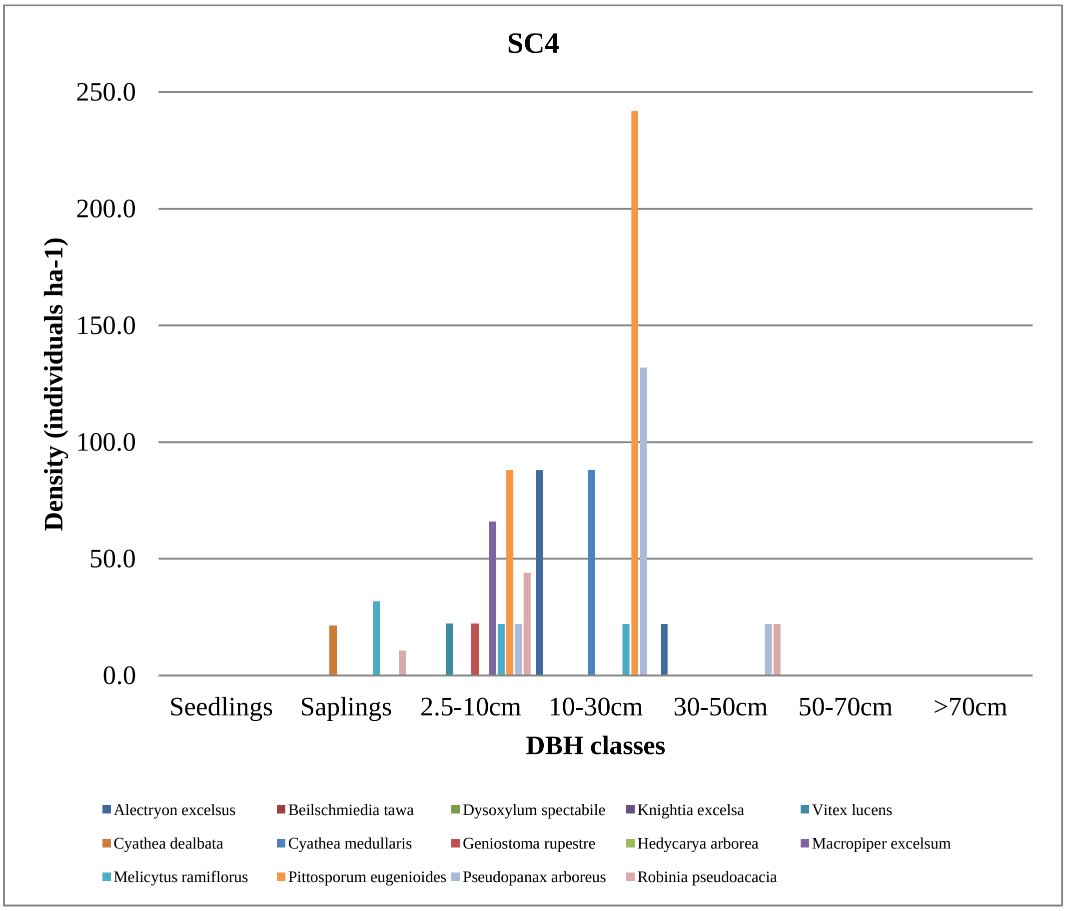

Figure 3.12: Density of individuals in seven size classes in category SC4. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

3.2.2 Formal vegetation name

Formal vegetation names show considerable variation in canopy dominants across the four semi-coastal forest categories (Table 3.7).

Table 3.7: Vegetation names for each of the four semi-coastal forest categories. Underlined species have a cover of ≥50%, species with no underlining and no brackets have a cover of 20-49%, round brackets indicate cover of 10-19% while square brackets indicate cover of 1-9%. Species in different canopy tiers are separated by a / whereas species within the same tier are separated by a -.

Category	Vegetation name
SC1	<u>*Beilschmiedia tawa*</u> - *Dysoxylum spectabile / (Macropiper excelsum) - (Cyathea dealbata)* forest
SC2	<u>*Cyathea medullaris*</u> - *Prunus campanulata / [Geniostoma rupestre var. ligustrifolium] - [Ligustrum sinense] - [Cyathea dealbata]* forest
SC3	*(Hoheria populnea) - (Pittosporum eugenioides) / (Pseudopanax arboreus) / (Tradescantia fluminensis)* forest
SC4	*Pittosporum eugenioides - (Pseudopanax arboreus) - (Robinia pseudoacacia)* forest

3.2.3 Vegetation Cover

Native and exotic vegetation cover in six height tiers for each of the four semi-coastal forest categories is detailed in Figure 3.13. The old-growth forest in category SC1 had very high canopy cover in the 12-25 m tier and the vegetation extended above 25 m. There was also moderate cover (above 30%) in the sub-canopy and small shrub tiers (5-12 m and 0.3-2 m respectively). No exotic species were recorded in SC1. The canopy in the naturally regenerating category (SC2) was in the 5-12m tier where cover was over 60%; at least 20% of which was exotic species. The graphs for the two planted categories (SC2 and SC3) both show high cover values in the 5-12 m tier and both categories include exotic species in every tier. The cover in the three lowest tiers of SC4 is less than in any other category, indicating a sparse understorey and groundcover.

3.2.4 Groundcover

Groundcover data from the semi-coastal forest plots (Figure 3.14) showed the highest cover of litter and native plants was in the old-growth sites (SC1). The highest cover of exotic plants was in SC2 and SC3 (22.5% and 23.3% respectively) and there were no exotic species recorded in the groundcover of the old-growth sites.

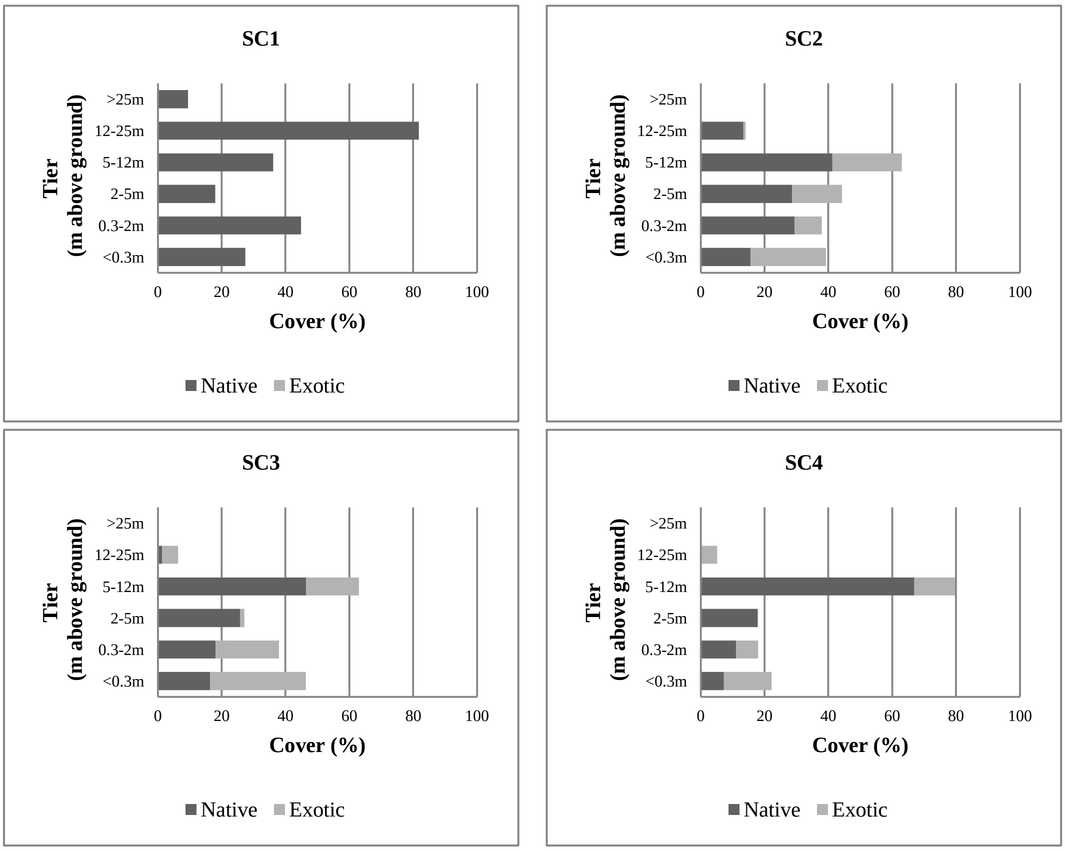

Figure 3.13: Cover of native and exotic species in each of six vegetation tiers of the four semi-coastal forest categories.

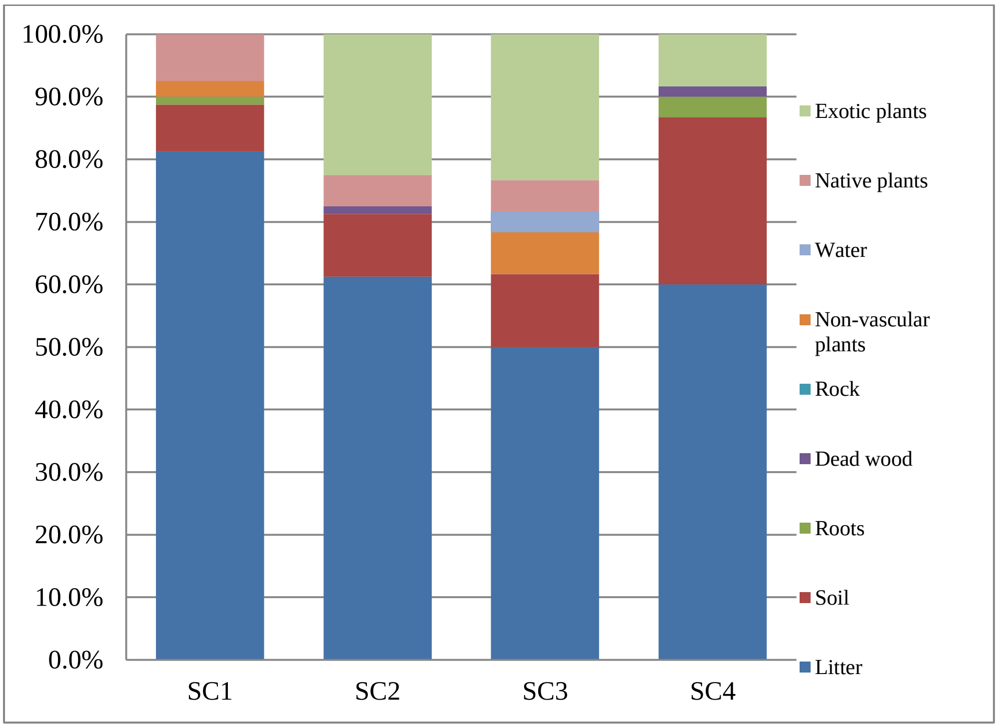

Figure 3.14: Groundcover in each of the four semi-coastal forest categories. Groundcover includes plants <30cm tall at the intercept point.

3.2.5 Species diversity

Diversity in the semi-coastal forest categories was similar throughout although SC3 was slightly more diverse (1-D = 0.81) compared with the other categories (Table 3.8). Category SC3 had the highest species richness and had only four less native species than SC1 which had the highest native species richness. The three regenerating categories SC2, SC3, and SC4 had relatively low species commonality with SC1 (11, 10, and 8 species respectively). The species missing from the younger forest categories include important canopy species like *Beilschmiedia tawa* and *Alectryon excelsus* as well as many understorey and epiphyte species.

Table 3.8: Species richness, diversity, and a comparison of the regenerating sites with the reference site (SC1) in terms of native species composition. Simpson's diversity index is based on pooled stem, sapling, and seedling data from all plots in each category, relativized by area, and only includes woody species whereas richness data are based on Recce cover data and includes non-woody species. The species listed are those that occurred in the reference site but not in the category they are listed under.

	SC1	SC2	SC3	SC4
Number of native species	40	20	36	34
Number of non-native species	0	13	23	16
Total species richness	40	33	59	50
Modified Simpson's diversity index (1-D)	0.73	0.74	0.81	0.72
Number of native species in common with CF1		11	10	8
Missing species		29	30	32
		Alectryon excelsus	*Asplenium bulbiferum*	*Asplenium bulbiferum*
		Asplenium bulbiferum	*Asplenium oblongifolium*	*Asplenium flaccidum*
		Asplenium flaccidum	*Asplenium polyodon*	*Asplenium oblongifolium*
		Asplenium oblongifolium	*Beilschmiedia tawa*	*Asplenium polyodon*
		Asplenium polyodon	*Blechnum chambersii*	*Beilschmiedia tawa*
		Beilschmiedia tawa	*Blechnum discolor*	*Blechnum chambersii*
		Blechnum discolor	*Blechnum filiforme*	*Blechnum discolor*
		Coprosma grandifolia	*Coprosma spathulata*	*Blechnum filiforme*
		Coprosma spathulata	*Dysoxylum spectabile*	*Coprosma grandifolia*
		Cyathea smithii	*Freycinetia banksii*	*Coprosma spathulata*
		Dysoxylum spectabile	*Geniostoma rupestre var. ligustrifolium*	*Cyathea smithii*
		Freycinetia banksii	*Hedycarya arborea*	*Dysoxylum spectabile*
		Hedycarya arborea	*Hymenophyllum demissum*	*Freycinetia banksii*
		Hymenophyllum demissum	*Lastreopsis glabella*	*Hedycarya arborea*
		Knightia excelsa	*Laurelia novae-zelandiae*	*Hymenophyllum demissum*
		Lastreopsis glabella	*Litsea calicaris*	*Lastreopsis glabella*
		Laurelia novae-zelandiae	*Lygodium articulatum*	*Laurelia novae-zelandiae*
		Litsea calicaris	*Metrosideros fulgens*	*Litsea calicaris*
		Metrosideros fulgens	*Metrosideros perforata*	*Lygodium articulatum*
		Metrosideros perforata	*Microsorum scandens*	*Metrosideros fulgens*
		Microsorum scandens	*Myrsine australis*	*Metrosideros perforata*
		Myrsine australis	*Oplismenus hirtellus subsp. Imbecillus*	*Microsorum scandens*
		Oplismenus hirtellus subsp. Imbecillus	*Pneumatopteris pennigera*	*Myrsine australis*
		Pseudopanax crassifolius	*Pseudopanax crassifolius*	*Oplismenus hirtellus subsp. Imbecillus*
		Rhopalostylis sapida	*Pyrrosia elaeagnifolia*	*Pneumatopteris pennigera*
		Ripogonum scandens	*Rhopalostylis sapida*	*Pseudopanax crassifolius*
		Schefflera digitata	*Ripogonum scandens*	*Pteris macilenta*
		Streblus heterophyllus	*Schefflera digitata*	*Pyrrosia elaeagnifolia*
		Vitex lucens	*Streblus heterophyllus*	*Rhopalostylis sapida*
			Vitex lucens	*Ripogonum scandens*
				Schefflera digitata

3.2.6 NMS and MRPP

An NMS ordination of the semi-coastal forest basal area data resulted in 3-dimensional plot with final stress of 7.585 after 88 iterations (Figure 3.15). Consistent with the coastal forest NMS the plot was rotated to align with the heat load variable. The three axes accounted for 73.1% of the variation in the community data with axis 1, aligned with heat load, accounting for 30.3%, axis 2 accounting for 28.7% and the final axis accounting for 14.1%.

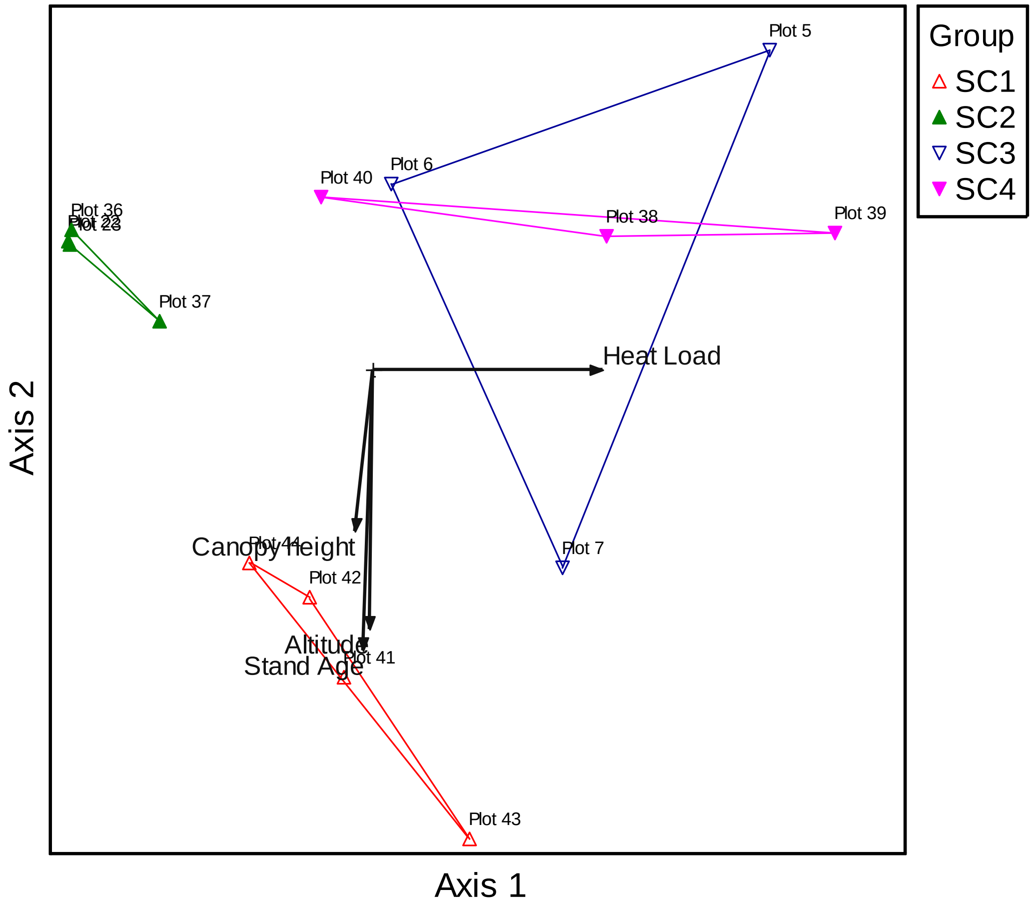

Figure 3.15: NMS ordination bi-plot of 41 species and 14 coastal forest plots based on un-relativized basal area data and eight environmental, biotic, and physical variables. Groups were pre-defined as per the study design.

