Community composition, assembly and priority effects in a volcanically disturbed alpine herbfield, Mount Taranaki, New Zealand

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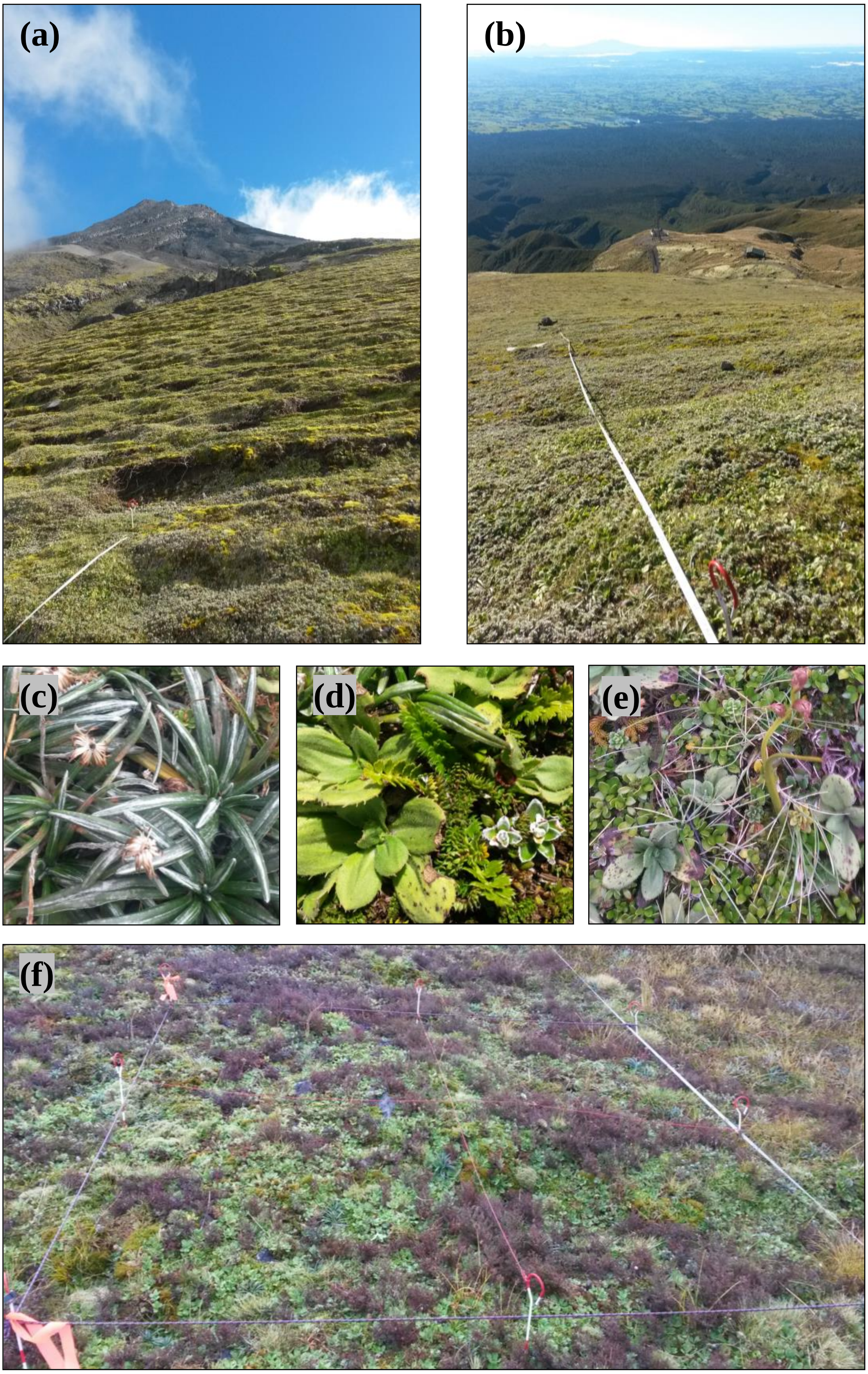

Frontispiece: **(a)** View from a North Egmont transect, looking up toward the summit of Mt Taranaki. **(b)** View from the same North Egmont transect looking toward Tongariro National Park. **(c)** *Celmisia gracilenta*. **(d, e)** Herbfield vegetation found in the plots. **(f)** A plot at Fantham's Peak.

Abstract

The New Zealand alpine flora is highly diverse, having evolved extensively over only c. 2 Ma. Examining how communities assemble and the effects of historical contingency may provide evidence for the mechanisms of rapid diversification of the New Zealand alpine flora. Evolutionary priority effects, in which the sequence of colonisation during community assembly can drive radiation of early arriving clades, has been tested in one South Island alpine community. The results showed genera belonging to older evolutionary lineages were more dominant and diverse in those communities, supporting the presence of priority effects.

Mount Taranaki in the North Island is geologically the youngest alpine zone in New Zealand, and supports a depauperate assemblage of alpine species compared to other New Zealand mountains. Mount Taranaki has had approximately 10 moderately sized eruptions in the last 500 years and is separated from other New Zealand alpine regions by 130 km. The present study sought to determine how the vegetation in the alpine herbfield of Mount Taranaki has been affected by various eruptions, and to test if priority effects have influenced those communities.

To quantify community composition in the Taranaki alpine herbfield, estimates of percent cover from 55 (2 x 2 m) plots were used to calculate relative species abundance at three sites within an altitudinal range of 1450–1650 m above sea level. Study sites were located at North Egmont, East Egmont and Fantham's Peak. Multivariate analysis using non-metric multidimensional scaling ordination of relative abundances was used to compare variations in composition between sites and elevations. To test for priority effects, time-calibrated molecular phylogenies of clade divergence (as age estimates) were compared to the relative abundances of genera within the plots using linear regression.

The results showed significant variation of species composition between sites, which correlates with the spatial pattern of the AD 1655 Burrell eruption. The eruption was directed toward East Egmont, and the plots there showed considerably lower species diversity compared to the other two sites. In addition, the inconsistency of species distribution between the sites indicated a lack of community convergence, suggesting herbfield vegetation is still in the early ages of assembly following eruptions. The test of priority effects showed no age-related abundance or richness relationships, therefore priority effects are unlikely to be contributing to community assembly in the Taranaki alpine herbfield. Instead, assembly appears to be influenced by the geological age and frequency of eruptions of Mount Taranaki, and its isolation from other alpine systems.

This is the first study to determine the effects of volcanic eruptions on the herbfield vegetation of Mount Taranaki, and it is recommended that plots be re-measured in the future to determine how those communities develop. Because no priority effects were evident on Mount Taranaki, further research on a range of older volcanic and non-volcanic alpine systems in the North Island would be valuable. This would further contribute to our understanding of how communities assemble and if and when priority effects become significant.

Keywords: alpine flora, community assembly, volcanic disturbance, Taranaki, priority effects, Burrell eruption

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Chapter One: Introduction

1.1 Background to the research area

Determining how communities assemble is no easy task. Disturbance, colonisation history and environmental factors must all be considered when attempting to predict species assemblages. Research by Lee et al. (2012) of historical and evolutionary influences on an alpine community in the Southern Alps highlighted the importance of colonisation history in structuring clade diversity and community composition. Lee et al. tested the hypothesis of Silvertown (2004) in which early colonists gain priority over later arrivals by niche pre-emption, and this ‘priority effect’ may strongly influence species radiation. Their study represented the first test of priority effects in the New Zealand flora. Because the alpine flora of New Zealand is highly diverse, yet has evolved rapidly over less than c. 2 Ma, the origins and diversification of this flora have been questioned at length (Raven 1973; Wardle 1978; McGlone 1985; Winkworth et al. 2005; Heenan & McGlone 2013).

In this thesis, I examine the influences on community assembly in the alpine herbfield of Mount Taranaki. First the alpine herbfield community composition is assessed and then related to the historical events affecting the vegetation on the mountain. Second, an analysis of priority effects in those communities is undertaken. The present research highlights how the recent formation of Mount Taranaki, periods of volcanic activity, dispersal and colonisation may have contributed to the species assemblages present within the Taranaki herbfield belt, and how this relates to the assemblages observed in the wider New Zealand alpine flora.

1.2 Research objectives and aims

There are two main research objectives in this thesis. The first objective is to determine how community composition varies between study sites on Mount Taranaki, and poses the following questions:

1. How does community composition vary between three study locations (North Egmont, East Egmont and Fantham’s Peak) on Mount Taranaki, and which species are most abundant?

2. How have recent eruptions affected vegetation composition within the herbfield belt on Mount Taranaki?

The second research objective is to determine the effects of dispersal and colonisation history in the Taranaki alpine herbfield. The questions asked to address this objective are:

1. Are priority effects present in the Mount Taranaki alpine herbfield communities?
2. How does diversity in the Mount Taranaki herbfield compare to other New Zealand alpine regions?

The aim of this research is to examine how community composition on the geologically young and frequently disturbed alpine habitat of Mount Taranaki compares to older alpine regions of New Zealand, such as the Southern Alps and central North Island volcanoes, in order to improve our understanding of how alpine communities assemble.

1.3 Outline of thesis

Chapter One: Introduction

This chapter provides a brief introduction to the thesis, and contains the research objectives and thesis outline.

Chapter Two: Community assembly and the diversity of the New Zealand alpine flora

In this chapter a review is undertaken of the ecological theories relating to community assembly. This chapter also provides an introduction to the New Zealand alpine habitats and vegetation.

Chapter Three: Variation of community composition within the Mount Taranaki alpine herbfield

This chapter provides an introduction to Mount Taranaki and the methods used to measure composition within the herbfield communities, in order to determine how species abundances and distribution vary between sites as a result of recent eruptions.

Chapter Four: Colonisation and priority effects in the Mount Taranaki herbfield

In this chapter I test if priority effects are present in the Taranaki alpine herbfield communities, and review the dispersal mechanisms that have led to colonisation of species on the mountain. This chapter highlights the low diversity and richness observed in the Taranaki alpine flora.

Synthesis

This concluding chapter summarises the results and main discussion points of this thesis, and draws together the key findings. Also included in this chapter are recommendations for future research.

1.4 References

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Chapter Two: Community assembly and diversity of the New Zealand alpine flora

2.1 Abstract

Predicting the assembly of ecological communities combines the theories of assembly rules, species pools, dispersal, ecological niches and adaptive radiation. Recent research has focused on the importance of historical contingency and priority effects as mechanisms of community assembly. The New Zealand alpine flora is rich in diversity and highly endemic, yet the alpine habitats of New Zealand are geologically young in contrast. Evolutionary priority effects may have been responsible for the rapid diversification of the New Zealand alpine flora, and the study by Lee et al. (2012) has provided evidence for this phenomenon in one South Island alpine community. Further research applying historical contingency and priority effects may assist in understanding the effects on community assembly and species diversity in the New Zealand alpine communities.

2.2 Introduction

Understanding the patterns and processes that affect development of ecological communities has long held interest for ecologists, drawing upon the classic theories of pioneers in the science to the more contemporary theories developed in recent years, in a bid to predict change in communities. Predicting how communities initially assemble is a goal of community ecologists, and is becoming more achievable by combining ecological theories from the classic paradigms of the community versus individualistic models of Clements (1916) and Gleason (1926), respectively, to the very recent idea of historical contingency as a driver of community assembly (Vannette & Fukami 2014; Fukami 2015; Tanentzap et al. 2015). These new developments in the study of community assembly combine assembly history and succession with phylogenetic, biogeographic and niche-based theoretical frameworks (Weiher et al. 2011). Together with the ever-improving models of functional trait-based ecology (eg. Lavorel & Garnier 2002; Laughlin et al. 2012; Laughlin & Laughlin 2013), these theories are set to significantly improve the science of predictive community ecology.

Biodiversity can be affected by the arrival of a species to a community, as immigration timing determines the amount of ecological energy available in a developing community, and experimental studies have shown that adaptive radiation and diversification can be altered based on the order in which species enter a community (Fukami & Morin 2003; Fukami et al. 2007). New Zealand, an island isolated from other continental landmasses for approximately 80 Ma, is rich in biodiversity. The New Zealand alpine flora alone contains over 750 species, many of which are endemic (Mark 2012). Interestingly, the high endemism is not only the product of extreme isolation over millions of years, but appears to be the result of rapid evolutionary pressures in the case of the alpine flora, as alpine habitats have only been available for colonisation since their formation in the late Pliocene (Heenan & McGlone 2013). If we consider that immigration history has influenced the diversification of the alpine flora of New Zealand over such a short evolutionary period, then the resulting community composition would be determined by the order of colonisation events. This theory has so far been tested in one New Zealand alpine community, providing evidence that early plant radiations had influenced community composition (Lee et al. 2012).

The first section of this chapter provides a review of the founding and novel theories in community ecology, including assembly rules, species pools, ecological niches, historical contingency and priority effects. The second half of this chapter contains a review of the geological development of the New Zealand alpine habitats and the origins and evolutionary history of the New Zealand alpine flora. The aim of the present review is to provide a theoretical background to the research chapters that follow in this thesis.

2.3 Community assembly theory

2.3.1 Classic theory

Throughout the history of ecological theory, there has been debate over the mechanisms of initial community assembly and ensuing changes in composition over time. Early ecologists tended to focus on simple biotic and abiotic influences on community assembly (Connell & Slatyer 1977), such as environmental resource constraints or the ability to cope with interspecific competition (Gleason 1926). The view held by Clements (1916) that community succession continues until a single climax community is reached was challenged by Gleason (1926, 1939), who proposed that the assemblages of species were not the result of an inevitable pattern of succession in which species cohorts would forever occur together. Gleason instead proposed that the development of cohorts happened independently as the result of an individual species ability to colonise. Gleason’s arguments were supported later by Whittaker (1953) and Egler (1954), and it is now widely accepted that the succession and pattern of development in communities are stochastic processes (Connell & Slatyer 1977; Pickett et al. 1987; Drake 1990). Communities are known to undergo multiple shifts in composition through time according to biotic and abiotic filters that can have varying effects on different species (Lavorel & Garnier 2002).

As discussed by Connell and Slatyer (1977), earlier models placed emphasis on competitive interactions and physical stressors as the main contributors of community assembly and the constituents of species that follow initial colonisation. Connell and Slatyer proposed three alternative models of succession, the first being that facilitation contributes to future community composition, and the further two models suggested tolerance and inhibition were also important mechanisms of succession. Facilitation in communities has been explored in greater detail since the publication by Bertness and Callaway (1994), in which they noted a predominance of facilitative relationships within communities where abiotic stress was higher, and so developed their now-popular stress gradient hypothesis. In comparison, Tilman’s (1985) resource-ratio hypothesis states resource competition is the primary limiting factor in community assembly, and places emphasis on community composition being controlled by lack of availability of two or more limiting resources. Connell and Slatyer, Bertness and Callaway, and Tilman each offer three contrasting theories of community assembly and succession which are only a few of many theories that demonstrate the multifaceted nature of community ecology, also serving to highlight the emphasis that has been placed on immediate environmental influences (biotic and abiotic) on community development. A common theme with these early theories is that they tended to exclude comprehensive historical analyses of past community states and composition, which, as noted by Drake (1991), can be the downfall of assembly studies as they are often undertaken within a short period and therefore disregard many of the processes that led the communities to their current states.

2.3.2 Assembly rules

Community assembly and ecological succession are similar concepts. Succession pertains to a turnover in community composition based on shifts in environmental factors as the community develops towards a (somewhat) predictable community state (Young et al. 2001; White & Jentsch 2004). In community assembly, immigration and species interactions result in variations in community composition, rather than environmentally mediated patterns in development, and the community has not yet converged towards a predictable state (Young et al. 2001; White & Jentsch 2004). Community development can be divided into one of two patterns: 'environmentally mediated patterns,' where species cohorts occur based on environmental preferences in their given habitat; and 'assembly rules,' which includes all forms of interspecific interactions (Wilson 2001). The concept of assembly rules, first proposed by Diamond (1975), is a set of 'rules' by which ecological communities assemble. The rules are based on competition and the ecological niche, allowing or forbidding particular species combinations (Diamond 1975). However, Diamond's assembly rules theory has been the source of much debate (e.g. Connor & Simberloff 1979; Case 1983; Gotelli & McCabe 2002; Ulrich 2004), arising from the difficulty of developing appropriate models with which to test assembly rules (Weiher et al. 1998; Gotelli & McCabe 2002). Patterns of assembly can be difficult to discern, being biotic, abiotic, or a combination of both (Wilson 2001), and of importance to this review is from which pattern of assembly a community develops, and the order in which influential events occur. The resulting community may first have been subjected to an environmentally mediated pattern i.e. the inability to withstand certain environmental circumstances, and the remaining species then undergo interspecific interactions, culminating in the present community (Keddy 1992; Wilson 2001). These patterns of development are what Keddy (1992) used to further develop Diamond's initial assembly rules theory, whereby noting that species must undergo a filtering process which may be either abiotic (environmental influences) or biotic (e.g. competition), in order to remove species that are not suited to a habitat. To use assembly rules to predict community composition, ecologists are required to examine the species pool and traits of the species belonging to the species pool in order to model which species will be capable of surviving (Keddy 1992).