The four forest categories are generally well separated and the ordination captures the developmental sequence to some degree although the two planted categories (SC3 and SC4) were not well differentiated from each other. Axis 1 was correlated with heat load (r^2 = 0.582) while axis 2 was strongly correlated to stand age (r^2 = 0.711) and altitude (r^2 = 0.658).

MRPP analysis showed a significant overall difference between groups (*A* = 0.326, p = 0.002). The moderately high chance-corrected agreement value (*A*) indicates a reasonably high level of similarity with groups. Pair-wise comparisons (Table 3.9) showed significant differences between all groups except SC3 and SC4. The comparison between SC1 and SC2 resulted in the strongest dissimilarity and had the highest within-group agreement.

Table 3.9: MRPP pair-wise comparisons between all semi-coastal forest categories. T is the test statistic, and A is the chance-corrected within group agreement.

Compared groups			T	A	p	Holm-Bonferroni correction of α
SC2	vs.	SC1	-4.00076	0.425926	0.006679	0.016667
SC3	vs.	SC2	-3.02525	0.19898	0.011942	0.02
SC4	vs.	SC1	-2.83045	0.272109	0.012581	0.025
SC3	vs.	SC1	-2.29478	0.171769	0.016874	0.033333
SC2	vs.	SC4	-2.34417	0.207483	0.021683	0.05
SC3	vs.	SC4	2.060408	-0.2381	0.9744	0.1

3.2.7 Temperature and Humidity

Temperatures in the semi-coastal forest sites ranged from an overall minimum temperature of -1.6 °C to an overall maximum of 24.8 °C (Table 3.10). Significant differences in average minimum temperature, average maximum temperature, average RH, average minimum RH, and average maximum RH were detected (minimum daily temperature: Welch $F(3,419.9) = 10.39$ $p < 0.001$; maximum daily temperature: $F(3,779) = 43.73$ $p < 0.001$); mean daily RH: $F(3,779) = 24.0$ $p < 0.001$; minimum daily RH: $F(3,779) = 36.39$ $p < 0.001$; and maximum daily RH: Welch $F(3,424.8) = 75.05$ $p < 0.001$) by ANOVA. The differences in mean daily temperature were not significant across the four categories (Welch $F(3,424.5) = 1.82$ $p = 0.143$). Furthermore, Tukey HSD tests revealed that there were no significant differences in average temperature between any of the four categories. However, the old-growth forest site (SC1) had a smaller temperature range than any of the other sites with higher average minimum temperature (all $p < 0.01$) and lower average maximum temperature (all $p < 0.001$). The youngest site (SC4) also had a significantly higher average daily maximum temperature than SC2 or SC3 ($p < 0.001$ for both).

Mean daily RH was higher in SC1 than in SC2 ($p = 0.03$) and SC4 ($p < 0.001$). However, SC3 had the highest mean daily RH at 90.7% which was significantly higher than all other sites (all $p < 0.001$). The old-growth site (SC1) had a smaller humidity range than the other sites with the highest mean daily minimum RH and the second lowest mean daily maximum RH. Site SC4, the youngest planted site, had the lowest average humidity, statistically significant compared with SC1 ($p < 0.001$) and SC3 ($p < 0.001$) but not compared with SC2 ($p = 0.32$).

3.2.8 Soil

The pH in this forest type was very low and ranged from 5.1 in SC1 to 5.8 in SC4 (Table 3.10), considerably lower than in the coastal forest sites. Olsen P values were very low in all sites. Total N, Available N, and Total C were highest at the old-growth SC1 site, and Total N and Total C were lowest in SC2. CEC was also lowest in SC2 and highest in SC1 although SC4 had a similarly high value. High levels of organic matter were found in the reference forest but he naturally regenerating site had relatively low organic matter. The two planted sites at Johnson reserve had moderate levels of organic matter but the youngest site (SC4) had relatively low available N.

Table 3.10: (a) Average physical and environmental characteristics of each semi-coastal forest category and (b) representative soil characteristics. The values for temperature and relative humidity represent the average of the daily mean temperatures; i.e. means for each day were first calculated using the hourly readings and then these means were averaged across the whole data collection period.

(a)

	Altitude (m asl)				Slope (°)				Heat Load				Average daily temperature (°C)				Average RH (%)				Canopy Height (m)			
	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.
SC1	145	120	180	25.17	17.5	10	30	8.66	0.79	0.59	0.92	0.14	11.4	2.0	22.4	2.79	88.0	54.8	100.0	7.00	21.25	17.00	26.00	4.43
SC2	15	10	20	5.77	26.3	15	35	8.54	0.67	0.52	0.80	0.12	11.5	-0.9	24.7	3.33	86.1	46.5	99.0	6.57	10.25	8.00	13.00	2.63
SC3	17	5	25	10.41	14.0	2	30	14.42	0.96	0.93	0.98	0.03	11.3	-1.6	23.5	3.49	90.7	48.1	100.0	7.12	8.00	5.00	10.00	2.65
SC4	12	10	15	2.89	18.3	10	25	7.64	0.91	0.70	1.06	0.19	12.1	-0.7	24.8	3.42	84.9	40.9	100.0	7.61	9.50	8.00	10.50	1.32

(b)

	pH	Olsen P (mg/L)	Available N (kg/ha)	Organic Matter (%)	TC (%)	TN (%)	C/N Ratio	K (me/100g)	Ca (me/100g)	Mg (me/100g)	Na (me/100g)	CEC (me/100g)	Total Base Saturation (%)
SC1	5.1	2	193	22	12.8	0.8	15.9	0.37	3	1.43	0.2	32	16
SC2	5.6	2	101	7	4.1	0.28	14.6	1.12	5.3	1.96	0.17	17	50
SC3	5.7	2	135	10.7	6.2	0.45	13.9	0.66	7.2	2.42	0.23	22	47
SC4	5.8	5	98	15.6	9	0.74	12.2	1.11	9.7	1.9	0.19	31	42

3.3 Swamp forest

3.3.1 Abundance of key swamp forest species

The data from the swamp forest sites showed that four large tree species dominated the old-growth site (SF1, Table 3.11). *Alectryon excelsus* had the highest density with over 2,500 stems per hectare although the basal area was relatively low (Table 3.11). *Laurelia novae-zelandiae* and *Beilschmiedia tawa* had the highest basal areas in SF1 but neither were present in any other category. *Dacrycarpus dacrydioides* was present in the two planted categories (SF3, SF4) as well as the old-growth site (SF1). Grey willow (*Salix cinerea*) had a high density in the youngest sites (SF4) as well as in SF2 where it also had a relatively high basal area.

Table 3.11: Mean basal area (BA, m^2ha^{-1}) and density (D, individuals ha^{-1}) comparison of key swamp forest species.

	SF1		SF2		SF3		SF4	
Canopy trees	BA	D	BA	D	BA	D	BA	D
Alectryon excelsus	3.1	2560.8	0.0	0.0	0.0	0.0	0.0	0.0
Beilschmiedia tawa	20.3	877.4	0.0	0.0	0.0	0.0	0.0	0.0
Dacrycarpus dacrydioides	12.0	50.0	0.0	0.0	4.6	332.1	0.0	252.2
Cordyline australis	2.6	12.5	0.0	38.3	48.0	1130.3	0.8	555.0
Laurelia novae-zelandiae	50.7	388.7	0.0	0.0	0.0	0.0	0.0	0.0
Leptospermum scoparium	0.0	0.0	0.0	0.0	0.4	66.9	0.3	1015.0
Salix cinerea	0.0	0.0	31.1	1752.4	0.0	0.0	0.0	1126.0
Sub-canopy trees & shrubs								
Melicytus ramiflorus	14.1	688.7	0.0	0.0	0.0	0.0	0.0	0.0
Coprosma robusta	0.0	0.0	0.0	49.7	2.2	1939.0	0.1	85.9
Total (all species)	103.9	11925.8	34.8	38396.9	56.3	3766.3	2.2	3333.5

In the understorey *Coprosma robusta* was present in all sites except the old-growth and was most dense in SF3. *Melicytus ramiflorus* was only present in the old-growth forest.

Total basal area ranged from just 2.2 m^2ha^{-1} in SF4 to 103.9 m^2ha^{-1} at White Pine Bush (SF1), while total density ranged from 3,333 individuals ha^{-1} in SF4 to 38,396 individuals ha^{-1} in SF2.

3.3.2 Population structure of key swamp forest species

Like the semi-coastal forest, the population structures of the swamp forest species show small trees and shrubs, mostly in cohort stands in the planted sites, and a more complex structure and large, continuously recruiting trees in the reference forest (Figure 3.16 - Figure 3.19).

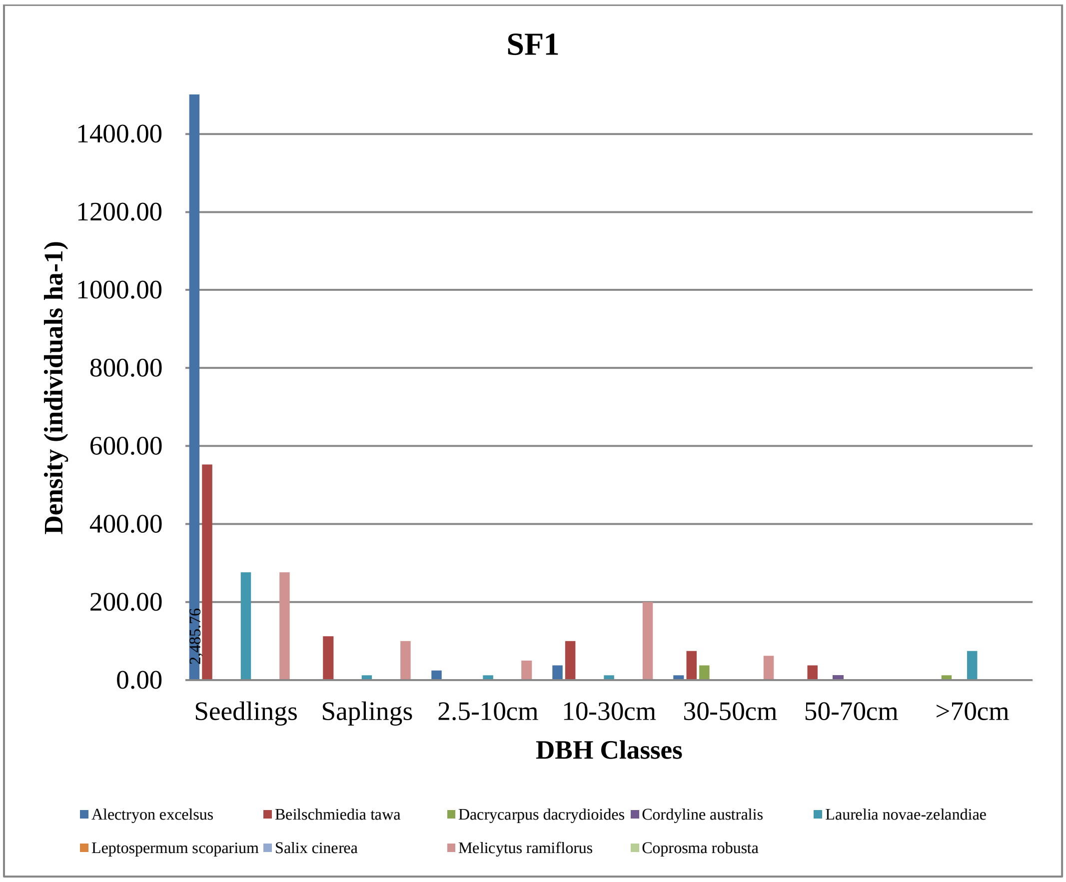

Figure 3.16: Density of individuals in seven size classes in category SF1. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall. Seedling bars have been truncated and the associated value is displayed inside the bar.

In the old growth forest (SF1) *Laurelia novae-zelandiae* and *Dacrycarpus dacrydioides* were both present in the largest size class but whereas *Laurelia* were present in several size classes including the seedlings, *Dacrycarpus* only occurred in one other class (20-50 cm DBH) and only at relatively low density (Figure 3.16). *Alectryon excelsus* seedling density was high (2485 ha^{-1}) but density was low in the larger classes and no *Alectryon* larger than 50cm DBH were recorded. *Beilschmiedia tawa* was present in a range of size classes from seedlings up to 50-70 cm DBH trees and showed a population structure which indicates continuous recruitment.

Melicytus ramiflorus was present in the classes from seedlings through to the 30-50 cm class. *Melicytus ramiflorus* showed moderate density in the seedling class and reduced over the following two size classes to peak again in the 10-30 cm class.

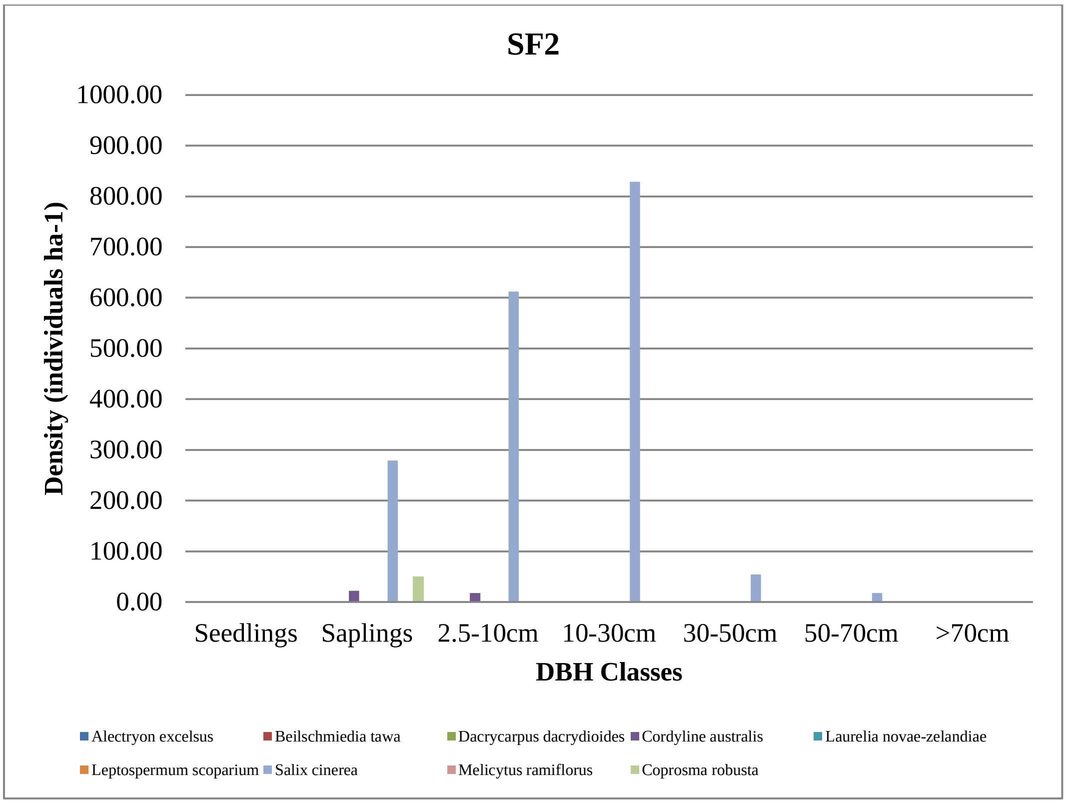

Figure 3.17: Density of individuals in seven size classes in category SF2. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

The SF2 category (Figure 3.17) was dominated by *Salix cinerea* which was present in from the seedling size class through to the 50-70 cm size class. *Salix cinerea* was most dense in the 10-30 cm size class. *Cordyline australis* was present in the sapling and 2.5-10 cm size classes at very low density and *Coprosma robusta* was present only in the saplings. Although not included in the graph, *Ligustrum sinense* was the most abundant plant with a density of more than 31,000 seedlings ha^{-1}.

In the >10 year old planted sites (SF3, Figure 3.18) *Dacrycarpus dacrydioides* was present in the 2.5-10 cm size class at low density and in the 10-30 cm class in moderate density.

Cordyline australis was present in all classes from the saplings through to the 50-70 cm class and was most dense in the 10-30 cm size class. Note that its presence in the 50-70 cm class is due to the way the data from multi-stemmed individuals was handled. *Coprosma robusta* was present in high density in the saplings and fell sharply to low density in the 10-30 cm class.