2.3.3 Species pools and dispersal

The term ‘species pool’ refers to both regional and local species belonging to a group of organisms with shared preferences for similar environmental conditions, allowing them to co-exist in a target community (Zobel 1997). The size of the species pool is considered an important influence on community diversity (Karger et al. 2015). The regional and local pools both have the ability to migrate into the target community, which is a habitat that provides the community with enough available niche space and favourable environmental conditions to support the incoming species, however local species migrate faster than regional species, as the local pool is closest (in geographical distance) to the target community (Zobel 1997). Consequently, target communities formed from large species pools are more susceptible to compositional changes through time, as greater species diversity can induce competition for niche space faster, when compared to a smaller species pool, and the possibility of random immigration increases (Chase 2003; Karger et al. 2015). Diversity in the target community also depends on the interactions (such as speciation and dispersal) occurring prior to immigration in the local and regional species pools (Ricklefs 1987). Competitive exclusion, availability of environmental resources, and disturbances, such as storm events or erosion, are important controls on diversity within the ‘actual’ species pool, which is the species assemblage found within the target community (Ricklefs 1987; Zobel 1997). It is therefore important to consider that the development of the actual species pool stems from spatiotemporal events creating patterns of assembly through evolutionary and biogeographical channels (Ricklefs 1987).

2.3.4 The ecological niche and adaptive radiation

If a species is to arrive at a community and surpass the various filters limiting their establishment, there must also be adequate niche space available (Gause 1932). Successful establishment of a species can be measured as the ability to grow to reproductive maturity, which is usually achieved by limiting resources within the niche to such a point where similar species cannot survive (Tilman 2004). Niche apportionment theory was first defined by MacArthur (1957) when examining niche overlap in tropical bird species, using the analogy of breaking a stick into smaller and smaller pieces to represent species abundances and resource availability within their given niche. Since MacArthur, a variety of mechanistic niche apportionment models have been developed in an attempt to explain and predict species relative abundances in communities (e.g. Pianka 1974; Sugihara 1980; Tokeshi 1990; Tokeshi & Schmid 2001; Mouillot et al. 2003). The mechanism of adaptive radiation is niche availability; given adequate ecological space, resources and reduced competition, some clades can radiate and diversify quickly (Schluter 1996). Adaptive radiation can be considered not just the product of time, because even though older clades may have had longer to diversify, it is likely that the immigration history of the clade (the timing and arrival of ancestral and derived species) is also highly influential (Fukami et al. 2007). Niche pre-emption, in which early arriving species reduce resource availability for later arriving species; and niche modification, wherein early colonists modify the available niche type, can strongly influence the trajectory of community assembly (Silvertown 2004; Buser et al. 2014; Fukami 2015).

2.3.5 Historical contingency and priority effects

A priority effect is the impact a species has on future community assembly by gaining priority over other species arriving later to a habitat, consequently determining the development of the community through the timing and order in which the initial colonist arrives (Silvertown 2004; Leopold et al. 2015). The subsequent species abundance and distribution of the community is arbitrated through either competitive exclusion (Gause 1932), or (less frequently) facilitative interactions where the colonist species positively interacts with the newly arrived species (Bertness & Callaway 1994; Fukami 2015). Priority effects can profoundly influence historical contingency, which is the effect of historical events on community assembly (Fukami 2015). For example, if the pattern of community assembly is governed by competition, then the historical contingency of that community is that the present species assemblage is the result of a prior competition event (Drake 1990, 1991; Fukami 2015).The previously mentioned, niche pre-emption is deemed an inhibitory priority effect (Fukami 2015). Priority effects may be weak, where only a few species are excluded, or strong, where many species are excluded from the community (Vannette & Fukami 2014; Fukami 2015). For a species to successfully induce priority effects, it must first be capable of surpassing environmental and biotic filters, then increase biomass sufficiently to exclude other species from establishing (Fukami 2015). The pattern of assembly may then be controlled by the strength of priority effects either strongly or weakly limiting niche availability for immigrating species. Priority effects have been tested in a variety of ecosystems (e.g. Shulman et al. 1983; Wilbur & Alford 1985; Peay et al. 2012; Brandt et al. 2016), and although a constraint to testing priority effects has been the difficulty in determining arrival histories, advances in molecular technologies are now capable of producing time calibrated phylogenies that can be used to estimate species radiations (Fukami 2015; Leopold et al. 2015).

2.4 Evolution of the New Zealand alpine flora

2.4.1 Geology and climate of the New Zealand alpine habitats

New Zealand has been separated from Australia since the late Cretaceous (c. 80 Ma), and sea level rise during the Oligocene reduced the landmass to about a third of its present day form (Fleming 1975; Gibbs 2006). As such, the New Zealand landmass has only existed in its current state for less than 25 Ma, the result of continental drift and upheaval that saw the Gondwanan relic gradually emerge from the ocean (Fleming 1975; Winkworth et al. 2005). Alpine zones in New Zealand are geologically very young, with the uplift of the Southern Alps reaching their maximum height in the late Pliocene (Cooper et al. 1987) due to tectonic collision of the Australian and Pacific plates which commenced only 7 Ma before present (Walcott 1998). The collision of the plates occurs at what is known as the Alpine Fault, and the resulting uplift termed the Kaikoura Orogeny (Cooper et al. 1987). The highest point in the Southern Alps is the permanently snow-clad Mount Cook (a.k.a Aoraki) at 3724 m a.s.l (above sea level), the tallest mountain on the New Zealand landmass.

The North Island alpine regions did not form until much later than the South Island mountains. In contrast to the plate collision below the Southern Alps, the central North Island is the location of volcanism stemming from convergence and subduction of the Pacific plate beneath the Australian plate, known as the Taupo Volcanic Zone, or TVZ (Reyners et al. 2006). Three prominent active volcanoes are located within the TVZ (Figure 2.1); Mount Ruapehu at 2797 m a.s.l, making it the tallest mountain in the North Island, Mount Ngauruhoe (2291 m) and Mount Tongariro (1978 m). The primarily andesitic eruptions of the TVZ volcanoes, located in Tongariro National Park, began 2 Ma before present, and all three continue to erupt frequently (Wilson et al. 1995). Volcanic activity in New

Zealand also occurs outside of the TVZ, as seen in the Taranaki region on the west coast, where frictional shear and deformation due to thinning of the continental crust has created magmatism below Mount Taranaki (Reyners et al. 2006; Zernack et al. 2012). Mount Taranaki (Figure 2.1**)** is an andesitic-dacitic stratovolcano 2518 m a.s.l and the second tallest mountain in the North Island, formed around 135 ka (Neall et al. 1986). Mount Taranaki, along with the three volcanoes of the TVZ, represent the extent of volcanic alpine habitats in the North Island.