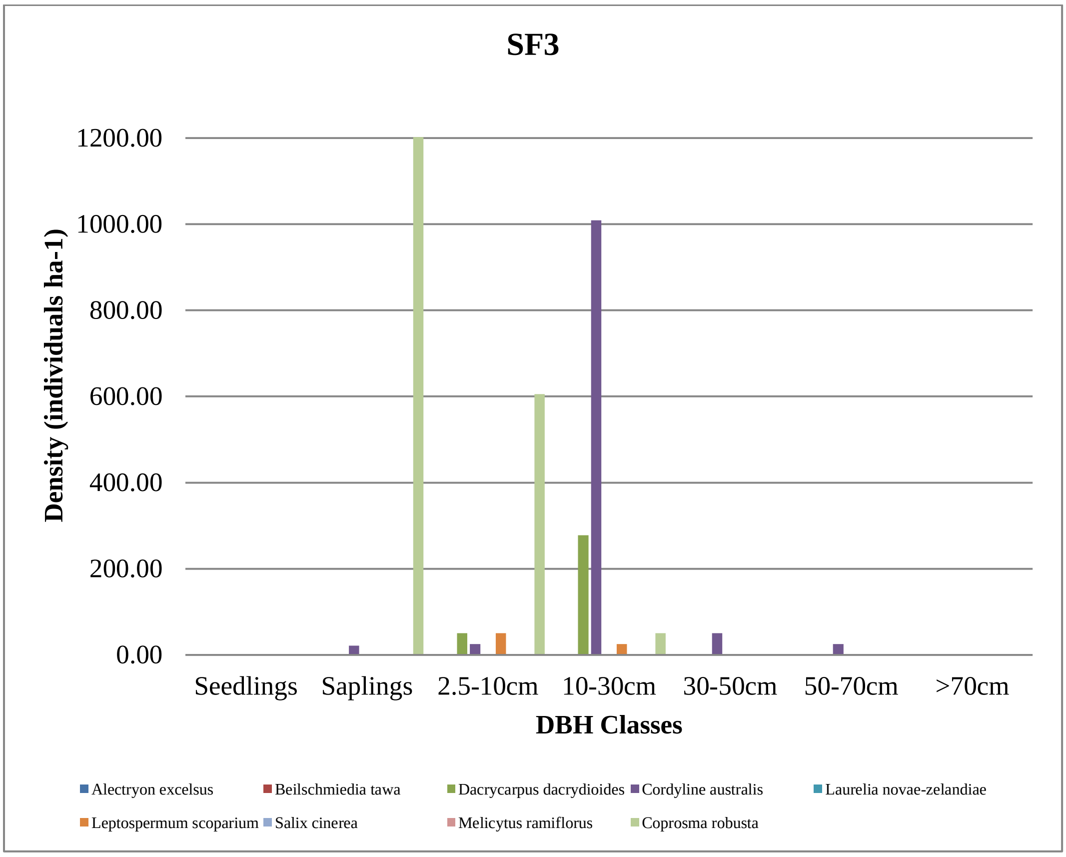

Figure 3.18: Density of individuals in seven size classes in category SF3. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

All of the key species present in the <10 year old planted site (SF4, Figure 3.19) showed a similar pattern; higher density in the smaller size classes, progressively decreasing to low densities in the middle size classes. *Dacrycarpus dacrydioides* was only present as saplings and grey willow was very dense in the seedlings but sparse in the saplings.

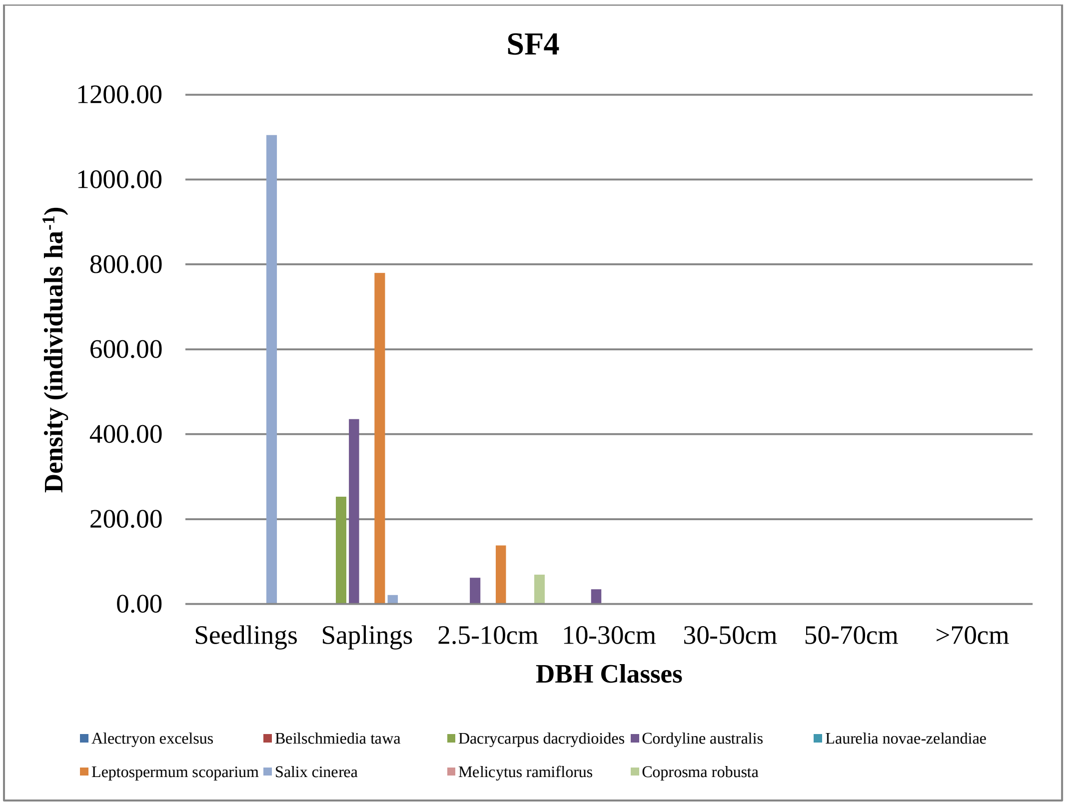

Figure 3.19: Density of individuals in seven size classes in category SF4. Saplings are >135 cm tall and <2.5 cm DBH while seedlings are >15 cm and <1.35 m tall.

3.3.3 Formal vegetation name

The considerable differences in the vegetation of each category are reflected in their names (Table 3.12).

Table 3.12: Vegetation names for each of the four swamp forest categories. Underlined species have a cover of ≥50%, species with no underlining and no brackets have a cover of 20-49%, round brackets indicate cover of 10-19% while square brackets indicate cover of 1-9%. Species in different canopy tiers are separated by a / whereas species within the same tier are separated by a -.

Vegetation Category	Vegetation name
SF1	*(Dacrycarpus dacrydioides) / Beilschmiedia tawa - Laurelia novae-zelandiae / [Melicytus ramiflorus] - [Rhopalostylis sapida]* forest
SF2	*Salix cinerea* forest
SF3	*Cordyline australis - (Dacrycarpus dacrydioides) / (Phormium tenax)* scrub
SF4	*Phormium tenax - (Leptospermum scoparium) - (Carex secta)* shrub-flaxland

3.3.4 Vegetation Cover

Cover data for the swamp forest categories presented in Figure 3.20 show clear differences between the old-growth forest of SF1 and the other three categories. The forest in SF1 had high cover in the top two tiers (12-25 m and >25 m) as well as moderately high cover in all other tiers which indicates reasonably dense vegetation in the understorey and groundcover tiers. Unlike its coastal and semi-coastal forest equivalents, SF1 did have some exotic species present, albeit in low abundance. The naturally regenerating sites (SF2) had an exclusively exotic canopy in the 5-12 m tier and moderate cover in the understorey tiers where exotic species were also dominant. The two planted categories (SF3 and SF4) had predominantly indigenous cover except in the groundcover tier (<30 cm) where there was a higher proportion of exotic species. The canopy in SF3 was between 2 m and 12 m high while that in SF4 was less than 2 m high.

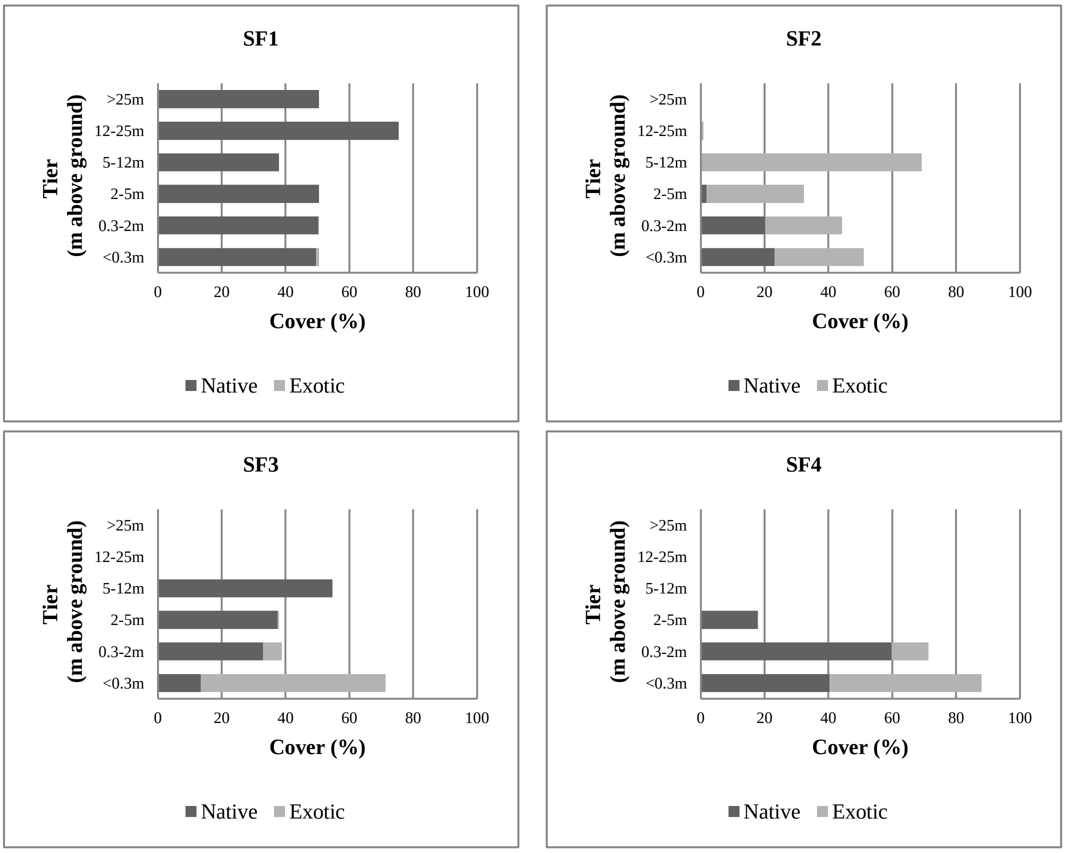

Figure 3.20: Cover of native and exotic species in each of six vegetation tiers in the four swamp forest categories.

3.3.5 Groundcover

Groundcover data for the swamp forest sites were consistent with the other forest types in that there was no exotic groundcover plants recorded in the old growth sites (Figure 3.21). The proportion of native plant cover was also highest in SF1, as was the dead wood. Exotic plant groundcover increased from SF2 (8.8%) through to SF4 (51.7%). The naturally regenerating category (SF2) had significant water cover which none of the other categories had. Litter cover was highest in SF3.

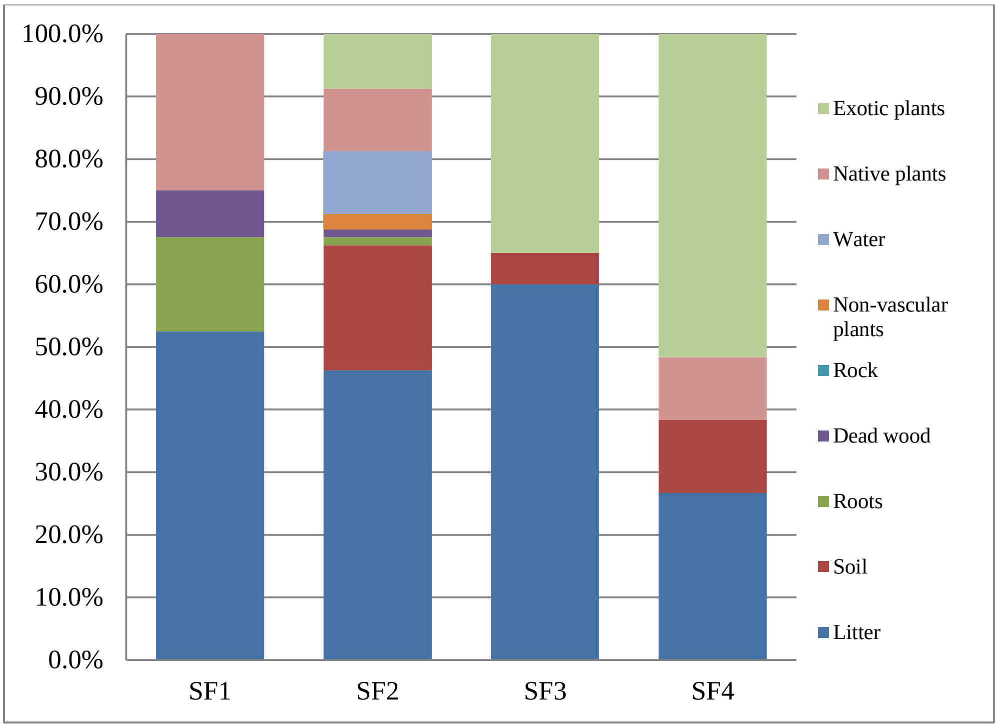

Figure 3.21: Groundcover in each of the four swamp forest categories.

3.3.6 Species diversity

The mature forest at White Pine Bush (SF1) had considerably more native species than the other swamp forest categories and was also the most diverse site (see Table 3.13). None of the regenerating sites were very similar to the reference site in terms of species composition and SC3 and SC4 had more non-native species than native ones.

Table 3.13: Species richness, diversity, and a comparison of the regenerating sites with the reference site (SF1) in terms of native species composition. The species listed are those that occurred in the reference site but not in the category they are listed under.

	SF1	SF2	SF3	SF4
Number of native spp	41	17	18	15
Number of non-native species	2	11	24	28
Total species richness	43	28	42	43
Modified Simpson's diversity index (1-D)	0.85	0.12	0.28	0.12
Number of native spp in common with CF1		6	4	2
Missing' species		36	39	40
		Alectryon excelsus Asplenium bulbiferum Asplenium oblongifolium Beilschmiedia tawa Blechnum chambersii Blechnum filiforme Carpodetus serratus Collospermum hastatum Coprosma areolata Corynocarpus laevigatus Cyathea dealbata Dacrycarpus dacrydioides Diplazium australe Freycinetia banksii Geniostoma rupestre var. ligustrifolium Hedycarya arborea Lastreopsis glabella Laurelia novae-zelandiae Litsea calicaris Macropiper excelsum Melicytus ramiflorus Metrosideros diffusa Metrosideros perforata Microlaena avenacea Microsorum scandens Oplismenus hirtellus subsp. Imbecillus Parsonsia heterophylla Pellaea rotundifolia Pneumatopteris pennigera Pteris macilenta Rhopalostylis sapida Ripogonum scandens Streblus heterophyllus Tradescantia fluminensis Uncinia uncinata Vitex lucens	Alectryon excelsus Asplenium bulbiferum Asplenium flaccidum Asplenium oblongifolium Asplenium polyodon Beilschmiedia tawa Blechnum chambersii Carpodetus serratus Collospermum hastatum Coprosma areolata Cyathea dealbata Dicksonia squarrosa Diplazium australe Freycinetia banksii Geniostoma rupestre var. ligustrifolium Hedycarya arborea Lastreopsis glabella Laurelia novae-zelandiae Ligustrum sinense Litsea calicaris Macropiper excelsum Melicytus ramiflorus Metrosideros diffusa Metrosideros perforata Microlaena avenacea Microsorum pustulatum Microsorum scandens Oplismenus hirtellus subsp. Imbecillus Parsonsia heterophylla Pellaea rotundifolia Pneumatopteris pennigera Pteris macilenta Pyrrosia elaeagnifolia Rhopalostylis sapida Ripogonum scandens Streblus heterophyllus Tradescantia fluminensis Uncinia uncinata Vitex lucens	Alectryon excelsus Asplenium bulbiferum Asplenium flaccidum Asplenium oblongifolium Asplenium polyodon Beilschmiedia tawa Blechnum chambersii Blechnum filiforme Carpodetus serratus Collospermum hastatum Coprosma areolata Corynocarpus laevigatus Cyathea dealbata Dicksonia squarrosa Diplazium australe Freycinetia banksii Geniostoma rupestre var. ligustrifolium Hedycarya arborea Lastreopsis glabella Laurelia novae-zelandiae Litsea calicaris Macropiper excelsum Melicytus ramiflorus Metrosideros diffusa Metrosideros perforata Microlaena avenacea Microsorum pustulatum Microsorum scandens Oplismenus hirtellus subsp. Imbecillus Parsonsia heterophylla Pellaea rotundifolia Pneumatopteris pennigera Pteris macilenta Pyrrosia elaeagnifolia Rhopalostylis sapida Ripogonum scandens Streblus heterophyllus Tradescantia fluminensis Uncinia uncinata Vitex lucens

3.3.7 NMS and MRPP

The autopilot mode in PC-Ord selected a 4-dimensional solution for the swamp forest NMS ordination. However, because the graphing capabilities of PC-Ord and the correlation statistics associated with it can only deal with three axes a manual NMS run was conducted with the same settings as for the other forest types, except that the number of axes was restricted to three. Final stress was 6.297 after 47 iterations. The resulting plot (Figure 3.22) was rotated to align with heat load. The three-axis solution accounted for 72.7% of the variation in the community data. Axis 1 was associated primarily with heat load (r^2 = 0.588), altitude (r^2 = 0.519), and species richness (r^2= 0.538), and accounted for 21.6% of the variation. Axis 2 was weakly related to species richness (r^2 = 0.321) and accounted for 38% of the variation, while axis 3 was weakly associated with canopy height (r^2 = 0.406) and accounted for 13.1% of the total variation.