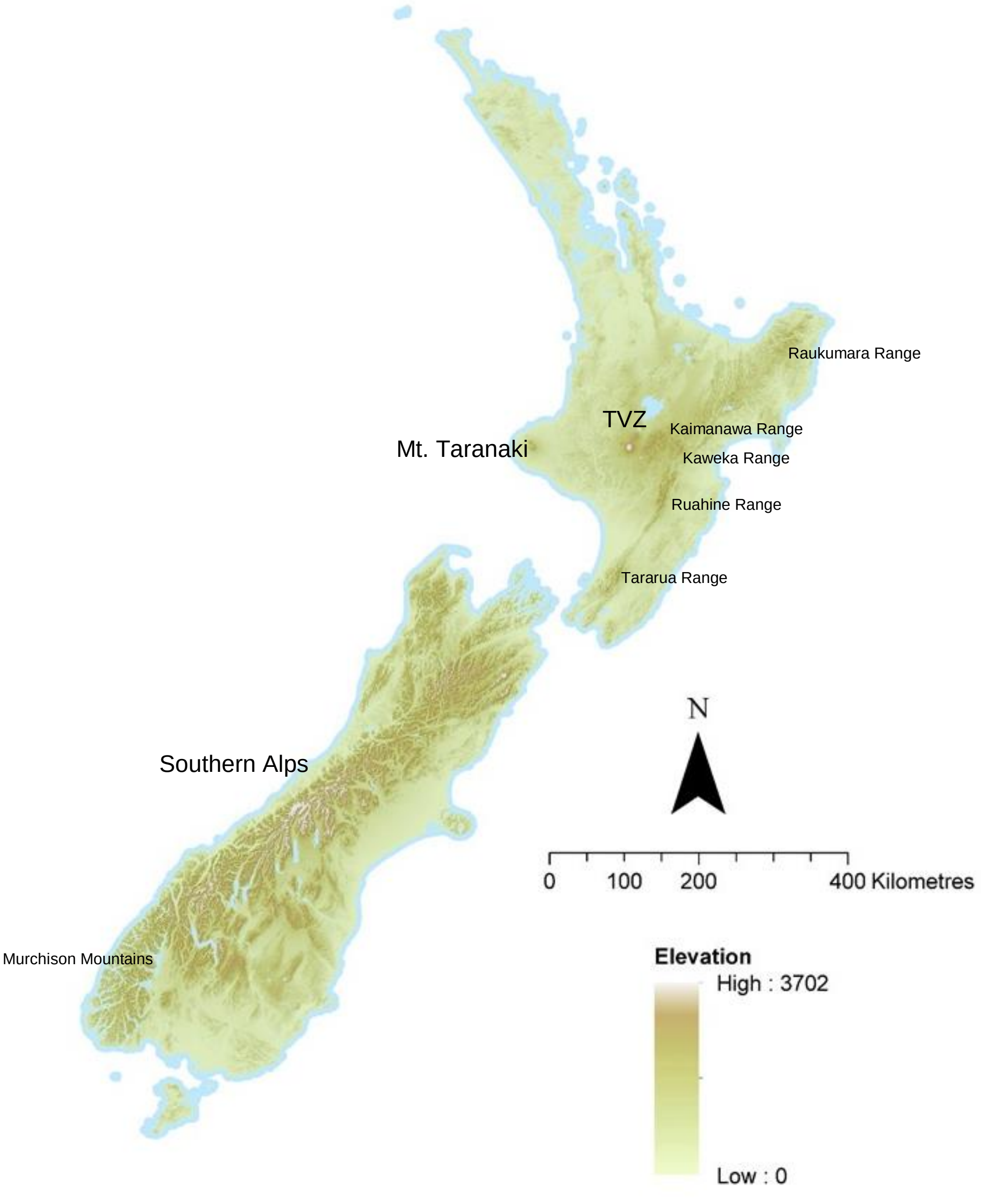

Figure 2.1 Map of New Zealand showing elevation (m a.s.l) of landmass and notable alpine to subalpine mountains and ranges. TVZ = Taupo Volcanic Zone, where Mts. Ruapehu, Ngauruhoe and Tongariro are located.

Alpine habitats in this review refer to subalpine to high alpine habitats, i.e. the area extending from the treeline up to the snowline, encompassing subalpine tussock field and herb-moss field. Alpine treelines in New Zealand decrease in altitude with increasing latitude, and range from approximately 900–1530 m a.s.l (Mark & Adams 1973; Cieraad & McGlone 2014). Treelines in New Zealand are a mixture of either 'abrupt' treelines consisting of southern beech (Nothofagaceae, *Fuscospora* and *Lophozonia*) or 'gradual' treelines comprising a mix of conifer-hardwood species (Wardle 2008; Cieraad & McGlone 2014). Mount Hikurangi (1752 m) in the Raukumara Range (Figure 2.1**)** is the tallest non-volcanic peak in the North Island and contains an extensive alpine herbfield. Subalpine regions of mixed geological origin exist in the North Island, with the ranges of Kaweka, Kaimanawa, Ruahine and Tararua all supporting alpine vegetation (Mark & Adams 1973).

Shifts in the New Zealand climate from warm, subtropical temperatures to rapid cooling that led to at least three glacial cycles, combined with the formation of the Southern Alps and North Island volcanoes, have given rise to unprecedented habitats for plant species to colonise (Raven 1973; McGlone et al. 2001; Heenan & McGlone 2013). Permanent snow cover occurs on the tallest peaks of the Southern Alps, and Mount Ruapehu, but the Mountains Taranaki, Tongariro and Ngauruhoe have, in recent years, undergone almost complete snowmelt in the summer months.

2.4.2 Alpine vegetation

The origins of the New Zealand alpine flora have been discussed at length, e.g. Wardle 1968; Raven 1973; Wardle 1978; McGlone et al. 2001; Winkworth et al. 2005. Dispersal patterns indicate that many species originate from Australia, others have ancestors in Southeast Asia and New Guinea, and phylogenetic evidence indicates some arrived via long-distance dispersal from the Northern Hemisphere and South America (Winkworth et al. 2005). Many New Zealand alpine species are likely to have evolved from lowland Tertiary ancestors already present, and fossil records indicate close relationships exist with the flora of New Guinea and Antarctica, pre-dating the break-up of Gondwana (Wardle 1978). Many species possibly travelled a migratory pathway from New Zealand to New

Caledonia, Southeast Asia and beyond (Wardle 1978), and from South America to New Zealand via Antarctica (Winkworth et al. 2005). The predominance of white flowers in the New Zealand alpine flora suggests evolution in the absence of specialised pollinators (Wardle 1978; Conran et al. 2014).

The vascular alpine plants of New Zealand are highly endemic (93%) with over 750 species belonging to c. 130 genera (Halloy & Mark 2003; Mark 2012), 53 of which contain more than 10 species throughout New Zealand (Tanentzap et al. 2015). Such high endemism and species richness suggests that this alpine flora has had an extensive time to diversify, but the geological evidence does not support this theory, as alpine habitats have existed for only a few million years (Heenan & McGlone 2013). It is therefore widely accepted that the New Zealand alpine flora must have undergone rapid diversification with the formation of these new habitats in order to attain such a high level of species richness (Raven 1973; Wardle 1978; Winkworth et al. 2005). Considering the ecological specialisation of many alpine species, the theory that a persistent alpine zone was only present from 0.95 Ma (modelled by Heenan & McGlone 2013) substantially increases the rate at which specialist species had to have evolved. The age progression of the New Zealand alpine zones is reflected in the number of species contained within each. The Southern Alps have, unsurprisingly, the greatest number of alpine species, the progressively younger volcanoes in the TVZ have fewer than the South Island, and the youngest, Mount Taranaki, is depauperate in comparison.

Lee et al. (2012) used data from the lower South Island alpine region to test whether the priority effect of niche pre-emption influenced community assembly. While the results suggested no relationship existed between species richness and the age of colonisation, there was evidence that older lineages were more abundant in the communities. A later study focused on the strength of priority effects with environmental variability, and showed that priority effects diminished with increasing abiotic strength, suggesting the strengths of priority effects can vary based on environmental influences (Leopold et al. 2015). Priority effects appear to exist in the South Island alpine flora, but there are no published studies testing priority effects in North Island alpine communities. Given that Mount Taranaki is the youngest and most isolated of the North Island alpine zones, research to test for the presence of priority effects may provide a unique opportunity to further explain the pattern and process controlling community assembly in the New Zealand alpine flora. Several endemic taxa belong to the alpine communities of Mount Taranaki (Clarkson 1986), yet colonisation of this region is no easy feat due to its isolation from other alpine systems. There are c. 460 ‘missing’ species known to inhabit the central North Island, including subalpine tussockland and alpine herbfield species that have not been found on Mount Taranaki (Clarkson 1986). The absence of these species may be mainly attributed to distance from seed source, i.e. dispersal barriers, and the frequency of disturbance that occurs on Mount Taranaki would further inhibit establishment (Clarkson 1986).

2.5 Conclusions

Community assembly is a complex process, and recent advances in knowledge are providing explanations for changes in pattern and process in communities. The unique assemblages of the New Zealand alpine flora may provide an opportunity to test the strength of priority effects within an evolutionary context. The vast diversity observed in the alpine flora of New Zealand may be, in part, the result of evolutionary priority effects. Many South Island alpine communities are older and less frequently disturbed, compared to the younger alpine zones of the North Island. Comparing studies of the more complex South Island floral communities could show the difference in the strength of priority effects. Further research could improve understanding of the underlying mechanisms of community patterns and process that lead to the assembly of species in ecological communities.

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Chapter Three: Variation of community composition within the Mount Taranaki alpine herbfield

3.1 Abstract

Mount Taranaki, New Zealand, has erupted approximately 10 times in the last 500 years. Consequently, vegetation on the mountain has been affected at different times and to varying degrees. Multiple studies of eruption effects on vegetation have focused on lowland forest. Here I present a study of variation in community composition and species abundance within the alpine herbfield of Mount Taranaki. Species relative abundances were measured in 55 plots at Fantham's Peak, East Egmont, and North Egmont. The results of non-metric multidimensional scaling ordination and rank-abundance analysis indicated the vegetation at East Egmont has been greatly affected by the AD 1655 Burrell eruption, as species diversity was much lower at East Egmont when compared to the other study sites. The results also showed that species composition varied between sites, and North Egmont had the greatest species richness. Species were found to be distributed according to their ecological preference, but the low diversity observed in the Mount Taranaki alpine flora indicates the herbfield communities are still undergoing initial community assembly following the various eruptions.

3.2 Introduction

The vegetation of Egmont National Park has been studied extensively through the years (e.g. Druce 1966; Clarkson 1981; McGlone et al. 1988; Clarkson 1990; Lees & Neall 1993; Efford et al. 2014), predominantly regarding how vegetation has been affected by the various volcanic eruptions of Mount Taranaki. There have been no studies on the compositional differences within the Taranaki herbfield belt since the extensive studies by Clarkson (1977, 1981) measuring change in community composition along the altitudinal gradient and vegetation response to volcanic disturbance. Although Clarkson's research included several comparisons of herbfield vegetation on the mountain, no study has yet focused solely on changes in the Taranaki herbfield communities.

The present study quantifies compositional variation between sites and altitudes within the Mount Taranaki herbfield communities, in order to determine if those communities have been affected differently following disturbances, namely volcanic eruptions, around the mountain. First an introduction of Mount Taranaki and the field methods used to measure the herbfield vegetation is provided. A detailed description of statistical methods used to analyse the vegetation data follows. Finally, the results and a discussion of the findings are presented along with concluding statements.

3.3 Mount Taranaki

3.3.1 Geology and eruption history

Mount Taranaki (also known as Mount Egmont) is a stratovolcano located in Egmont National Park, on the west coast of the North Island, New Zealand (latitude 39.2968°S, longitude 174.0634°E). Mount Taranaki is isolated from other New Zealand alpine zones, the nearest being Mount Ruapehu, some 130 km to the east in the central North Island. Currently in a dormant state, the 2518 m a.s.l. cone of Mount Taranaki is basaltic to andesitic-dacitic in composition (Turner et al. 2009), formed from eruptions spanning the last 10,000 years following the collapse of at least two original cones in the same site (Lees & Neall 1993; Alloway et al. 1995; Zernack et al. 2011). Representing the westernmost extent of volcanic activity in New Zealand, Mount Taranaki is the most recent volcano in what is known as the Taranaki Volcanic Succession (Neall et al. 1986; Zernack et al. 2009). The volcanic succession began in Taranaki with Paritutu and the Sugar Loaf Islands (1.75 Ma) before shifting southeast to the Kaitake (0.57 Ma) and Pouakai (0.25 Ma) ranges, ending with the Taranaki Volcano, where volcanism initially commenced c. 120–130,000 years before present (Grant-Taylor 1964; Lees & Neall 1993; Locke et al. 1993; Downey et al. 1994). Though no major eruptions have occurred since the AD 1655 Burrell eruption (Downey et al. 1994), there have been approximately 10 distinct eruptions in the last 500 years (Neall et al. 1986), with the c. AD 1785–1820 Sisters eruption considered to be the most recent (Platz et al. 2011). Fantham’s Peak (Māori name Panitahi; 1962 m a.s.l) is a prominent feature of Mount Taranaki, although not visible from New Plymouth City, the largest nearby urban centre to Egmont National Park. Fantham’s Peak is a secondary satellite cone on the southern flanks of the Taranaki Volcano, with a disputed age (e.g. Downey et al., 1994; Turner et al.

2009) of c. 3300 years. The upper slopes of the mountain are littered with tephra of varying eruptive origins (Roverato et al. 2015), creating gravel and boulder fields intermixed with steep eroding scree slopes. The cyclic building and collapse of Egmont Volcano has resulted in mass avalanche and lahar debris flows which have transported material to the wider ring-plain surrounding the lower slopes of the mountain, creating the hummocky landscape and deeply dissected gorges that are characteristic of Egmont National Park (Zernack et al. 2009).

3.3.2 Weather and climate

Due to its coastal location, the general climate of the Taranaki region is temperate-maritime, where seasonal fluctuations in temperature and weather patterns are observed (McGlone et al. 1988). As the summit of Mount Taranaki is not more than 23 km from the coast on all but its eastern side, the mountain is strongly affected by marine weather patterns bringing frequent rain upon prevailing westerly winds, and the eastern flanks are exposed to south-easterly flows which also influence precipitation (Marcus & Moore 1983). Records from the National Institute of Water and Atmospheric Research (NIWA) for the years 1981–2010 measured mean annual rainfall at North Egmont (approximately 942 m a.s.l.) as 7029 mm, with an annual average of 212 rain days (up to 0.1 mm rainfall) and 192 wet days (greater than 1 mm rainfall; NIWA 2014). North Egmont mean daytime summer temperatures for the same period were less than 14 °C, and mean daytime winter temperatures were less than 2 °C (NIWA 2014). Efford (2012) detected no irregularities in temperature ranges at the treeline (1000–1100 m a.s.l.) over the winter and spring months (July through November). Wind gusts of up to 172 km hr^{-1} have previously been recorded at The Plateau (East Egmont, 1144m a.s.l), and wind speeds are fastest in the afternoon following mixing of rising air from lowlands, with spring being the windiest season and summer the calmest (NIWA 2014). The altitude of Mount Taranaki causes precipitation to fall as snow during periods of cooler temperatures, although the upper slopes can remain above freezing level even in winter and therefore precipitation remains as rainfall (Marcus & Moore 1983). In winter the snowline extends to around 1100 m (Marcus & Moore 1983), and can reach altitudes as low as 900 m, however, the depth of snowpack has decreased since the 1920s (Efford et al. 2012). Snowfall is also known to occur over the summer months on the upper slopes.

3.3.3 Alpine vegetation

The montane treeline on Mount Taranaki extends to 1100 m a.s.l before giving way to subalpine scrub that reaches up to 1300 m (Clarkson 1986). The subalpine to alpine zone ranges from 1400–1675 m, with red tussock *Chionochloa rubra* subsp. *rubra*[1] and silver tussock *Poa cita* being the dominant vegetation at altitudes up to 1500 m, where true herbfield begins (Clarkson 1986). The herbfield extends to 1650 m (McGlone et al. 1988), and the limit of continuous vegetation is around 1750 m, where, at higher altitudes, vegetation consists mainly of patches of *Racomitrium* moss among the rocky slopes (Clarkson 1986). The Mount Taranaki species list compiled originally by Druce (1992) lists over 65 species that have been found to grow above 1220 m. Within the true herbfield, the most common species are the mountain daisies *Celmisia* spp., the prostrate, dwarf shrubs of *Gaultheria depressa* var. *novae-zelandiae* and *Coprosma perpusilla* subsp. *perpusilla*, the small grass *Poa colensoi*, and herbs such as *Anaphalioides alpina* and the highly fragrant *Anisotome aromatica*. In areas with less drainage, the dwarf comb sedge *Oreobolus pectinatus* forms dense cushions, often found alongside the mountain foxglove *Ourisia macrophylla* subsp. *macrophylla* and mountain buttercup *Ranunculus nivicola*. At the species level, Mount Taranaki shares all of its alpine flora with other New Zealand mountains, but does contain several subspecies and varieties thought to be endemic to Egmont National Park such as *Wahlenbergia pygmaea* subsp. *drucei, Celmisia major* var. *brevis* and *Celmisia glandulosa* var. *latifolia.* The Mount Taranaki flora also contains the alpine shield fern *Polystichum cystostegium*, whose absence from the rest of the North Island but widespread South Island distribution is intriguing.

3.4 Methods

3.4.1 Study sites

The study was conducted at three locations within the alpine zone of Mount Taranaki (Figures 3.1 and 3.2a-c). The northern sites near Tahurangi were located along and below the North Ridge, beside the popular summit hiking route (Figure 3.2a). Several of the sites along the Northern Ridge were adjacent to the original summit route, as remnants of wooden steps were found among the vegetation. The

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[1] Nomenclature follows the New Zealand Plant Conservation Network (February 2017).

present summit route passes through Hongi's Valley before joining the Northern Ridge at a higher altitude, and the lower transect was located within the lower reaches of Hongi's Valley. The East Egmont sites needed to be beyond the boundaries of the ski field as the vegetation within the ski field is controlled by mowing prior to the first snowfall each year (Efford et al. 2012). The frequent mowing and removal of sub-alpine shrub and tussock has enabled species normally found at higher altitudes to colonise the ski field (Efford et al. 2012), so the ski field itself was not sampled, as community composition there is strongly influenced by human intervention. The eastern sites (Figure 3.2b) were therefore adjacent to Manganui ski field, with the lower transect located on the southern side of the ski field as low visibility conditions on the sampling day prevented any further exploration. The southern sites were located below the secondary cone of Fantham's Peak (Figure 3.2c) These sites were located on the northern side of the Fantham's Peak summit route, and carefully selected to avoid overlap with the zig-zagged track of boulders and scree that is used as the main access route to Syme Hut, a public alpine hut at the summit of Fantham's Peak.