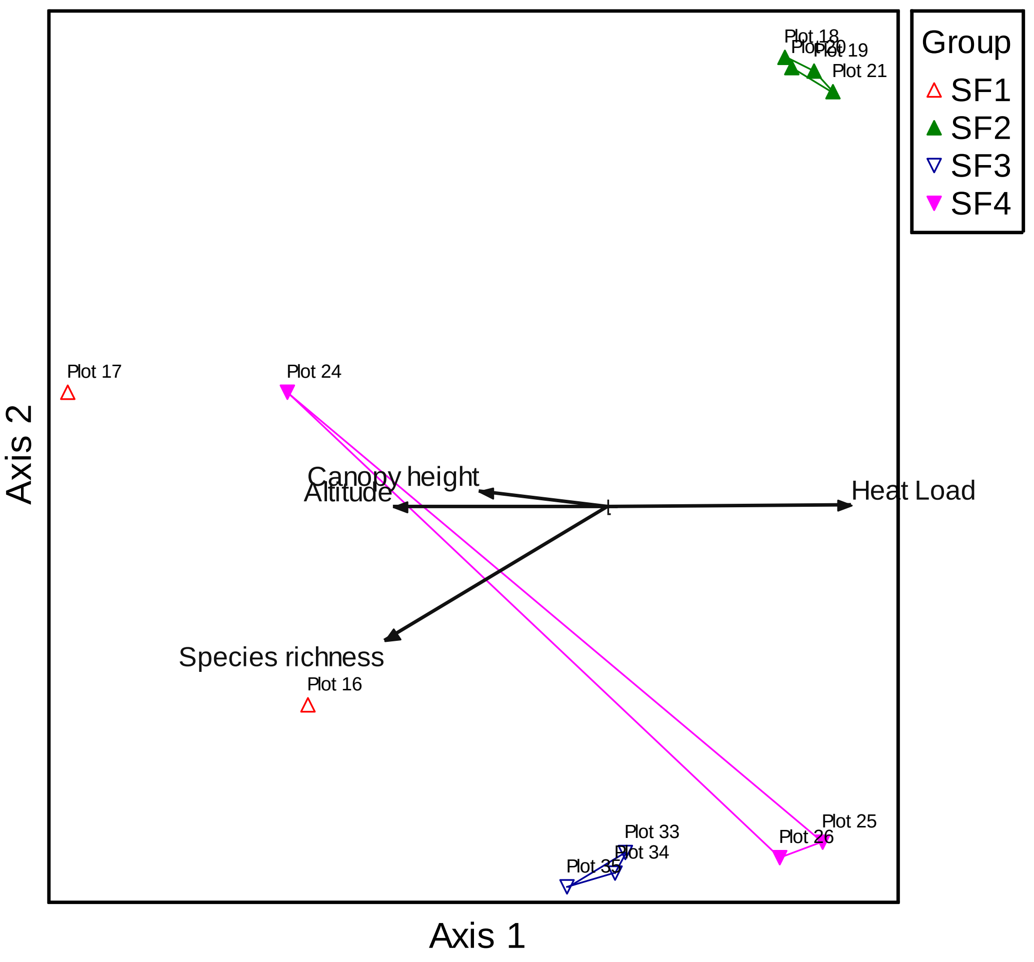

Figure 3.22: NMS ordination bi-plot of 25 species and 12 swamp forest plots based on un-relativized basal area data and eight environmental, biotic, and physical variables. Groups were pre-defined as per the study design.

The ordination plot shows a deviation from the hypothesised successional sequence: The planted plots are more closely related to the reference sites than the naturally regenerating site and the ordination shows considerable variation within the SF4 and SF1 categories.

MRPP analysis (Table 3.14) showed a significant difference between forest categories (A = 0.511, $p < 0.001$). Pair-wise comparisons showed significant differences between all groups tested although SF1 was excluded from the analysis as previously discussed.

Table 3.14: MRPP pair-wise comparisons between all swamp forest categories. T is the test statistic, and A is the chance-corrected within group agreement.

Compared groups			T	A	p	Holm-Bonferroni correction of α
11	vs.	13	-3.18727	0.255102	0.01193595	0.033333
11	vs.	12	-3.53688	0.421769	0.0100882	0.05
13	vs.	12	-2.44949	0.190476	0.0248198	0.1

3.3.8 Temperature and Humidity

Temperatures in the swamp forest sites ranged from an absolute minimum of -2.4 °C to an absolute maximum of 29.3 °C (Table 3.15). Both of these extremes were recorded in the youngest planted site (SF4). Average temperatures ranged from 10.2 °C in SF1 to 12.2 °C in SF3. ANOVA showed significant variation in and between groups for all six variables (average mean daily temperature: $F(3,848) = 13.37$, $p < 0.001$; minimum daily temperature: $F(3,848) = 13.76$ $p < 0.001$; maximum daily temperature: Welch $F(3,469) = 92.1$ $p < 0.001$); mean daily RH: Welch $F(3,468.3) = 89.4$ $p < 0.001$; minimum daily RH: $F(3,848) = 91.7$ $p < 0.001$; and maximum daily RH: Welch $F(3,460) = 141.8$ $p < 0.001$). The reference forest (SF1) had a significantly cooler mean daily temperature than all other sites (all $p < 0.001$) as well as a significantly cooler mean maximum daily temperature (all $p < 0.001$). There was no significant difference between the average daily temperatures for the other three sites but SF4 had a significantly lower average daily minimum than SF2 and SF3 ($p = 0.002$ and $p < 0.001$ respectively).

The average RH at SF1 (91.4%) was significantly higher than the other three sites (all $p < 0.001$), as was the average daily minimum RH (all $p < 0.01$). SF4 was the second most humid site with average RH in that category significantly higher than in SC2 and SC3 (both $p < 0.001$).

Table 3.15: (a) Average physical and environmental characteristics of each coastal forest category and (b) representative soil characteristics. The values for temperature and relative humidity represent the average of the daily mean temperatures; i.e. means for each day were first calculated using the hourly readings and then these means were averaged across the whole data collection period.

(a)

	Altitude (m asl)				**Slope (°)**				**Heat Load**				**Average daily temperature (°C)**				**Average RH (%)**				**Canopy Height (m)**			
	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.
SF1	15	15	15	0.00	0.0	0	0	0.00	0.98	0.98	0.98	0.00	10.2	-1.1	23.7	3.74	91.4	49.6	100.0	5.03	22.00	22.00	22.00	0.00
SF2	5	5	5	0.00	0.0	0	0	0.00	0.98	0.98	0.98	0.00	11.9	-1.3	26.4	3.42	84.5	36.3	100.0	6.22	9.63	6.00	13.00	3.64
SF3	4	3	5	1.15	0.0	0	0	0.00	0.98	0.98	0.98	0.00	12.2	0.3	24.7	3.25	83.3	43.6	97.1	6.39	7.67	7.00	8.00	0.58
SF4	5	5	5	0.00	0.0	0	0	0.00	0.98	0.98	0.98	0.00	11.5	-2.4	29.3	3.76	87.2	39.9	100.0	6.53	2.17	1.80	2.50	0.35

(b)

	pH	**Olsen P (mg/L)**	**Available N (kg/ha)**	**Organic Matter (%)**	**TC (%)**	**TN (%)**	**C/N Ratio**	**K (me/100g)**	**Ca (me/100g)**	**Mg (me/100g)**	**Na (me/100g)**	**CEC (me/100g)**	**Total Base Saturation (%)**
SF1	6	25	111	8.5	13.4	4.9	0.37	0.89	6.8	2.12	0.09	16	61
SF2	5.5	4	44	14.6	8.5	0.72	11.7	0.38	4.3	1.21	0.59	29	22
SF3	5.2	8	151	9.2	12.1	5.4	0.44	0.14	2.4	0.42	0.19	15	21
SF4	5.4	4	96	6.4	3.7	0.26	14.2	0.22	2.3	0.43	0.28	14	23

3.3.9 Soil

In the swamp forest, pH ranged from 6 in SF1 to 5.2 in SF3 (Table 3.15). Available N and TN were considerably higher in SF1 and SF3 than in the other two sites and TC showed similar results. Organic matter levels were relatively low in SF4 and only moderate in the other sites. CEC was highest in SF2 while the other three sites had moderate levels. All sites except the reference site had very low levels of phosphorus and low base saturation.

3.4 Results of study-wide analyses

3.4.1 Ordination of all forest categories

NMS ordination of averaged category data resulted in a 2-dimensional plot with final stress of 14.273 after 96 iterations. The NMS plot shows considerable overlap of each forest type in ordination space (Figure 3.23). Axis 1 accounted for 20.9% of the variance in the data and had a strong positive correlation with maximum temperature (r^2 = 0.799) and introduced species richness (r^2 = 0.591), and was negatively correlated with minimum RH (r^2 = 0.757) and canopy height (r^2 = 0.587). Axis 2 accounted for 14.6% of the variance in the data and had a weak negative correlation to soil volume weight (r^2 = 0.434) and total nitrogen (r^2 = 0.429).

The coastal forest categories were spread in an almost linear fashion along axis 1 apparently due in part to the *Metrosideros*-dominant forest in CF1 and CF2 having shared species with SC1 (particularly *Hedycarya*, *Knightia*, and *Macropiper*), whereas CF5 shared some species with SF4 (*Pittosporum colensoi*, *Leptospermum scoparium*, and *Myoporum laetum*) and had higher exotic species richness and maximum temperature. The swamp forest categories were widely spread in ordination space due to diversity in both composition and environmental characteristics with the outlying CF2 apparently influenced by the presence of *Salix cinerea*, *Coprosma tenuicaulis*, and *Ligustrum sinense* which each had moderate associations with axis 2 (r^2 values of 0.514, 0.432, & 0.525 respectively). The semi-coastal forest categories were reasonably tightly grouped but were associated with a suite of species not found in the other forest types or only present in low abundance.

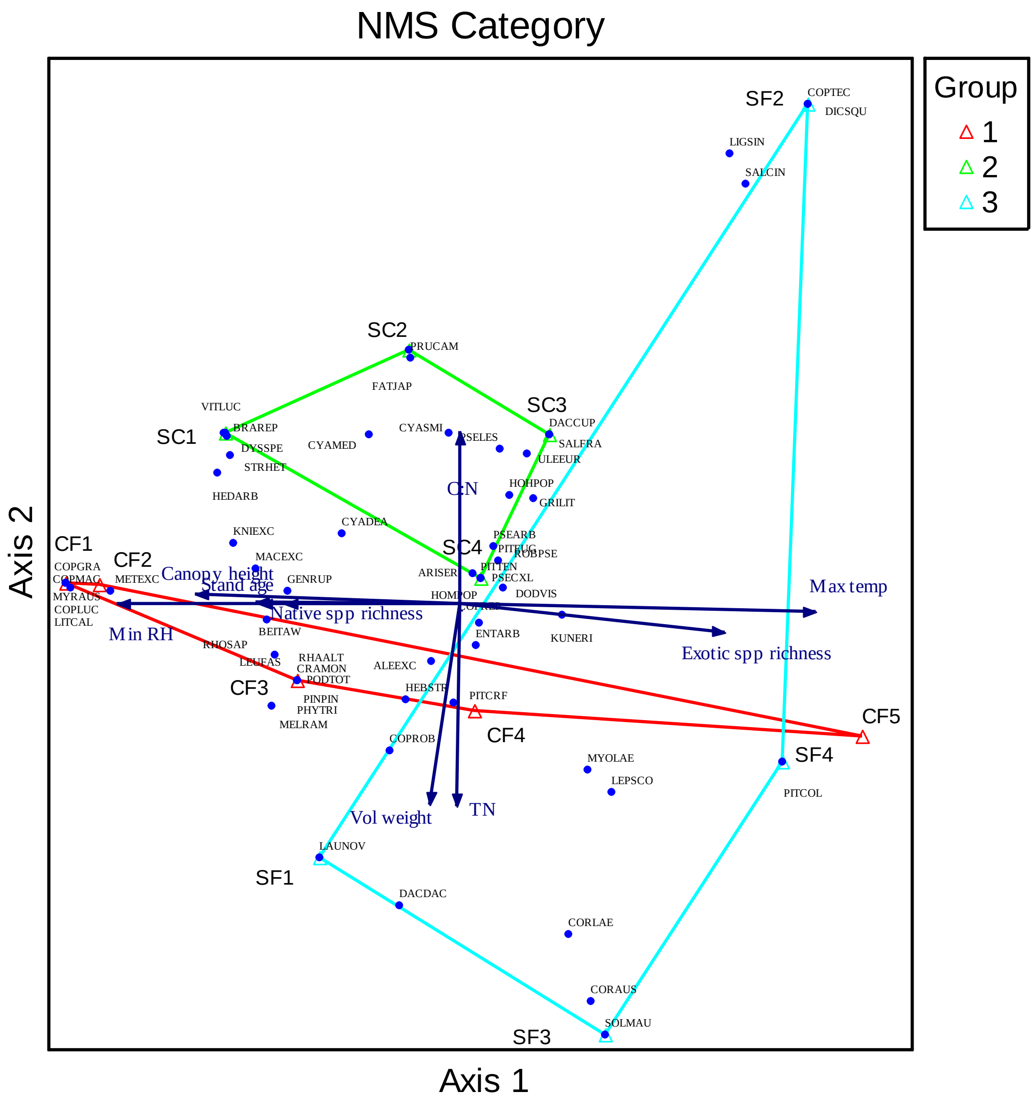

Figure 3.23: NMS ordination plot of all forest categories in the study. Average basal area and environmental data were used in this ordination and an environmental data overlay has been added.

3.4.2 Relationships between vegetation and environmental characteristics

Analysis of vegetation characteristics and associated environmental and physical conditions across all study sites showed some associations relevant to the study. As expected, basal area and density increased with stand age ($r_s(13) = 0.730$, $p = 0.004$ and $r_s(13) = 0.749$, $p = 0.003$ respectively) which mirrors the development of the vegetation from small plants and simple structure to large trees and a complex, multi-storey structure.

Stand age also had a strong negative correlation with both temperature range (the difference between maximum and minimum temperatures; $r_s(13) = -0.606$, $p = 0.028$) and RH range ($r_s(13) = -0.851$, $p = 0.0002$), i.e. older vegetation had smaller fluctuations in temperature and humidity levels. Interestingly, heat load was correlated with maximum temperature ($r_s(13) = 0.632$, $p < 0.0205$) but not with average daily temperature which could be the result of variation amongst plots in the same categories and the use of only one temperature and humidity sensor per category.

Stand age was negatively associated with exotic species richness ($r_s(13) = -0.927$, $p < 0.0001$), and positively associated with native species richness ($r_s(13) = 0.554$, $p = 0.049$). Exotic species richness also showed a strong negative correlation with stem density ($r_s(13) = -0.708$, $p = 0.007$). Stem density was also correlated to soil organic matter ($r_s(13) = 0.597$, $p = 0.031$), while native species richness was correlated with available N ($r_s(13) = 0.522$, $p = 0.067$) although this relationship was not statistically significant.

Trends in ground cover were also apparent. Litter cover increased with stand age (($r_s(13) = 0.583$, $p = 0.036$) possibly indicating greater litter production in older forests. The increase in litter apparently replaced exotic plants which, reflecting overall species richness, decreased in the ground cover as stand age increased (($r_s(13) = -0.672$, $p = 0.012$).

Chapter Four: Discussion and Recommendations

This chapter follows the structure of the previous results chapter with one section each for coastal forest, semi-coastal forest, and swamp forest. The results of the present study are discussed in relation to the existing knowledge of succession in New Zealand vegetation, succession and assembly theory, and the practice and theory of restoration ecology.

As expected, the results of the study illustrate significant differences in vegetation composition and structure across the various age categories in each forest type. Indications of the likely developmental sequence and trajectory of the various forest types are evident.

A number of factors influencing the success of the restoration sites is this study are examined and recommendations are made for the management of current and future projects.

4.1 Coastal Forest

4.1.1 Regeneration and succession in coastal forest

Of key importance to the coastal forest ecosystem being restored on Mauao is *Metrosideros excelsa* which in natural successions colonises highly disturbed coastal sites quickly and dominates them for many hundreds of years (Clarkson 1990; Atkinson 2004). The development of coastal *Metrosideros excelsa* forest has been well documented by Percy (1956), Atkinson (2004) and Bylsma (2012). Although these accounts vary slightly because of the differing conditions at the individual study sites the basic model of forest development and succession is the same: *Metrosideros* produces masses of wind-dispersed seed and can establish quickly after a disturbance, often alongside *Kunzea ericoides* and *Leptospermum scoparium*, themselves both wind-dispersed pioneer species. The shorter lifespans of *Leptospermum* and *Kunzea* mean that eventually *Metrosideros excelsa* comes to dominate the canopy vegetation. Within 50 to 100 years a suite of bird-dispersed species, including *Myrsine australis, Melicytus ramiflorus, Litsea calicaris*, *Vitex lucens, Dysoxylum spectabile*, *Corynocarpus laevigatus*, *Macropiper excelsum, Pseudopanax lessonii, Pseudopanax arboreus,* and *Geniostoma rupestre* var. *ligustrifolium* begin to colonise the established vegetation (Atkinson 2004; Bylsma 2012). The exact combination and abundance of these species depends on a number of factors including salt influence, soil moisture and fertility, and seed availability (Atkinson 2004). Of the species listed above, *Vitex, Dysoxylum, Litsea,* and *Corynocarpus* have the potential to become part of the forest canopy but only *Dysoxylum* and *Corynocarpus* are capable of regenerating under a dense canopy, whereas *Vitex* and *Litsea* either have to establish relatively early in the succession when light levels are still high enough, or in canopy gaps (Percy 1956; Smale & Kimberley 1983; Atkinson 2004).

The final documented stage of the coastal forest succession is the establishment of highly shade tolerant tree species (Atkinson 2004). The most common of these in the Bay of Plenty is *Beilschmiedia tawa* which has very low light requirements and can regenerate under its own canopy (Smale & Kimberley 1983). The fruits of *Beilschmiedia* are prone to desiccation and it requires moist forest environments in which to regenerate (Burrows 1999) so the trees arriving before *Beilschmiedia* in the developing vegetation must alter the habitat considerably to facilitate its establishment.

Although *Metrosideros* dominant forest is not a stable end-point in the absence of major disturbance its persistence for 300 or more years makes a forest dominated by *Metrosideros* a reasonable goal for restoration on Mauao.

4.1.2 Comparison of planted and naturally regenerating sites with the reference forest

The forest on Tuhua was surveyed for use as a reference site against which to compare the restored and naturally regenerating sites on Mauao. On Tuhua, large multi-stemmed *Metrosideros excelsa* almost completely dominated the canopy which reached as much as 26 m tall. *Knightia excelsa* was also present in the canopy although large trees were very sparse. A sub-canopy layer dominated by *Melicytus ramiflorus, Myrsine australis,* and *Coprosma macrocarpa* but including *Litsea calicaris,* and *Hedycarya arborea* was on average less than 10m tall. The groundcover was very sparse being dominated by a thick litter of *Metrosideros* leaves. Species richness was relatively low compared with the semi-coastal broadleaved forest and swamp forest reference sites. *Metrosideros* diameter measurements and the diameter age relationship data from Bylsma (2012) indicate that the *Metrosideros* at this site were at least 120 years old.

The complete lack of *Metrosideros* seedlings or saplings was entirely expected as *Metrosideros* is incapable of regenerating in shaded conditions or amongst other vegetation (Bergin & Hosking 2006). *Litsea*, along with *Dysoxylum* appear to be in a position to gradually succeed the *Metrosideros* canopy as it begins to senesce over the next 100 or 200 years. *Litsea* was present at high density in the seedling and sapling classes along with occasional *Dysoxylum*, *Corynocarpus*, and *Vitex*.

4.1.2.1 Old growth forest on Mauao: Category CF2

The old-growth forest on Mauao (CF2) was also at least 120 years old with individual stem diameters of more than 50 cm not uncommon. This forest is broadly similar to the Tuhua reference site in that it is dominated by mature *Metrosideros excelsa* but the canopy was slightly lower (less than 25 m). The sub-canopy and shrub layer were sparser than the Tuhua forest and seedling density was much lower. The old-growth forest on Mauao had only 15 species in common with the Tuhua site which was slightly more than half of the total species present. This significant difference in species composition may be partly attributable to climatic conditions but increased disturbance and the impact of browsing animals may also play a part. Of particular note was the difference in abundance of *Myrsine australis* which on Tuhua was a significant part of the understorey whereas on Mauao it was present only as saplings, and then only at low density. Atkinson (2004) suggested that *Myrsine australis* is more likely to be a major part of the understorey below *Metrosideros* at lower fertility sites with lower salt-spray whereas *Melicytus ramiflorus* will be more prominent in high fertility, high salt sites. However, soil fertility at both sites was similar with Tuhua arguably being the more fertile. The salt content of the wind is likely to be higher around the lower slopes of Mauao where the mature forest is because the area is exposed to the northerly and north-westerly weather but the presence of the tree fern *Cyathea medullaris* suggests that salt winds are not a major issue.

The key mid- and late-successional canopy species were also missing from the Mauao forest. These include *Dysoxylum spectabile*, *Litsea calicaris*, *Vitex lucens*, and *Beilschmiedia tawa*. *Vitex* is present elsewhere on Mauao (both planted and naturally occurring) while the others are completely absent (Bibby et al. 1999) although there is a single large *Litsea* on nearby Motuotau Island (BD Clarkson pers. comm.). *Cyathea medullaris* and *C. dealbata* were a significant component of the understorey in this forest (approximately 20-25% total cover) which may be another factor influencing the establishment of these mid-succession tree species. Tree-ferns can create very low light environments and develop a deep litter of fallen fronds and Atkinson (2004) noted that dense stands of tree ferns can inhibit the establishment of tree species.

Bylsma (2012) found many different understorey assemblages in her study of Bay of Plenty *Metrosideros* forest and reported that the composition of forest on Tuhua was distinct from the mainland forests. This suggests that Tuhua is not an ideal reference site for Mauao restoration projects but nevertheless provides a satisfactory general target ecosystem.

4.1.2.2 Naturally regenerating sites: Category CF3

The naturally regenerating areas on Mauao (CF3) contain very little *Metrosideros excelsa* which is present only as scattered trees. These areas were quite variable low forest and scrub in which *Coprosma robusta, Geniostoma rupestre* var. *ligustrifolium,* and *Cyathea medullaris* were important components. Several pest plant species including *Lonicera japonica* and *Asparagus scandens* were also present and are likely to be affecting vegetation development and successional trends. Although these naturally regenerating areas will not become *Metrosideros* forest without further suitable disturbance events they had the highest species richness and highest native species richness of all of the coastal forest sites. This may reflect the history of disturbance and planting and the more sheltered sites this forest type occupied. The composition and structure of this naturally regenerating forest also illustrates how vegetation development can follow a number of trajectories, especially where there is on-going disturbance by people.

4.1.2.3 Restoration plantings >10 years old: Category CF4

The older of the two restoration categories had a closed canopy of up to 8 m in height comprising a mix of species including *Metrosideros excelsa, Cordyline australis, Pittosporum eugenioides, Pittosporum crassifolium, Dodonea viscosa,* and *Leptospermum scoparium*. All of the species making up the canopy appeared to have been planted and the sapling and seedling tiers were very sparse with only

Macropiper excelsum represented in the tall seedling size class. However, there were reasonably high densities of small ephemeral seedlings which included *Geniostoma, Melicytus, Dodonea viscosa, and Entelia arborescens.* Although 26 native species were recorded in this category only six of them were also found in the reference forest, partly reflecting the different structure and conditions. No ground ferns except *Pteris tremula* and *Doodia australis* were present, and there were no tree ferns or lianes. The light levels under the canopy appeared to be low compared to other forest categories and the humidity was lower than at other sites, which may contribute to the lack of regeneration and recruitment into the larger size classes. However, rabbits are prolific in the more open areas on Mauao and these are undoubtedly having an effect on the regeneration of native forest plants. Rabbits have been reported to browse *Metrosideros excelsa*, *Melicytus ramiflorus*, *Pseudopanax arboreus*, *Coprosma* species, and *Hedycarya arborea* and can affect vegetation succession in coastal areas (Ogle 1990; Norbury 1996). Without rabbit control or a reduction in rabbit browse pressure it is unlikely that the full range of understorey and mid- and late-successional canopy species will establish.

4.1.2.4 Restoration plantings <10 years old: Category CF5

The youngest restoration category had only a broken canopy reaching about 2.5m in height. This comprised of *Leptospermum scoparium*, *Kunzea ericoides*, *Metrosideros excelsa*, and *Phormium cookianum*. The *Leptospermum* and *Kunzea* were frequently taller than the *Metrosideros* and were more abundant in terms of basal area, density, and canopy cover. The majority of the tree and shrub species in this category had been planted but *Leptospermum* appears to have established naturally as well. The exotic *Ulex europaeus* and *Cortaderia selloana* are present but at the time of the survey both species had recently been sprayed with herbicide and most were dead. As expected, this youngest and most open vegetation category was subject to the largest extremes in temperature and humidity having not yet developed sufficient vegetation to moderate the effects of external environmental conditions. There was considerably more vegetation in the groundcover than in the older restoration sites but most species were light-loving grasses and herbs and most were exotic. Rabbit browse and other sign was common and many rabbits were seen in these areas.

For the restoration of tall *Metrosideros excelsa* forest restoration on Mauao one of the most important considerations is whether the existing restoration sites have the right components in place to allow them to develop into *Metrosideros* forest or whether additional planting or other management will be required. Natural *Metrosideros* stands in the Bay of Plenty can progress from 1000-2000 stems ha^{-1} in juvenile stands to <400 stems ha^{-1} in old-growth forests, associated with an increase in basal area from <20 m^2ha^{-1} to about 50 m^2ha^{-1} (Bylsma 2012). The densities of *Metrosideros* in the planted categories CF4 and CF5 were 584 individuals ha^{-1} and 358 individuals ha^{-1} respectively; considerably less than were reported by Bylsma (2012). Despite this it seems likely that *Metrosideros* will remain in a mixed canopy and given its longevity compared with the other species present will eventually come to dominate the forest, or at least become a significant component of the canopy. Mixed stands of *Metrosideros* and *Kunzea* have developed like this in Matata Scenic reserve (Bylsma 2012). Indeed, Atkinson (2004) noted that dense restoration plantings of *Metrosideros* will result in very slow development of a diverse canopy and understorey so the mixed nature of the plantings on Mauao may be beneficial for a faster turnover of species.

4.2 Semi-coastal broadleaved forest

Although the original forest in the Tauranga area was cleared long before the arrival of Europeans, palynology studies have shown that the district was probably mostly covered in a mixed podocarp-broadleaved forest (Newnham et al. 1995; Giles et al. 1999). Given the forest pattern in other lowland areas of New Zealand, and in the nearby Kaimai and Otanewainuku forests, it is likely that undisturbed sites featured tall podocarps such as *Dacrydium cupressinum, Dacrycarpus dacrydioides,* and *Prumnopitys ferruginea* emergent over a canopy of *Beilschmiedia tawa, Dysoxylum spectabile,* and *Vitex lucens. Alectryon excelsus, Knightia excelsa,* and *Litsea calicaris* were probably also common canopy components. Succession in this specific forest type has not been studied in detail but the habitat requirements of the main canopy species are well documented. *Beilschmiedia tawa,* the dominant tree in many lowland forests, is a late-successional species which requires deep forest conditions in which to germinate (Knowles & Beveridge 1982). *Dysoxylum spectabile* is also shade tolerant and can regenerate in deep forest (Smale & Kimberley 1983) but can enter the succession earlier than *Beilschmiedia* (Atkinson 2004). *Vitex* has relatively high light requirements compared with *Beilschmiedia* and requires light gaps or a relatively open canopy to establish (Atkinson 2004). None of these species except perhaps *Vitex* can be planted on bare sites at the start of a restoration project but require a vegetated, somewhat sheltered habitat in which to establish.

4.2.1 Comparison of the planted and naturally regenerating semi-coastal sites with the reference forest

The two reference sites for the semi-coastal broadleaved forest categories comprised a canopy dominated by *Beilschmiedia tawa* with a significant component of *Dysoxylum spectabile*. *Beilschmiedia* trees up to 78 cm DBH were recorded but trees in the 30-50 cm DBH size class were most abundant. A lack of *Beilschmiedia tawa* in the sapling and seedling size classes and low abundance of trees in the 2.5-10 cm DBH size class suggests that it is not a self-sustaining population. In comparison, Smale & Kimberley (1983) reported *Beilschmiedia* saplings (<5cm DBH) in excess of 100 stems ha^{-1} in mature *Beilschmiedia*-dominated forest at Rotoehu, while Carswell et al. (2007) reported *Beilschmiedia* seedling densities of 1667 stems ha^{-1} in forests adjacent to Te Urewera National Park. *Beilschmiedia* densities in the swamp forest reference site at White Pine Bush were 552 individuals ha^{-1} and 112 individuals ha^{-1} in the seedling and sapling classes respectively.

The ability of *Beilschmiedia* to regenerate in deep forest (Knowles & Beveridge 1982) suggests that continuous recruitment should be happening in the reference forests, but *Beilschmiedia* is known to grow in stands with a population structure that does not reflect continuous recruitment (Ogden 1985). *Beilschmiedia* seedlings and saplings were noted in other parts of the forest and insufficient sampling intensity may partly explain the results in this study, but in any case the abundance of *Beilschmiedia* in the understorey is very low which suggests that other factors may also be involved. Predation of seeds by possums and rats has been recorded (Knowles & Beveridge 1982; Moles & Drake 1999; Overdyck et al 2013) and neither of the forest areas surveyed as reference sites is subject to consistent pest control and are likely to have moderate to high possum numbers. Other reported factors influencing *Beilschmiedia* germination failure are desiccation of fruits and seed predation by the larvae of a moth (*Cryptaspasma querula*) which can destroy large quantities of seed (Knowles & Beveridge 1982).

Burns et al. (2011) also found lower than expected levels of *Beilschmiedia* seedlings and saplings in a study of *Beilschmiedia*-dominated forest fragments in the Waikato. Even more than 20 years after the exclusion of livestock *Beilschmiedia* seedlings and saplings were not considered abundant enough to sustain the existing canopy (Burns et al. 2011). Edge effects (lower humidity levels and high light levels) and interspecific competition were cited as possible reasons for the low levels of *Beilschmiedia* regeneration (Burns et al. 2011).

The *Dysoxylum spectabile* population structure in the semi-coastal reference forests reflected the findings of Smale & Kimberley (1983): Large trees were present but the smaller size classes were much more abundant and high densities of seedlings and saplings were recorded. This reverse-J population structure (refer Figure 3.9) is typical of continuous recruitment of a canopy tree and *Dysoxylum* in the smaller size classes appears to be in sufficient abundance to replace the existing canopy or sub-canopy trees. Smale & Kimberley (1983) reported that *Dysoxylum* seedlings were more abundant under a mixed *Beilschmiedia*-*Dysoxylum* canopy in Rotoehu forest than *Beilschmiedia* seedlings were, and a reciprocal replacement regime was in place whereby *Beilschmiedia* replaced *Dysoxylum* in the canopy and vice versa. It is possible that this may also be the case in the sites surveyed for this study.

Occasional large *Knightia* and *Vitex* were also present in the canopy and there was a reasonably well developed sub-canopy of *Hedycarya arborea, Melicytus ramiflorus*, *Cyathea medullaris*, and *C. dealbata.* Below about 6m in height *Macropiper excelsum* was the dominant understorey shrub and seedlings of all of the species mentioned except *Beilschmiedia* were well represented.

The microclimate conditions across all of the semi-coastal forest categories largely reflected the developmental stage of the vegetation. Although the average temperature was no different between sites the range of temperatures in the established forest was smaller than the temperature range in the restoration sites. The situation was similar for humidity although the naturally regenerating forest was the most humid. Temperature and humidity data for the driest months of the year was not collected but it is likely that over these months the differences in temperature and humidity ranges between the established and the developing vegetation is most marked. This may have implications for seed germination and regeneration and succession. Seeds prone to desiccation such as *Beilschmiedia* (Knowles & Beveridge 1982) may have less opportunity to germinate in the young developing stands than in the more established ones, especially since *Beilschmiedia* fruits ripen in what is often the driest part of the year.

4.2.1.1 Naturally regenerating sites: Category SC2

The vegetation surveyed at naturally regenerating sites within the city (category SC2) is likely to have developed in the last 50 or 60 years after complete clearance, although disturbance by domestic stock has probably continued to have been relatively high during the development of the vegetation as well. The current vegetation is most likely to have developed following earlier colonisers because the dominant species in these sites is *Cyathea medullaris* which requires the moist conditions and shelter provided by vegetative cover in order to establish. Remnant moribund gorse (*Ulex europaeus*) in at least one plot suggests that the *Cyathea medullaris* canopy may have developed through stands of gorse, which is a reasonably common progression elsewhere in the Tauranga area (pers. obs.). *Cyathea medullaris* reached as much as 13 m in height and overtopped a sub-canopy of indigenous and exotic shrubs including *Geniostoma rupestre* var. *ligustrifolium*, *Melicytus ramiflorus*, *Ligustrum sinense*, and *Prunus campanulata*. This vegetation had a low native species richness compared to the reference forest and only 11 species in common with it (33% of total species richness). *S*pecies present in the reference forests but not in the naturally regenerating forest included several ground ferns, lianas, and epiphytes; species associated with well-developed forest. In addition, none of the major canopy species from the reference forest were present but the reasons for this are not clear. The absence of *Beilschmiedia* is not particularly unusual as the vegetation was still reasonably open and light, temperature, and humidity levels may have been too extreme, but *Vitex, Knightia, Dysoxylum* and *Alectryon excelsus* should be capable of establishing in these conditions. Microclimate conditions at this site were similar to those in the reference forest although there was a slightly wider range of temperature and humidity compared with the older site. Lack of local seed sources of these later-successional species and competition from exotic species are probable reasons for their absence and these factors are discussed in section 4.4.1 below.

Without the common mid-succession tree species the developmental trajectory of this vegetation is not at all clear. *Melicytus* has the potential to become a more significant component of the canopy as there was a reasonable density of small trees and saplings of this species and it is known to be a significant canopy component in some low stature regenerating forest (Dungan et al. 2001). High seedling density of *Prunus campanulata*, a bird dispersed deciduous tree from East Asia (Popay et al. 2010), indicate that this species may also play a significant part in the trajectory of this vegetation. *Prunus campanulata* can regenerate in semi-shaded forest and scrub environments and appears to compete successfully with native species for canopy space (pers. obs.).

Chinese privet (*Ligustrum sinense*) was present in the seedling tier at a density of almost 5,000 individuals ha^{-1}, similar to the density of *Geniostoma*. *Ligustrum sinense* is capable of forming dense stands that exclude native species and is capable of regenerating under its own canopy and continually occupying a site (Grove & Clarkson 2005). The presence of these to pest plants suggests that these sites could well become completely dominated by exotics, especially if *Ligustrum sinense* becomes dominant in the understorey.

4.2.1.2 Planted restoration sites >25 years old: Category SC3

The canopy in the >25 year old restoration plantings was dominated by the species that were originally planted but *Cyathea medullaris*, *Salix cinerea*, and *S. fragilis* were also canopy components. This forest category was more diverse than any other semi-coastal forest category and had the highest exotic species richness. Only ten species were in common with the reference forests but microclimate conditions were similar, albeit slightly more humid.

The structure of the vegetation was relatively simple with a dense canopy overtopping a usually sparse understorey and a groundcover of litter or exotic herbs and grasses. *Alectryon excelsus* and *Knightia excelsa* were the only two species with the potential to become canopy components in tall forest but both were present at very low density and there was no evidence to suggest that either species was naturally regenerating. The understorey was dominated by exotic species but *Melicytus ramiflorus, Macropiper excelsum, Entelia arborescens, Cyathea medullaris,* and *Cyathea dealbata* appear to have colonised naturally. Apart from the tree ferns, these species are bird-dispersed which confirms that seed dispersal vectors are in place; at least for small-seeded locally available species. This is a vital ecosystem function and indicates that at least some functionality has been restored to these systems.