The effect of eroding scree and erupted volcanic debris within the Taranaki alpine zone has created patchiness in the vegetation. The higher altitudinal fellfield was dominated by mosses, and many of the lower elevations contained gullies in which boulders have come to rest, as well as areas with steep bluffs. Therefore, placing long transects to encompass the desired altitudinal range was impractical so a systematic, stratified, spatial sampling method was chosen to account for altitudinal variation in the herbfield species, and to enable transects to be placed in areas where there was enough continuous vegetation to sample. The altitudinal intervals of the transects were 1650–1600 m (plots numbering 1–5), 1600–1550 m (plots 6–10), 1550–1500 m (plots 11–15), and 1500–1450 m (plots 16–20). Certain criteria were applied when selecting sites for transects:

1. The transect did not intersect a walking track.
2. The transect was not dominated (> 50% by initial visual estimate) by moss, tussock, or scree/bare soil.
3. Angle of hill slope remained moderately consistent for the length of the transect (i.e. no sudden changes in slope).
4. In the interest of field safety, transect sites were not within close proximity to cliff faces where loose debris could fall and cause injury.

Transects were oriented upslope to downslope. A quadrat measuring 2 x 2 m was selected as the sample size, adapted from the recommendation of Kent (2011) as the appropriate size for grassland, dwarf heath and tall herb communities. The quadrats were positioned along each transect with 2 m intervals between, totalling five quadrats (plots) per 20 m transect. Four transects were placed between 1650 and 1450 m at each site, except for Fantham’s Peak where only three transects were sampled as heavy snow fall obscured the site before the study could be completed. A total of 11 transects with 55 plots were sampled.

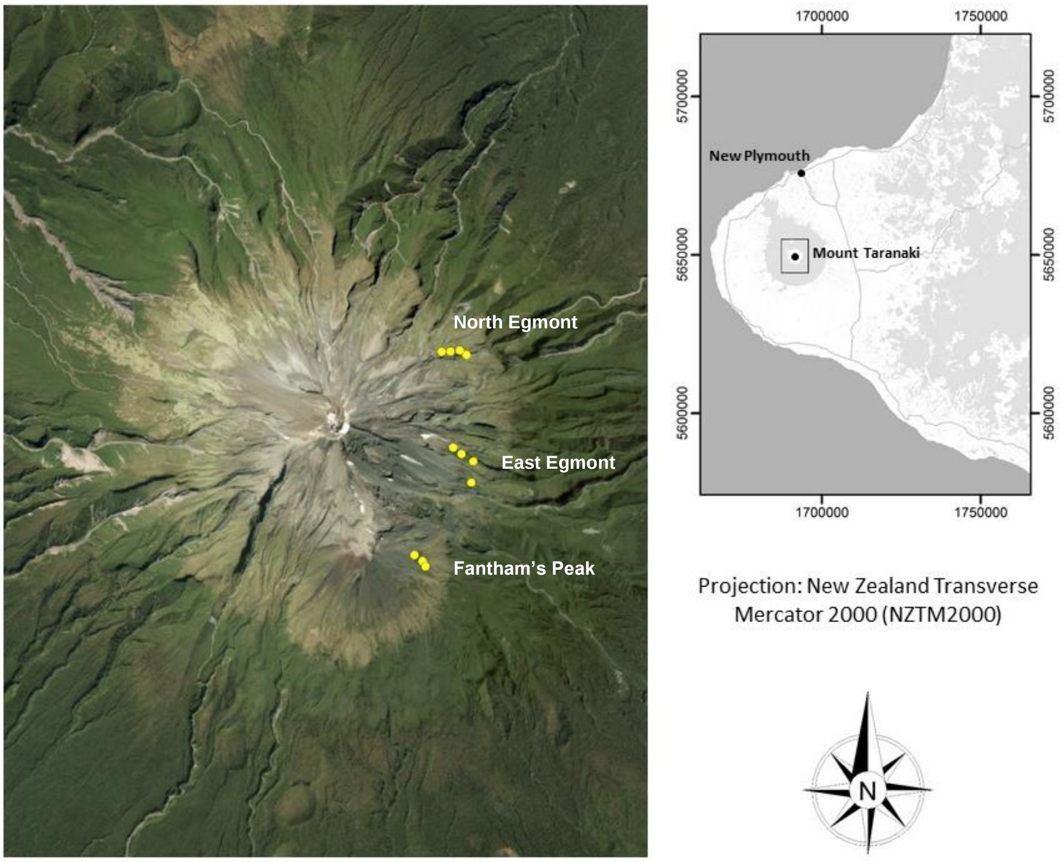

Figure 3.1 Map of study area, Mt Taranaki, New Zealand. Inset (right) shows location of Mt Taranaki on the west coast of the North Island. Box in inset represents extent of larger map on left. Yellow points are locations of transects in the herbfield at North Egmont, East Egmont, and Fantham’s Peak. Larger map image sourced from Land Information New Zealand.

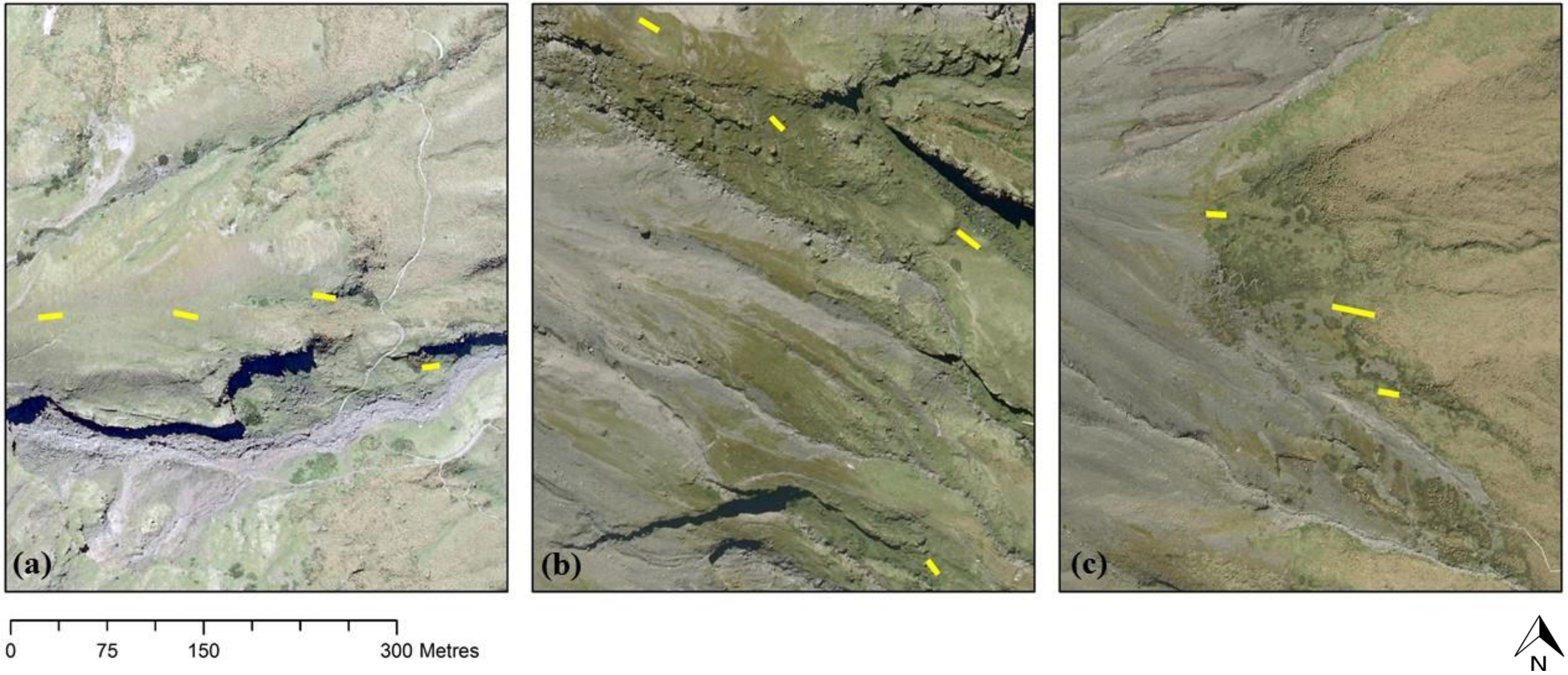

Figure 3.2 Maps of Mt Taranaki study sites at **(a)** North Egmont, **(b)** East Egmont and **(c)** Fantham’s Peak. Yellow lines represent transects at different elevations at each site. Map image sourced from Land Information New Zealand.