The groundcover and seedling species in this forest category are indicative of the variation in the vegetation and the placement of the plots. Light-loving species such as *Berberis glaucocarpa* and *Ulex europaeus* which were both present as seedlings at high density contrast with *Tradescantia fluminensis* which is a species of darker, damper environments (Popay et al. 2010).

4.2.1.3 Planted restoration sites >10 years old: Category SC4

The >10 year old restoration site had a dense canopy between eight and ten metres high which was dominated by planted, fast-growing native species. *Pittosporum eugenioides, Pseudopanax arboreus,* and *Robinia pseudoacacia* were the dominant species by cover. *Alectryon excelsus* and *Vitex lucens* had also been planted and were reasonably common. This category had only eight species in common with the reference forest and was the least diverse site in the semi-coastal categories. Ground ferns were limited to species such as *Pteris tremula* and *Doodia australis* which are adapted to lighter and drier sites, and there were no epiphytes or lianas except *Rubus cissoides*, a plant well suited to scrub and open vegetation.

Macropiper excelsum was regenerating naturally and was present as plants up to five metres tall. *Geniostoma rupestre* var. *ligustrifolium* and *Melicytus ramiflorus* were also regenerating naturally. The groundcover tier was generally very sparse although *Tradescantia fluminensis* infestations were present in some parts of the site and tended to dominate those areas. Like the older restoration plantings, the trajectory and future canopy composition of this site is not clear but some speculations can be made from the available information. The presence of naturally regenerating forest understorey species such as *Geniostoma* and *Melicytus* suggest that dispersal vectors are in place and that the planted trees have altered the habitat sufficiently for these species to establish. It seems likely that the understorey will continue to develop as long as seed sources are available and competition from exotic plants is managed. *Melicytus* may succeed the existing canopy where longer-lived trees like *Alectryon* and *Vitex* are not present but without the arrival of other mid- and late-successional tree species through natural or artificial means these restoration sites will probably continue to cycle through small, easily dispersed tree and shrub species without ever developing into tall forest.

4.3 Swamp forest

4.3.1 Comparison of the planted and naturally regenerating swamp forest sites with the reference forest

The forest at White Pine Bush comprised large *Dacrycarpus dacrydioides* to at least 25m in height emergent over a mixed canopy of angiosperm trees including *Beilschmiedia tawa*, *Laurelia novae-zelandiae*, and *Alectryon excelsus*. Below this canopy a dense understorey of small trees and shrubs including *Melicytus ramiflorus*, *Cyathea dealbata,* and *Rhopalostylis sapida* had a total cover of at least 50%. The forest was diverse and only two non-native species were recorded.

Overall stem density was much lower than in the coastal reference forest on Tuhua and the semi-coastal reference forests, reflecting a much lower density of seedlings. *Dacrycarpus dacrydioides* had a density of just 50 individuals ha^{-1} which was slightly lower than the 57.9 stems ha^{-1} reported by Smale (1984) for the same forest remnant. The density of mature *Dacrycarpus* stands can vary considerably: Wardle (1974) reported stands of 200 trees ha^{-1} (although the size classes included in this number were not clear), Whaley et al. (1997) reported 371 stems ha^{-1}, and Duncan (1993) reported *Dacrycarpus* density in mature stands of up to 825 stems ha^{-1}. Robertson & Hackwell (1995) reported *Dacrycarpus* in <70 year old stands at 2739 stems ha^{-1} which illustrates self-thinning of *Dacrycarpus* as the stand ages. No *Dacrycarpus dacrydioides* smaller than 30cm DBH were recorded in the current study, indicating a lack of regeneration of this species. In contrast Smale (1984) recorded numerous small seedlings and saplings but concluded from the lack of mid-sized stems that the mortality rate in the small size classes was high and that the current *Dacrycarpus* population would decline. These differences are likely due to the difference in sampling intensity between the two studies; Smale (1984) measured every tree in the remnant greater than 8cm DBH and sampled the seedlings and saplings, whereas only two 400m^2 plots were measured in the current study.

In contrast to the population structure of *Dacrycarpus,* those of *Beilschmiedia tawa, Laurelia novae-zelandiae* and *Alectryon excelsa* indicate continuous recruitment and these species appear to be self-sustaining. *Alectryon* in particular had very high seedling abundance but low abundance in the larger classes indicating high seedling mortality. *Beilschmiedia* and *Laurelia* together made up more than 55% of the canopy cover.

The soil at White Pine Bush was moderately fertile with high levels of phosphorus compared to other sites in the study and moderate levels of available nitrogen, organic matter, and the trace elements.

These results are consistent with the literature dealing with *Dacrycarpus dacrydioides* successions. *Dacrycarpus* is associated with alluvial floodplain forest and often establishes in relatively even aged stands on newly deposited alluvium after floods or when a river changes course (Wardle 1974; Duncan 1993). Without major disturbance and the laying down of new alluvium *Dacrycarpus* forest eventually gives way to angiosperm-dominated forest (Wardle 1974; Smale 1984; Duncan 1993). *Dacrycarpus* is not particularly shade tolerant and is incapable of competing effectively with angiosperms and ferns, particularly on fertile sites where higher soil phosphorus levels favour angiosperm and fern establishment (Coomes et al. 2005; Carswell et al. 2007). Thus, it appears that White Pine Bush is transitioning from *Dacrycarpus* forest to *Beilschmiedia-Laurelia* forest as predicted by Smale (1984).

4.3.1.1 Naturally regenerating forest in Kopurererua Valley: Category SF2

The vegetation in category SF2 comprised a tract of *Salix cinerea* forest in the Kopurererua reserve. This forest was included in the survey because it is situated within the Kopurererua Valley restoration area, and it is growing on a floodplain which is likely to have once been covered in *Dacrycarpus dacrydioides* forest. In addition, it represents at least 60 years of vegetation development in the urban environment without management by people. The vegetation was entirely dominated by *Salix cinerea* that reached about 13 m in height although the majority of the canopy was well below 12 m. This forest had only six species in common with the reference forest and had the lowest species richness of all of the swamp forest sites. Indigenous species were restricted to the understorey tiers and none of the key swamp forest canopy species was present. This site had a higher water table than the other sites that were surveyed.

Salix cinerea is a vigorous competitor and can take advantage of newly disturbed areas or new depositions of alluvium in much the same way as *Dacrycarpus*. However, it is very fast growing and can regenerate very effectively from vegetative fragments (Radtke et al. 2012), which means it can recover dominance quickly after minor disturbances. Research in the Hamilton basin showed that *Salix cinerea* could out-compete *Dacrycarpus* when both were establishing at newly disturbed sites and form a canopy despite the presence of *Dacrycarpus* (Coleman 2010). Once it had formed a canopy *Salix cinerea* could prevent further recruitment of *Dacrycarpus* and prevent it from establishing or penetrating the canopy (Coleman 2010). Given this evidence from a neighbouring district and the lack of any other potential canopy species in the SF2 sites it seems likely that without management or major disturbance the *Salix cinerea* canopy will remain.

4.3.1.2 Restoration plantings >10 years old: Category SF3

The plantings at Te Maunga comprised a mix of species forming a broken canopy to around 8m tall. *Cordyline australis* was by far the most abundant in terms of density and basal area but *Dacrycarpus dacrydioides, Corynocarpus laevigatus, Coprosma robusta,* and *Phormium tenax* were all significant components of the vegetation. All of these species had been planted but it appeared that some older naturally occurring *Cordyline australis* were present amongst the planted ones. High densities of small ephemeral *Dacrycarpus* seedlings were recorded (<15 cm tall) but no seedlings >15 cm or saplings indicate that the light environment and other conditions are not suitable for recruitment into the larger size classes. However, with the goal of *Dacrycarpus dacrydioides* forest in mind, the density of the planted individuals (332 individuals ha^{-1}) will likely be sufficient to establish a *Dacrycarpus*-dominated canopy in time, although other species such as *Corynocarpus laevigatus* are likely to remain a part of the canopy.

The temperature and humidity results reflect both the site locality and the developmental stage of the vegetation. The reference forest was cooler and more humid but this is to be expected in tall forest in a sheltered valley away from the coast. In comparison, the restoration sites (both SF3 and SF4) were more exposed to coastal winds and the open nature of the vegetation is unlikely to be able to influence microclimate to the same extent as tall forest. The soil test results are comparable to the reference forest results in everything except phosphorus which was considerably higher in the reference forest. Similarly, low phosphorus levels were recorded in all of the categories across the study except for at White Pine Bush and on Tuhua. Phosphorus is known to be depleted over the course of vegetation development so that it can become limiting in late successional forests (Wardle et al. 2004; Coomes et al. 2005). Given that the vegetation at both Tuhua and White Pine Bush is less than 500 years old and therefore relatively young the phosphorus levels may be an indication of the time since the last major disturbance or surface-laying event. Whatever the case, the implications of low phosphorus levels for restoration plantings may be important although no statistically significant associations were found between phosphorus levels and vegetation metrics. While podocarps such as *Dacrycarpus* have an advantage over angiosperms because of more efficient use of phosphorus (Coomes et al. 2005) establishment of vegetation through planting may require the use of fertiliser at many of the restoration sites in Tauranga. Currently, slow release fertiliser is often added to the soil when undertaking revegetation in Tauranga and it is apparent from the current study that that there is a need for it. To avoid enhancing conditions for exotic weeds fertiliser should be applied directly into the hole when planting a tree rather than in a broadcast manner.

4.3.1.3 Restoration plantings <10 years old: Category SF4

The youngest planted sites in the Kopurererua Valley comprised a mixed and very open canopy of planted tree and shrub species interspersed with exotic grasses and herbs. *Phormium tenax* was the dominant species by cover but *Cordyline australis, Dacrycarpus dacrydioides, Leptospermum scoparium,* and *Pittosporum colensoi* were common. In a natural swamp forest succession *Dacrycarpus* forms very dense stands in excess of 2000 stems ha^{-1} so although the density of kahikatea recorded in SF4 (252 individuals ha^{-1}) is likely to result in *Dacrycarpus* becoming a significant component of the canopy as the forest develops, the vegetation is unlikely to follow a trajectory consistent with natural stands. However, with no other large tree species recorded at the site and the natural establishment of other native trees unlikely, *Dacrycarpus* could still become the dominant tree under the current management regime.

4.4 Application of relevant succession and assembly theory and discussion of factors influencing restoration success

Having a basic understanding of the ecology of the key species in the habitat being restored and how these species interact to assemble the desired vegetation is important if the restoration is to be successful. Succession theory and assembly theory each attempt to explain how an ecosystem develops after a disturbance and when and which species arrive (Young et al. 2001). Whereas traditional succession models are linear and describe a continuum from a degraded state to one or two possible stable end points assembly theory is more focussed on how a community is assembled from the available species pool of the area through interactions between species, the timing of their arrival, and abiotic influences and includes multiple resultant stable states (Young et al. 2001; Lockwood & Samuels 2004; Temperton & Hobbs 2004).

The development of the three forest types examined in this study can be explained in part by traditional successional models but also by newer assembly theory based models.

Aspects of the facilitation, inhibition, and tolerance models described by Connell & Slatyer (1977) can be seen in all of the natural successions associated with the forest types studied here. *Metrosideros excelsa*, with its longevity, dense canopy and deep litter can inhibit the establishment of other plants but it also facilitates the establishment of understorey species and eventually the trees which replace it in the canopy (Atkinson 1960, 2004). The establishment of *Beilschmiedia tawa* is an example of both facilitation and tolerance. The species arriving before *Beilschmiedia* must alter the habitat sufficiently to facilitate its establishment but *Beilschmiedia* must also tolerate the low-light conditions and often grows very slowly, remaining in the understorey for long periods and putting on mainly root growth which is important for it to be able to take advantage light gaps when they form (Knowles & Beveridge 1982; Smale & Kimberley 1983). One of the key aspects of the facilitation model is that the pioneer species that arrive and establish first after a disturbance modify the environment to make it less suitable for other pioneer species (Connell & Slatyer 1977). In the coastal forest and swamp forest systems *Metrosideros excelsa* and *Dacrycarpus dacrydioides* are respectively the key pioneer species and because they are incapable of establishing in heavily shaded conditions they must arrive soon after a disturbance to be able to establish and to initiate a natural successional trajectory. However, in severely degraded systems like those found in urban Tauranga the arrival of the key species at the desired time to facilitate the succession is not a foregone conclusion.

While the traditional successional models can be fitted to the natural successions in these forest types the concepts of ecological thresholds and filters are more useful for describing the development of vegetation in severely depleted systems. Ecological filters define what species from the regional species pool can enter an assembling community and when (Hobbs & Norton 2004). Filters represent biotic and abiotic factors that can prevent a species from arriving and surviving at a site such as climate, substrate, and seed availability (Hobbs & Norton 2004). In a natural system filters work to assemble a native vegetation community that reflects the local conditions but in a highly degraded urban environment many of the same filters, as well as novel ones, may act to exclude native species after a disturbance in favour of exotic weeds. In undertaking restoration we manipulate or bypass filters in order to restore the system to the desired state (Hobbs & Norton 2004).

This failure of key species to establish after a disturbance is an example of a restoration threshold (Suding & Hobbs 2009). Thresholds exist when a system is degraded to such an extent that it requires restoration effort beyond just removing the stressor that caused the degradation in order to reverse the decline (Hobbs & Norton 1996). Alternatively, thresholds can be considered as barriers that must be overcome in order to change the developmental trajectory of the ecosystem (Hobbs & Norton 1996; Temperton & Hobbs 2004; Suding & Hobbs 2009). Where the dispersal of key native species is failing, or competition from exotic weeds is too strong, planting can be considered a means to overcome a threshold and direct the development of the vegetation along a more appropriate or desirable trajectory (see Figure 4.1). If key native species are not planted then it is likely that denuded sites in Tauranga city would become dominated by weeds. For example, the restoration plantings on Mauao were initiated because fire destroyed the previous vegetation and the decision was made by the reserve managers to replace it. While it would have been interesting to study the natural succession that would have initiated after these fires it is highly likely that the prevalent weeds of the area; *Ulex europaeus, Erica lusitanica,* and *Cortaderia selloana,* would have established much more quickly than *Metrosideros, Kunzea,* and *Leptospermum* or at least as quickly, so that the natural succession described by Atkinson (2004) would probably not have occurred. Planting these sites allowed the development of vegetation dominated by native species and the succession towards *Metrosideros* forest to begin. A study by Smale et al. (2001) of a forest restoration at Aratiatia further illustrates this situation. There, planted stands >30 years old resembled natural stands and were beginning to naturally regenerate whereas non-planted areas of the same age were dominated by the exotic broom *Cytisus scoparius* which was apparently replacing itself (Smale et al. 2001). Without planting, a means to overcome the threshold of native plant establishment, these sites would not have developed a native canopy but would have remained as exotic shrubland.

Planting is an important first step in restoring forest ecosystems in Tauranga, but what to plant is also an important consideration. Here the individual requirements and capabilities of the key species in each target ecosystem need to be considered. As discussed previously, the dominant canopy species in the coastal and swamp forest systems examined in the present study are pioneer species. Because of their pioneering traits these species can be planted on bare sites at an appropriate stem density with other associated pioneer species and managed to develop into forest. Given enough time and management of threats *Metrosideros*-dominated plantings are likely to develop into forest similar in structure and composition to the old-growth forest already on parts of Mauao and the swamp forest sites would at least develop a *Dacrycarpus*-dominated canopy.

The succession to mature semi-coastal broadleaved forest is more complicated because of the habitat requirements of the key canopy species *Beilschmiedia tawa, Dysoxylum spectabile,* and *Vitex lucens*. In this case it is not advisable to plant the key species on a completely denuded site. Instead, a nurse crop of fast growing species is required to facilitate the establishment of the mid- and late-succession species which typify the target forest. In this system the composition of the initial plantings may not be so important because they are there to perform the function of creating suitable forest conditions. Research on Banks Peninsular showed that the initial composition of the plantings did not matter and that natural regeneration under planted stands of a non-local native species was similar to regeneration under natural stands (Reay & Norton 1999). However, their study sites were located within 450 m of undisturbed natural forest which would have provided a good seed source for the restored stands. The initial composition of plantings may be more important where seed sources of desirable species are not in such close proximity (McClanahan & Wolfe 1993) or where the initial composition dictates the subsequent succession (e.g. Grant 2006).

In most of sites surveyed in the present study recruitment of the mid- and late-successional canopy and understorey species is failing and this could be considered another biotic threshold based on environmental filters which exclude native species. Without addressing this lack of recruitment the trajectory the sites will follow beyond the initial composition is likely to be very different from what would occur in a natural succession where all ecological functions and processes are intact. There are a number of reasons why this could be happening and some of these are discussed in the next section.

4.4.1 Ecological factors influencing the success of forest restoration in Tauranga

There are a range of factors that can influence whether a restoration is successful or not, including management regime (MacKay et al. 2011; Sullivan et al. 2009), invasion by pest plants (Sullivan et al. 2009), seed dispersal (Sullivan et al. 2009; MacKay et al. 2011; Overdyck & Clarkson 2012), and edge effects. These all represent ecological filters and aspects of these factors are discussed below.

4.4.1.1 Management regime and pest plant invasion

Results from this study suggest that exotic weeds are negatively impacting some of the restoration sites and all of the naturally regenerating sites. Personal experience in restoration and revegetation has shown that managing weeds can be costly and time consuming in the years following planting and although exotic species richness decreases with stand age, weed control in urban restoration in New Zealand is an on-going problem.

In a study of restored gully vegetation in Hamilton City, MacKay et al. (2011) found that high quality post-planting maintenance (weed control and clearing exotic herbs and grasses to reduce competition) was important for restoration success. All of the restoration sites examined in the present study are managed by the Tauranga City Council who has strict maintenance regimes in place and weeds were generally well controlled in the restoration sites studied. The detrimental effects of pest plants are well known and are not covered in detail here. However, results suggest that reserves with naturally regenerating vegetation receive less weed control attention than revegetation sites and this is something that should be addressed.

4.4.1.2 Seed availability and dispersal

The restorations sites in Tauranga City are relatively isolated from natural forest remnants. Mauao represents the biggest patch of forest in the city and Motuotau Island, 600m off the Mt Maunganui beach is also covered in *Metrosideros* forest. The next nearest significant patch of coastal forest is 24 km to the northwest at Bowentown. The nearest lowland forest patches containing key species such as *Beilschmiedia tawa* and *Dysoxylum spectabile* are at least 6 km to the southeast in the Papamoa hills. Many of the more common understorey shrubs such as *Macropiper*, *Geniostoma*, and *Melicytus* are present in the study sites or in other reserves and there are mature *Alectryon*, *Corynocarpus*, and *Vitex* in reserves or planted as street trees around the city. *Litsea*, one of the key successional species in coastal *Metrosideros* forest, is present in McCardel's Bush (a few trees) and there is a single tree on Motuotau Island (BD Clarkson pers. comm.). While some understorey species are nearby and are being dispersed to restoration sites many key species are failing to recruit. The distance of these sites from a seed source is likely to be one of the main reasons for this.

Two separate urban restoration studies have shown that distance from a native seed source affects the success of urban restoration projects. In a study in Auckland, Sullivan et al. (2009) found that restoration plantings closer to natural stands of native vegetation were colonised by higher numbers of native plant species and MacKay et al. (2011) reported that proximity to a natural seed source was a determinant of restoration success. In contrast, Dungan et al. (2001) reported that seed dispersal was not limiting to natural succession in rural restoration sites in the Port Hills. However, in highly modified urban areas seeds arriving at restoration sites may be more likely to be exotic than native. For example, seed rain in urban Hamilton forest patches was found to contain a higher proportion of exotic species than native ones (Overdyck & Clarkson 2012). Furthermore, woody species were least well represented in persistent seed banks which were predominantly exotic herbs (Overdyck & Clarkson 2012). However, Overdyck & Clarkson (2012) reported that restoration plantings of more than 20 years old had lower exotic species richness in the seed banks and understorey despite no change in exotic species richness in the seed rain. These older restorations sites may offer some resistance to the establishment of many exotic species such as herbs and grasses which are adapted to open habitats (Overdyck & Clarkson 2012). These studies suggest that seed dispersal can be a significant issue for urban restoration sites.

Many of the key species in the target ecosystems are bird-dispersed and their ability to arrive at a site may be limited by the presence of appropriate bird species and the availability of a seed source which is close enough for a bird to carry seed from. Large fruited trees like *Vitex* and *Beilschmiedia* require large birds to disperse their fruit. Of the birds likely to visit restoration sites in Tauranga only kereru and tui have been reported to disperse *Beilschmiedia* fruit (Clout & Hay 1989; Kelly et al. 2010), while kereru, tui, and Indian myna have been reported to disperse *Vitex* (Clout & Hay 1989; Dijkgraaf 2002; Kelly et al. 2010). Smaller-fruited species require smaller birds and introduced birds such as blackbird and song thrush are known to disperse a wide range of native seeds (Kelly et al. 2010). Kereru can have home ranges of many thousands of hectares and can travel many kilometres in a day (Powlesland et al. 2011). They are capable of dispersing native seeds very long distances but are much more likely to disperse seed within 500 m of where they ate it (Wotton & Kelly 2012). Hence with the nearest major seed source for *Beilschmiedia* or *Dysoxylum* more than 6 km away there is a chance that seed from these species may be introduced by kereru, or possibly even tui, but the quantity of seed will be very low. Propagule pressure, or the amount of seed arriving at a site, has a strong effect on the likelihood that a species will establish there (Lockwood et al. 2005; Simberloff 2009). Even if seeds are able to arrive at a site they are then subjected to a further set of environmental filters including predation and microclimate conditions that may or may not be suitable for germination and survival. In broadcast seeding trials in Hamilton up to 37% of fleshy-fruited seeds were predated on the ground by rats, mice, and possums (Overdyck et al. 2013) If seeds escape predation, the conditions at the site then need to be right from them to germinate and survive beyond the seedling stage to have any influence on the vegetation community. So, in urban forest patches isolated from natural seed sources, with high exotic presence in the seed rain and limited or no pest animal control the likelihood of species such as *Beilschmiedia* of *Dysoxylum* establishing in sufficient numbers to influence the composition of the canopy appears to be very low.

4.4.1.3 Edge effects

Many of the revegetation plantings in Tauranga city are small or are an irregular shape. In some cases plots measured for this study were within 15m of the patch edge. The largest plantings are on Mauao and in the Kopurererua Valley where some plantings are 100-200m wide. Small forest patches have a high proportion of edge which can affect regeneration and the vegetation dynamics (Young & Mitchell 1994; Norton 2002; Burns et al. 2011). Forest edges are the transition area where the microclimate grades from fluctuating conditions in open country to relatively stable conditions in the forest interior (Norton 2002). Edges have higher light, are less moist, and are subjected to higher wind speeds than the forest interior (Davies-Colley et al. 2000; Norton 2002): These factors are collectively known as edge effects. Edge effects can affect canopy cover, understorey composition and abundance of forest species as well as enabling the invasion of pest plants (Young & Mitchell 1994; Norton 2002) simply because conditions favour open habitat species rather than forest interior ones. Edge environments typically extend 40-50m into the forest (Young & Mitchell 1994; Davies-Colley et al. 2000) but this distance is affected by adjacent land use, aspect, and topography, as well as the density of vegetation at the edge (Young & Mitchell 1994; Didham & Lawton 1999; Norton 2002). Given the small size of the restoration sites surveyed in the present study and elsewhere in Tauranga and the evidence summarised here it seems unlikely that forest microclimate conditions will be reached in any but the largest of the restoration sites. Suggestions for mitigating edge effects are outlined in section 4.7 below.

4.5 Theoretical model for Tauranga City restoration sites

Despite an abundance of theoretical models relevant to ecological restoration, none provide simple answers to actual restoration questions (Suding & Hobbs 2009). However, models can be useful in making decisions about how a restoration is approached. The theoretical model of the restoration of forest vegetation in Tauranga City in Figure 4.1 illustrates the environmental thresholds and multiple stable states that are possible and the potential effects of different management. This model is largely conjecture but it is based broadly on the results of this study, the literature, and personal experience.

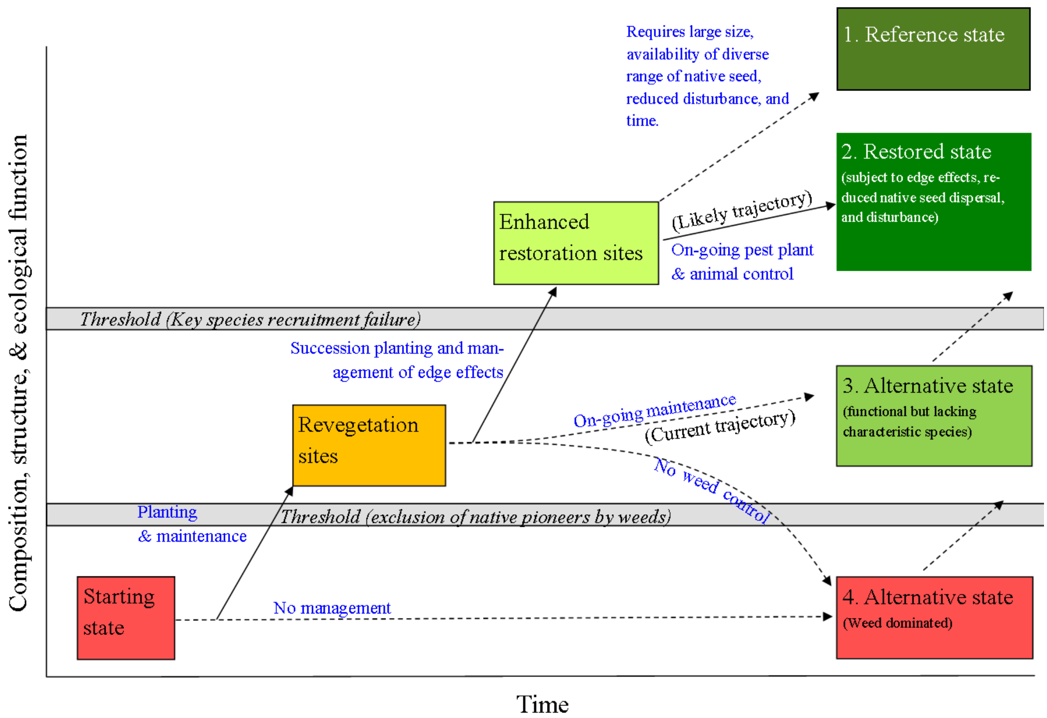

Figure 4.1: A theoretical vegetation development diagram for restoration sites in Tauranga City. Boxes represent the various states of the vegetation, arrows represent developmental trajectories and blue text represents management inputs or drivers of developmental change.

The reference state in the top-right of the diagram is likely to be unattainable in an urban setting, but a functioning forest ecosystem with many of the components of the reference forest (State 2, Figure 4.1) should be achievable at larger sites, with succession planting and management of weeds and pests. Alternative state 3 represents the current trajectory of the restoration sites under the current management. This state would have some ecological function restored and would be dominated by natives but would be lacking the characteristic species of the target forest type. Without any management or planting current restoration plantings may decline to become weed-dominated. Similarly, bare sites are likely to become weedy and unlikely to develop a native vegetation cover. Transition from state 4 to state 3, and 3 to state 2 is possible with appropriate management intervention.

4.6 Summary

Results from this study show that the initial establishment of native vegetation and associated maintenance and weed control is being done to a high standard in Tauranga City, and in the Kopurererua Valley and on Mauao this will result in forest dominated by representative tree species. However, vegetation development beyond early-successional and easily dispersed native species is not occurring, probably as a result of limited availability of seed and browsing by pest animals (in the case of Mauao), but also because of the young age of many plantings and their size and shape. This lack of succession represents a developmental threshold which will require specific management to be overcome. Nevertheless, improving vegetation structure, composition, and diversity, as well as microclimate conditions and ecosystem function (seed dispersal) as stands age are positive results and indicate that as time goes on, and with the current level of management, restoration sites in Tauranga will continue to improve. Vegetation development or recovery takes a long time and while positive results can be seen after 20 years (Burns et al. 2011; Overdyck & Clarkson 2012) reaching a state anywhere near the reference state is likely to take many, many years more.

Management inputs to ameliorate some of the issues preventing successional development may help to keep the restoration sites on the desired trajectory towards the target forest types. However, given their small scale and isolation, many of the revegetation and restoration plantings in Tauranga City will never be restored to a pre-disturbance state. These sites can still provide valuable habitat for native birds and insects however, and if appropriate species are planted they can help to restore native species to the urban seed rain.

Specific management recommendations for each forest type are outlined in section 4.7 below.

4.7 Recommendations

4.7.1 Coastal forest

1. When planting new sites *Metrosideros excelsa* should be planted at a density of 1000 – 2000 plants ha^{-1} which equates to approximately 50% of the planting mix when using a typical 1.5 m between plants. *Kunzea ericoides,* and *Leptospermum scoparium* should be the other major components of the initial mix.
2. Key understorey and successional canopy species should be deliberately introduced into the system because natural recruitment of these species appears to be failing. *Vitex lucens* can be planted within two or three years of other plantings in relatively open vegetation such as that found in the youngest restoration plantings surveyed in this study. *Vitex* should also be planted in gaps in older vegetation or where the canopy has thinned. *Litsea calicaris* can also be planted in gaps or lighter areas in older vegetation. The highly shade tolerant *Dysoxylum spectabile* and *Beilschmiedia tawa* should be planted in the old-growth forest on Mauao and in the older restoration plantings. These plantings should be relatively sparse: as little as 100 plants ha^{-1}.
3. Most of the other understorey species are present on Mauao but recruitment of a number of shrub and small tree species into the seedling and sapling tiers is failing and the high rabbit numbers are a likely cause. The rabbit population on Mauao needs to be reduced considerably to allow natural regeneration to occur. Establishing a monitoring programme for seedlings and saplings would give a good indication of recruitment success and the effect of rabbit control.
4. Pest plant control has been very successful on Mauao and this has undoubtedly contributed to the success in establishing the initial restoration plantings. This high level of weed control should be continued.

4.7.2 Semi-coastal broadleaved forest

1. Initial plantings should be diverse and include both fast-growing pioneer species and some of the key mid-succession trees such as *Alectryon excelsus, Vitex lucens, Dacrydium cupressinum,* and *Melicytus ramiflorus*.
2. In addition, initial plantings should include species such as *Aristotelia serrata* and *Coprosma* to attract frugivorous birds.
3. Revegetation sites should include a dense buffer planting around the perimeter to help reduce edge effects. Plant a species that remains bushy down to ground-level so that it reduces airflow and direct sunlight in the understorey near the edge. *Phormium tenax* works well in this role but *Leptospermum scoparium* will also work. Adding buffer plantings to existing restoration plantings should be considered.
4. When planning new plantings large areas and robust shapes will help to reduce edge effects.
5. Where patches are small and likely to be subject to on-going edge effects long-lived but light loving species such as *Kunzea ericoides, Dacrydium cupressinum, Podocarpus totara* and *Weinmannia racemosa* could be planted.
6. Successional species should be added to the restoration sites by either planting (preferred) or direct seeding. Key late-successional canopy and understorey species including *Beilschmiedia tawa* and *Dysoxylum spectabile* can begin to be added four or five years after the initial planting when canopy closure has occurred. This is much earlier than they would arrive in natural systems but there environmental conditions prevent germination, not necessarily the ability of the plants to survive once past the seedling stage. These species should each be planted at densities of 100-300 stems ha^{-1} (5.5-10 m apart).
7. Other forest species including lianes, shrubs, sedges, grasses and ferns can be added within 10-15 years after the initial planting but the individual requirements of each species will need to be checked prior to planting them.
8. A high level of weed control should continue to be maintained. Weeds such as *Tradescantia fluminensis* and *Hedychium gardnerianum* that can prevent regeneration of native species should especially be targeted.

9. Pest animal control should also be considered to reduce predation of seeds and native animals.

4.7.3 Swamp forest

1. Where conditions are suitable (i.e. gley soils but not completely waterlogged) and *Dacrycarpus dacrydioides* forest is the goal, *Dacrycarpus* should be planted at a density of at least 2000 stems ha^{-1}. This equates to approximately 45% of the species mix in a 1.5m spaced planting.
2. *Dacrycarpus* can be planted into a bare site amongst other suitable pioneers including *Leptospermum scoparium, Coprosma propinqua, C. tenuicaulis, Phormium tenax,* and various species of *Carex*.
3. Weed control to maintain an indigenous understorey and exclude *Salix cinerea* and *Ligustrum sinense* is critical.
4. Pest animal control should also be considered to reduce predation of seeds and native animals.

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Appendices

Appendix 1: Vascular plant species list.