3.4.2 Community composition

Measuring vegetation

Because much of the herbfield vegetation had creeping growth habits, it was not feasible to count individuals of a given species. Therefore, community composition was measured by visually estimating the percent cover (out of 100%) of each species found within the plot, as in Lee et al. (2012). Exposed soil and rock cover were also given cover values, but were ultimately excluded from statistical analyses. Visual estimates were made where 1% of the plot was equal to 40 cm^2, and 'cover' was determined by spread, rather than height. When a species had cover values less than one percent it was given a value as low as 0.25% to indicate presence. To reduce observer subjectivity and bias, the visual estimates were carried out by the same person throughout the entire study.

All vegetation found within the plots was recorded (including all vascular, non-vascular, native or non-native), totalling 43 species (or 'types', in the case of mosses and lichens) across all plots and sites (Table 3.1). A full list of species names, families and common names is included in the Appendix (Table A2) of this thesis. Naming hereafter will refer only to genus, with the exception of when more than one representative of a genus is present, then both genus and species will be listed. Subsequent references of genera with more than one species within the same sentence will be shortened to the abbreviated genus followed by the species name (e.g. *Celmisia gracilenta* to *C. gracilenta*).

Point intercept was used as an additional method of quantifying vegetation. Due to the size of the quadrat, the usual pin frame method of point intercept (Kent 2011) required modification, as a 2 x 2 m pin frame would not have been easily transported between sites (as the 1 x 1 m frame used in Efford et al. 2012). Point intercept was achieved by laying a tape measure across the plot, starting with the outside edge at the top/upslope edge of the quadrat (perpendicular to the transect), then moving the tape measure across the entire quadrat. At every 25cm intercept, the species that fell directly below the point of intercept was recorded, giving a total of 81 points per quadrat.

Table 3.1 List of species and plant types recorded within plots in the Mt Taranaki herbfield.

Species code	**Binomial**	**Taxonomy/life form**
ANAalp	*Anaphalioides alpina*	Composite dicot herb
ANIaro	*Anisotome aromatica*	Dicot herb
BLEpen	*Blechnum penna-marina* subsp. *alpina*	Fern
BRAele	*Brachyglottis elaeagnifolia*	Dicot shrub
CARdru	*Carex drucei*	Sedge
CELgla	*Celmisia glandulosa*	Composite dicot herb
CELgra	*Celmisia gracilenta*	Composite dicot herb
CERfon	*Cerastium fontanum* subsp. *vulgare**	Dicot herb
CHAcol	*Chaerophyllum colensoi*	Dicot herb
CHIrub	*Chinochloa rubra* subsp. *rubra*	Grass - tussock
COLcan	*Colobanthus canaliculatus*	Dicot herb
COPper	*Coprosma perpusilla* subsp. *perpusilla*	Dicot shrub - creeping
CORplu	*Coriaria plumosa*	Dicot shrub
CORpte	*Coriaria pteridoides*	Dicot shrub
DRAfil	*Dracophyllum filifolium*	Dicot shrub
EPIgla	*Epilobium glabellum*	Dicot herb
EPIper	*Epilobium pernitens*	Dicot herb
EUPcun	*Euphrasia cuneata*	Dicot herb
FORten	*Forstera tenella*	Dicot herb
GAUdep	*Gaultheria depressa*	Dicot shrub - creeping
GERsp.	*Geranium* sp.†	Dicot herb
GUNmon	*Gunnera monoica*	Dicot herb
HUPaus	*Huperzia australiana*	Clubmoss
HYMmul	*Hymenophyllum multifidum*	Fern
HYPrad	*Hypochaeris radicata**	Dicot herb
KELdie	*Kelleria dieffenbachii*	Dicot herb
LOBang	*Lobelia angulata*	Dicot herb
LUZban	*Luzula banksiana*	Rush
LUZcol	*Luzula colensoi*	Rush
LYCfas	*Lycopodium fastigiatum*	Clubmoss
OREpec	*Oreobolus pectinatus*	Comb sedge
OURmac	*Ourisia macrophylla* subsp. *macrophylla*	Dicot herb
PENpum	*Pentachondra pumila*	Dicot shrub - creeping
POAcol	*Poa colensoi*	Grass
POLcys	*Polystichum cystostegium*	Fern
PRAcol	*Prasophyllum colensoi*	Orchid
RANniv	*Ranunculus nivicola*	Dicot herb
SAGpro	*Sagina procumbens**	Dicot herb
VERodo	*Veronica odora*	Dicot shrub
VIOcun	*Viola cunninghamii*	Dicot herb
WAHpyg	*Wahlenbergia pygmaea* subsp. *drucei*	Dicot herb
Lichens	†	Lichen
Mosses	*Racomitrium*†, *Polytrichum*†	Moss

*= non-native; † = not identified to species.

Environmental variables

Slope and aspect were recorded for each transect. Slope was recorded using a handheld Suunto Optical Reading Clinometer from the end (downslope) of the transect, facing upslope, the clinometer was positioned so it aligned with the top of the transect and recorded in degrees (from horizontal) and percent (rise/run x 100). Aspect was measured standing at the top (upslope) of each transect, where a compass was aligned with the direction of the transect. The present research follows the methodology of Lee et al. (2012) in focussing on slope, altitude, aspect, and mean local rainfall as proxies for environmental variables. Subsequent studies also used the same variables (e.g. Leopold et al. 2015; Tanentzap et al. 2015). Therefore, the measurement of soil pH, soil moisture and temperature (both soil and ambient) were omitted from the present study. Slope and aspect of each of the transects is listed in Table 3.2. A full list of attributes of the study sites is included in Table A.3 of the Appendix.

Table 3.2 The site attributes slope angle (°) and aspect (degrees from north and 16-wind compass directions) recorded for the Mt Taranaki transects. FP = Fantham's Peak; EE = East Egmont; NE = North Egmont.

Transect	Slope	Aspect
FP 1–5	34°	120° ESE
FP 6–10	27°	130° ESE
FP 11–15	27°	75° ENE
EE 1–5	20°	165° SSE
EE 6–10	31°	135° SE
EE 11–15	17°	105° ESE
EE 16–20	32°	135° SE
NE 1–5	23°	65° ENE
NE 6–10	18°	75° ENE
NE 11–15	28°	75° ENE
NE 16–20	25°	75° ENE

3.4.3 Statistical analyses

To determine which species differed in composition between sites, percent cover was converted to relative abundance (RA) to represent the proportion of cover of each species. Relative abundance of a species was calculated using Equation 1 below, where total % Plot *A* was equal to 100.

Equation 1

$$RA\ Sp.1 = \frac{(\%\ cover\ Sp.1)}{(total\ \%\ Plot\ A)}$$

The statistical program PC-ORD (Version 6, MjM Software) was used to complete non-metric multidimensional scaling (NMS) ordination analyses of the RA data, using the Sørensen (Bray-Curtis) distance measure. Ordination, a form of indirect gradient analysis, is widely used by community ecologists. In particular, NMS is considered to be highly appropriate for analysis of plant communities (Prentice 1977). Ordination seeks to display patterns within ecological communities by using multivariate data transposed into a matrix based on a distance measure of the researcher's choosing and projecting that data onto (usually) a two- or three-dimensional space (Beals 1984). An ordination diagram is constructed from the distance matrix, and similarities (i.e. community composition) are represented within the ordination space as distances between ordination points. The Sørensen (Bray-Curtis) measure is an example of a semi-metric city block distance measure that calculates shared abundances as a proportion of the total community abundance, calculating dissimilarities (distances) from a centroid rather than directly between species, as in Euclidean distance (McCune et al. 2002; Peck 2010).

PC-ORD features a tool that enables a second matrix of environmental or categorical variables to be overlaid on the main matrix, in this case, the species RA data matrix, for simultaneous comparisons of relationships between the main matrix variables and second matrix variables. Convex hulls were applied to group the data based on plot location (Fantham's Peak, East Egmont, North Egmont) and elevation range (plots 1–5, 6–10, 11–15, 16–20) through categorical coding in the second matrix. Slope, aspect and altitude measurements were used to create a bi-plot which was overlaid on the main matrix to determine correlations of those environmental variables with the ordination axes. Both plot and species ordinations were carried out for the herbfield data set in this study. Any species that occurred in less than 5% of the plots were removed prior to ordination to reduce data noise (McCune et al. 2002). No monotonic transformations or relativisations were performed, as preliminary analyses to which monotonic transformations were applied to the data produced little difference in ordination statistics. As data used for the NMS were already proportional values (relative species abundances), relativisations would have only resulted in shrinking the differences between large and smaller abundances. Because the aim of the ordinations was to compare differences between elevations and locations, it was deemed to be of greater ecological significance to retain those differences in relative abundances, rather than make them appear more similar (McCune et al. 2002).