Acmena smithii (poir.) Merr. & l.m.perry	monkey apple	Exotic
Actinidia chinensis planch.	kiwifruit	Exotic
Adiantum cunninghamii	maidenhair fern	Native
Adiantum hispidulum	rosy maidenhair	Native
Agapanthus praecox subsp. Orientalis (f.m.leight.) F.m.leight. (1965)	Agapanthus	Exotic
Agrostis stolonifera	creeping bent	Exotic
Ailanthus altissima	tree of heaven	Exotic
Alectryon excelsus	titoki	Native
Anagallis arvensis	scarlet pimpernel	Exotic
Anthoxanthum odoratum	sweet vernal	Exotic
Araujia sericifera brot.	moth plant	Exotic
Aristotelia serrata	makomako, wineberry	Native
Asparagus scandens	climbing asparagus	Exotic
Asplenium bulbiferum	pikopiko, hen & chicken fern	Native
Asplenium flaccidum g.forst.	drooping spleenwort	Native
Asplenium oblongifolium	shining spleenwort	Native
Asplenium polyodon	sickle spleenwort	Native
Astelia banksii	shore kowharawhara, coastal astelia	Native
Machaerina rubiginosa	Baumea	Native
Beilschmiedia tawa	tawa	Native
Berberis glaucocarpa	barberry	Exotic
Blechnum chambersii	lance fern	Native
Blechnum discolor	crown fern	Native
Blechnum filiforme	thread fern	Native
Blechnum novae-zealandiae	kiokio	Native
Brachyglottis repanda	rangiora	Native
Calystegia sepium	pink bindweed	Native
Cardamine debilis	New Zealand bittercress	Native
Carex geminata	rautahi	Native
Carex lambertiana	forest sedge	Native
Carex lurida	sallow sedge	Exotic
Carex maorica	Maori sedge	Native
Carex ovalis	oval sedge	Exotic
Carex secta	purei	Native
Carex species		
Carex testacea	speckled sedge	Native
Carex virgata	pukio	Native
Carpodetus serratus	putaputaweta	Native
Centella uniflora	Centella	Native
Cerastium glomeratum	annual mouse-ear chickweed	Exotic
Cistus albidus	rock rose	Exotic
Collospermum hastatum	kahakaha	Native
Conyza albida	fleabane	Exotic
Coprosma areolata	thin-leaved coprosma	Native
Coprosma grandifolia	kanono	Native
Coprosma lucida	shiny karamu	Native
Coprosma macrocarpa subsp. Minor	large seeded coprosma	Native
Coprosma propinqua	mingimingi	Native
Coprosma propinqua × robusta		Native
Coprosma repens	taupata	Native
Coprosma robusta	karamu	Native
Coprosma spathulata subsp. Spathulata		Native
Coprosma tenuicaulis	hukihuki, swamp coprosma	Native
Cordyline australis	ti, cabbage tree	Native
Coriaria arborea	tutu	Native

Cortaderia selloana	pampas grass	Exotic
Corynocarpus laevigatus	karaka	Native
Crataegus monogyna	hawthorn	Exotic
Crocosmia ×crocosmiiflora	montbretia	Exotic
Cyathea dealbata	ponga, silver fern	Native
Cyathea medullaris	mamaku	Native
Cyathea smithii	katote	Native
Cyperus eragrostis	umbrella sedge	Exotic
Cyperus ustulatus	giant umbrella sedge	Native
Dacrycarpus dacrydioides	kahikatea	Native
Dacrydium cupressinum	rimu	Native
Dactylis glomerata	cocksfoot grass	Exotic
Daucus carota	wild carrot	Exotic
Deparia petersenii (kunze) m.kato (1977)		Native
Dianella nigra	turutu	Native
Dichondra repens	Mercury Bay weed	Native
Dicksonia squarrosa	wheki	Native
Digitalis purpurea	foxglove	Exotic
Diplazium australe		Native
Dodonaea viscosa	akeake	Native
Doodia australis (parris) parris	rasp fern	Native
Dysoxylum spectabile	kohekohe	Native
Earina mucronata	peka-a-waka, spring earina	Native
Ehrharta erecta	veldt grass	Exotic
Elaeocarpus dentatus	hinau	Native
Entelea arborescens	whau	Native
Erica lusitanica	Spanish heath	Exotic
Euphorbia peplus	milkweed	Exotic
Fatsia japonica	Fatsia	Exotic
Freycinetia banksii	kiekie	Native
Fumaria muralis w.d.j.koch	scrambling fumatory	Exotic
Galium palustre l.	marsh bedstraw	Exotic
Geniostoma rupestre var. ligustrifolium	hangehange	Native
Glyceria maxima	reed sweetgrass	Exotic
Gomphocarpus fruticosus	swan plant	Exotic
Griselinia littoralis	kapuka, broadleaf	Native
Haloragis erecta	toatoa	Native
Hebe stricta	koromiko	Native
Hedera helix	English ivy	Exotic
Hedycarya arborea	porokaiwhiri, pigeonwood	Native
Hedychium gardnerianum	kahili ginger	Exotic
Hoheria populnea a.cunn.	houhere, lacebark	Native
Holcus lanatus	Yorkshire fog	Exotic
Homalanthus populifolius graham (1827)	Queensland poplar	Exotic
Hymenophyllum demissum	filmy fern	Native
Hymenophyllum dilatatum	filmy fern	Native
Hypochaeris radicata l.	catsear	Exotic
Isachne globosa	swamp millet	Native
Juncus articulatus	jointed rush	Exotic
Juncus effusus	soft rush	Exotic
Knightia excelsa	rewarewa	Native
Kunzea ericoides	kanuka	Native
Lastreopsis glabella	smooth shield fern	Native
Laurelia novae-zelandiae	pukatea	Native
Lemna disperma	common duckweed	Native
Leontodon taraxacoides	hawkbit	Exotic

Leptospermum scoparium	manuka	Native
Leucanthemum vulgare	oxeye daisy	Exotic
Leucopogon fasciculatus	mingimingi	Native
Ligustrum lucidum w.t.aiton	tree privet	Exotic
Ligustrum sinense	Chinese privet	Exotic
Litsea calicaris	mangeao	Native
Lonicera japonica	Japanese honeysuckle	Exotic
Lotus pedunculatus	lotus	Exotic
Ludwigia palustris	water purslane	Exotic
Lygodium articulatum	mangemange, tangle fern	Native
Macropiper excelsum	kawakawa	Native
Malva parviflora l.	small-flowered mallow	Exotic
Melicytus ramiflorus	mahoe	Native
Mentha pulegium	pennyroyal	Exotic
Metrosideros diffusa	white rata	Native
Metrosideros excelsa	pohutukawa	Native
Metrosideros fulgens	rata	Native
Metrosideros perforata	white rata	Native
Microlaena avenacea	bush rice grass	Native
Microlaena stipoides	meadow rice grass	Native
Microsorum pustulatum subsp. Pustulatum	kowaowao, hound's tongue fern	Native
Microsorum scandens	mokimoki, fragrant fern	Native
Morelotia affinis	Morelotia	Native
Muehlenbeckia complexa	small-leaved pohuehue	Native
Myoporum laetum	ngaio	Native
Myosotis laxa subsp. Caespitosa (schultz) hyl. Ex nordh.	forget-me-not	Exotic
Myriophyllum propinquum	water milfoil	Native
Myrsine australis	mapou	Native
Nothofagus menziesii	silver beech	Native
Olearia furfuracea	akepiro	Native
Oplismenus hirtellus subsp. Imbecillis (r.br.) U.scholz		Native
Oxalis species	oxalis	Exotic
Parsonsia capsularis	New Zealand jasmine	Native
Parsonsia heterophylla	New Zealand jasmine	Native
Paspalum dilatatum	Paspalum	Exotic
Pellaea rotundifolia	round-leaved fern	Native
Pennisetum clandestinum	kikuyu grass	Exotic
Persicaria hydropiper (l.) Spach (1841)	water pepper	Exotic
Phormium cookianum	wharariki, mountain flax	Native
Phormium tenax	harakeke, flax	Native
Phyllocladus trichomanoides	tanekaha	Native
Physalis peruviana	Cape gooseberry	Exotic
Phytolacca americana	pokeweed	Exotic
Phytolacca octandra	inkweed	Exotic
Pinus pinaster	cluster pine	Exotic
Pinus radiata	radiata pine	Exotic
Pittosporum colensoi	kohuhu	Native
Pittosporum crassifolium	karo	Native
Pittosporum eugenioides	tarata, lemonwood	Native
Pittosporum tenuifolium	kohuhu	Native
Pittosporum umbellatum	haekaro	Native
Plantago lanceolata	naroow-leaved plantain	Exotic
Pneumatopteris pennigera	piupiu, gully fern	Native
Podocarpus totara	totara	Native
Polystichum neozelandicum subsp. neozelandicum	black shield fern	Native
Pomaderris amoena colenso (1886)	tauhinu	Native

Prunella vulgaris	selfheal	Exotic
Prunus campanulata maxim.	Taiwan cherry	Exotic
Pseudopanax arboreus	whauwhaupaku	Native
Pseudopanax crassifolius (sol. Ex a.cunn.) K.koch	horoeka, lancewood	Native
Pseudopanax crassifolius × lessonii		Native
Pseudopanax lessonii	haupara	Native
Pteridium esculentum	braken	Native
Pteris macilenta	sweet fern	Native
Pteris tremula	shaking brake	Native
Pyrrosia elaeagnifolia	leather fern	Native
Ranunculus flammula	spearwort	Exotic
Ranunculus repens	buttercup	Exotic
Rhabdothamnus solandri	taurepo	Native
Rhamnus alaternus l.	Italian evergreen buckthorn	Exotic
Rhopalostylis sapida	nikau	Native
Ripogonum scandens	kareao, supplejack	Native
Robinia pseudoacacia l. (1753)	black locust	Exotic
Rubus cissoides	tataramoa, bush lawyer	Native
Rubus fruticosus	blackberry	Exotic
Rubus phoenicolasius	Japanese wineberry	Exotic
Rumex conglomeratus	clustered dock	Exotic
Rumex sagittatus	climbing dock	Exotic
Salix cinerea	grey willow	Exotic
Salix fragilis	crack willow	Exotic
Schefflera digitata	pate	Native
Selaginella kraussiana	African clubmoss	Exotic
Senecio bipinnatisectus	Australian fireweed	Exotic
Setaria palmifolia	palm grass	Exotic
Solanum mauritianum scop. (1788)	woolly nightshade	Exotic
Solanum nigrum	black nightshade	Exotic
Sonchus oleraceus	sow thistle	Exotic
Sophora microphylla	kowhai	Native
Sporobolus africanus	rat's tail	Exotic
Streblus heterophyllus	turepo	Native
Trachycarpus fortunei (hook.) H.wendl.	Chinese windmill palm	Exotic
Tradescantia fluminensis	wandering Jew	Exotic
Trifolium repens	white clover	Exotic
Ulex europaeus	gorse	Exotic
Uncinia banksii	fine-leaved bastard grass	Native
Uncinia uncinata	kamu, bastard grass	Native
Verbascum thapsus	woolly mullein	Exotic
Verbena bonariensis	purple-top	Exotic
Veronica arvensis	field speedwell	Exotic
Viola odorata	violet	Exotic
Vitex lucens	puriri	Native
Zantedeschia aethiopica	arum lily	Exotic

Appendix 2: Location and physical characteristics of each of the 45 plots included in the survey.

Plot	**Category**	**Site**	**Easting** (NZTM)	**Northing** (NZTM)	**Altitude (m asl)**	**Aspect (mag. ^{0})**	**Physio-graphy**	**Slope (^{0})**	**Canopy height (m)**
1	CF1	Tuhua	1888884	5866569	90	110	Ridge	5	25
2	CF1	Tuhua	1888668	5865834	45	180	Terrace	5	20
3	CF1	Tuhua	1888418	5866375	40	180	Terrace	5	26
4	CF1	Tuhua	1887757	5867105	75	150	Gully	4	19
5	SC3	Johnson Reserve	1880271	5818905	25	250	Face	30	9
6	SC3	Johnson Reserve	1880129	5819079	5	265	Gully	2	10
7	SC3	Johnson Reserve	1880248	5818841	20	230	ridge	10	5
8	CF5	Mauao	1879891	5830848	80	355	Face	35	1.8
9	CF5	Mauao	1879688	5830786	55	290	Face	25	2.5
10	CF5	Mauao	1879933	5830781	120	355	Face	30	1.8
11	CF5	Mauao	1879818	5830819	90	325	Face	30	2.5
12	CF3	Mauao	1879731	5830248	100	195	Face	35	5
13	CF3	Mauao	1879924	5830193	130	170	Face	20	3
14	CF3	Mauao	1879758	5830445	180	20	Face	37	13
15	CF3	Mauao	1880072	5830601	100	55	Face	25	3
16	SF1	White Pine Bush	1946450	5785541	15	310	Terrace	0	22
17	SF1	White Pine Bush	1946552	5785453	15	0	Terrace	0	22
18	SF2	Kopurererua Valley	1875695	5820903	5	0	Floodplain	0	13
19	SF2	Kopurererua Valley	1875820	5821163	5	0	Floodplain	0	7
20	SF2	Kopurererua Valley	1876153	5821540	5	0	floodplain	0	12.5
21	SF2	Kopurererua Valley	1876492	5821776	5	0	Floodplain	0	6
22	SC2	Kopurererua Valley	1875662	5821302	20	100	Face	30	13
23	SC2	Kopurererua Valley	1875430	5821112	20	135	Face	35	8
24	SF4	Kopurererua Valley	1876676	5822177	5	0	Floodplain	0	1.8
25	SF4	Kopurererua Valley	1876837	5822167	5	0	Floodplain	0	2.5
26	SF4	Kopurererua Valley	1876870	5822119	5	0	Floodplain	0	2.2
27	CF4	Mauao	1879870	5830929	40	320	Face	20	4.5
28	CF4	Mauao	1879709	5830865	50	250	Face	25	5
29	CF4	Mauao	1880135	5830415	60	55	Face	25	7.7
30	CF2	Mauao	1879466	5830396	30	210	Ridge	30	15
31	CF2	Mauao	1879544	5830632	50	320	Face	30	24
32	CF2	Mauao	1879599	5830533	100	270	Face	30	22
33	SF3	Te Maunga	1885330	5823411	3	0	floodplain	0	8
34	SF3	Te Maunga	1885032	5823593	5	0	floodplain	0	8
35	SF3	Te Maunga	1885370	5823436	3	0	floodplain	0	7
36	SC2	Kaitemako	1879772	5819999	10	95	Face	25	12
37	SC2	Kaitemako	1880006	5820147	10	150	Face	15	8
38	SC4	Johnson Reserve	1880428	5819644	10	315	Face	20	10
39	SC4	Johnson Reserve	1880125	5819385	10	35	Face	10	8
40	SC4	Johnson Reserve	1879981	5819077	15	100	Face	25	10.5
41	SC1	Armani	1855372	5831607	140	65	Face	10	26
42	SC1	Armani	1855501	5831564	120	180	Face	15	24
43	SC1	Blaymires	1887816	5815155	140	140	Gully	15	17
44	SC1	Blaymires	1887641	5815222	180	135	Face	30	18
45	CF1	Tuhua	1888672	5865889	45	180	Terrace	5	18

Appendix 3: (a) Average physical and environmental characteristics of each category and (b) representative soil characteristics. Average daily temperature and Relative Humidity (RH) are the average of the daily means at each site.

(a)

	Altitude (m asl)				**Slope** (°)				**Heat Load**				**Daily temperature** (°C)				**D RH** (%)				**Canopy Height** (m)			
	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.	$\bar{x}$	Min	Max	s.d.
CF1	59	40	90	22.19	4.8	4	5	0.45	0.94	0.93	0.94	0.00	13.2	6.0	20.4	2.46	87.2	51.0	100.0	7.44	21.60	18.00	26.00	3.65
CF2	60	30	100	36.06	30.0	30	30	0.00	0.95	0.77	1.07	0.16	12.8	3.9	23.1	2.72	83.9	48.8	100.0	7.39	20.33	15.00	24.00	4.73
CF3	128	100	180	37.75	29.3	20	37	8.10	0.79	0.66	0.90	0.10	12.1	3.5	23.1	2.87	86.6	46.5	100.0	7.92	6.00	3.00	13.00	4.76
CF4	50	40	60	10.00	23.3	20	25	2.89	0.95	0.83	1.06	0.12	13.3	4.1	24.8	2.67	82.9	43.8	100.0	9.22	5.73	4.50	7.70	1.72
CF5	86	55	120	26.89	30.0	25	35	4.08	1.04	1.01	1.07	0.03	14.3	2.8	31.5	2.61	76.2	29.6	100.0	11.11	2.15	1.80	2.50	0.40
SC1	145	120	180	25.17	17.5	10	30	8.66	0.79	0.59	0.92	0.14	11.4	2.0	22.4	2.79	88.0	54.8	100.0	7.00	21.25	17.00	26.00	4.43
SC2	15	10	20	5.77	26.3	15	35	8.54	0.67	0.52	0.80	0.12	11.5	-0.9	24.7	3.33	86.1	46.5	99.0	6.57	10.25	8.00	13.00	2.63
SC3	17	5	25	10.41	14.0	2	30	14.42	0.96	0.93	0.98	0.03	11.3	-1.6	23.5	3.49	90.7	48.1	100.0	7.12	8.00	5.00	10.00	2.65
SC4	12	10	15	2.89	18.3	10	25	7.64	0.91	0.70	1.06	0.19	12.1	-0.7	24.8	3.42	84.9	40.9	100.0	7.61	9.50	8.00	10.50	1.32
SF1	15	15	15	0.00	0.0	0	0	0.00	0.98	0.98	0.98	0.00	10.2	-1.1	23.7	3.74	91.4	49.6	100.0	5.03	22.00	22.00	22.00	0.00
SF2	5	5	5	0.00	0.0	0	0	0.00	0.98	0.98	0.98	0.00	11.9	-1.3	26.4	3.42	84.5	36.3	100.0	6.22	9.63	6.00	13.00	3.64
SF3	4	3	5	1.15	0.0	0	0	0.00	0.98	0.98	0.98	0.00	12.2	0.3	24.7	3.25	83.3	43.6	97.1	6.39	7.67	7.00	8.00	0.58
SF4	5	5	5	0.00	0.0	0	0	0.00	0.98	0.98	0.98	0.00	11.5	-2.4	29.3	3.76	87.2	39.9	100.0	6.53	2.17	1.80	2.50	0.35

(b)

	pH	**Olsen P** (mg/L)	**Available N** (kg/ha)	**Organic Matter** (%)	**TC** (%)	**TN** (%)	**C/N** Ratio	**K** (me/100g)	**Ca** (me/100g)	**Mg** (me/100g)	**Na** (me/100g)	**CEC** (me/100g)	**Total Base Saturation** (%)
CF1	6.8	47	97	10.7	6.2	0.37	16.6	1.17	19.2	6.39	1.15	32	86
CF2	6.5	3	142	7.5	13.5	4.3	0.32	0.53	11.5	2.65	0.3	17	90
CF3	6.2	5	188	9.4	11.4	5.4	0.48	1.24	8	3.8	0.38	19	73
CF4	6.8	8	202	9.3	10.4	5.4	0.52	1.73	10.1	4.84	0.28	20	84
CF5	6	3	101	6.7	12.6	3.9	0.31	0.61	4.2	2.19	0.22	13	56
SC1	5.1	2	193	22	12.8	0.8	15.9	0.37	3	1.43	0.2	32	16
SC2	5.6	2	101	7	4.1	0.28	14.6	1.12	5.3	1.96	0.17	17	50
SC3	5.7	2	135	10.7	6.2	0.45	13.9	0.66	7.2	2.42	0.23	22	47
SC4	5.8	5	98	15.6	9	0.74	12.2	1.11	9.7	1.9	0.19	31	42
SF1	6	25	111	8.5	13.4	4.9	0.37	0.89	6.8	2.12	0.09	16	61
SF2	5.5	4	44	14.6	8.5	0.72	11.7	0.38	4.3	1.21	0.59	29	22
SF3	5.2	8	151	9.2	12.1	5.4	0.44	0.14	2.4	0.42	0.19	15	21
SF4	5.4	4	96	6.4	3.7	0.26	14.2	0.22	2.3	0.43	0.28	14	23