Following NMS, permutational multivariate analysis of variance (perMANOVA) was used to evaluate any significant differences in community composition between groups (elevation range and site), to further clarify visual inspections made of the ordination diagrams. Due to data balancing limitiations perMANOVA was only conducted on plot numbers 1–15 for each of the three sites (i.e. Fantham's Peak and East Egmont plots 16–20 were removed from the data set prior to perMANOVA), as only 15 plots were sampled at Fantham's Peak compared to 20 each at East Egmont and North Egmont, and perMANOVA requires sample sizes to be even. Additional *t*-tests and post hoc comparisons between species distributions were conducted using STATISTICA (Version 12, StatSoft) to determine exactly which species distributions differed between sites and altitudes.

Community dominance was determined by using the RA data to compare dominance and evenness of species at the three sites and four altitudinal ranges, using PC-ORD to produce rank-abundance values and richness, evenness and diversity statistics. The ranked abundances were also used to compare species distributions and abundances across sites and altitudes, where RA of the top 10 abundant species was plotted along the elevation gradient at each site.

The point intercept data was converted to presence/absence, and compared to the percent cover method in which RA values were also converted to presence/absence. Graphing the presence/absence data from both methods enabled direct comparison of the two techniques to determine if species RA were over or underestimated using point intercept.

3.5 Results

3.5.1 Variation in community composition

Ordination and perMANOVA

The species that occurred in less than 5% (= 3 plots) of plots were *Brachyglottis*, *Dracophyllum*, *Lobelia*, *Huperzia* and *Polystichum*, which were consequently excluded from the NMS analysis. The NMS ordination was best suited to a two-dimensional (2-D) solution, as indicated by the NMS scree plot and the Monte Carlo randomisation test (250 permutations; $P = 0.004$). The final stress for the 2-D solution was 14.8 following 80 iterations, with a final instability of 0.000. The axes coefficients show 87% of variation between the distance matrix and the ordination distance is accounted for (Axis 1 $r^2 = .155$, Axis 2 $r^2 = .713$, cumulative $r^2 = .868$).

Ordination of the remaining 38 species showed a reasonable amount of variation in species relative abundances across the plots (Figure 3.3). A note that some species codes differ to those presented earlier in Table 3.1, in the ordination (listed first) to the current species code (listed second): DRAdie = KELdie, FORbid = FORten, HEBodo = VERodo, OREcol = CHAcol. The distribution of the species across the ordination space from Axis 1 to the top of the plot shows a progression of species abundances that relates to the ecological distribution of species across the communities (represented by dashed lines). Group 1 shows species that are often found in more freely drained, higher altitudinal sites, for example, *Gaultheria*. Group 2 shows species that usually exist within fertile sites such as the non-native species *Hypochaeris* and *Cerastium*. Group 3 is a subset of fertile species that prefer less well-drained sites, for example *Celmisia glandulosa*. Group 4 contains lower altitudinal species, like the tussock *Chionochloa*. The bi-plot overlay of the environmental variable aspect shows that species distributions correlate to aspect (i.e. site), rather than altitude or slope, as only variables with r^2 values greater than .25 were included in the bi-plot. However, the strength of the association was less than 30% (Table 3.3).

The plot ordination (Figure 3.4) shows similarity in composition was maintained along each transect, other than the North Egmont transect at 1500–1450 m elevation, and the Fantham's Peak 1600–1550 m transect. The two transects mentioned appeared to contain plots that were dissimilar to each other in composition. The North Egmont plots along each transect shared similar compositions to each other, and the lowest elevation transect for East Egmont had the most similarity along the transect, more than any of the other sites. It appeared that community compositions were not shared at each altitude between sites, other than at East and North Egmont 1500–1450 m transects. The bi-plot overlay in Figure 3.4 indicates aspect was the only environmental variable that had a significant positive relative relationship with the axes (as in Table 3.3). The East Egmont plot composition appears to be most closely associated with aspect, compared to the North Egmont and Fantham's Peak plots.

The perMANOVA results indicate statistically significant variation ($P < 0.05$) between group interactions (plot location and elevation range; Table 3.4). The pairwise comparisons show significant differences exist in composition across the Mount Taranaki herbfield communities, and can be attributed to the location and elevation of the plots (both $P < 0.05$), supporting the visual differences observed between sites and elevation ranges in the ordination. The additional post hoc analysis of species variation between sites and altitudes are included as appendices (Tables A1.1 and A1.2).

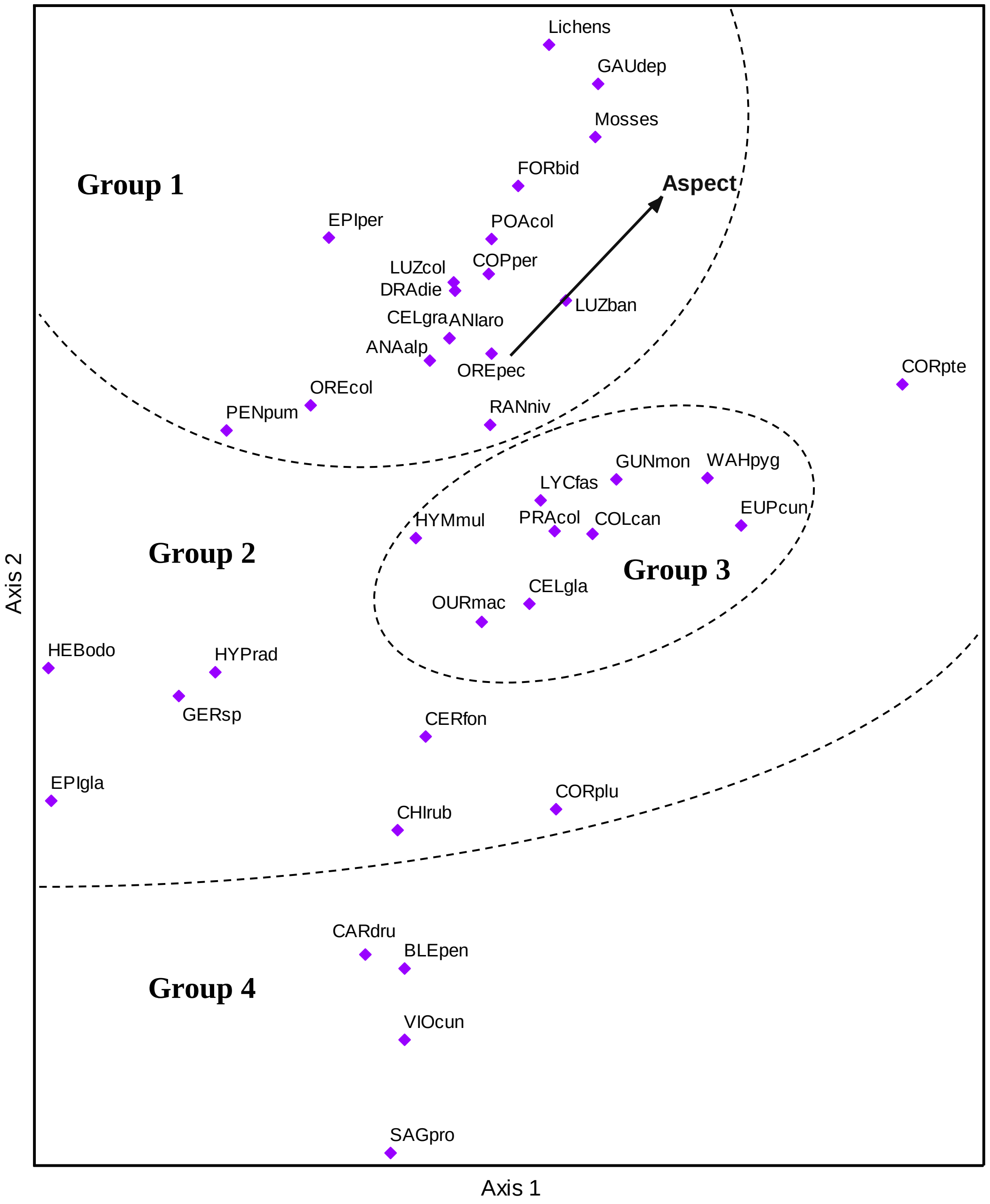

Figure 3.3 Non-metric multidimensional scaling (2-D) of distribution and abundance of 38 species across all plots in the Mt Taranaki herbfield. The dashed lines group species with similar ecological associations; group 1 shows higher elevation species, group 2 represents species in more fertile sites, group 3 contains species preferring wet sites and group 4 are lower altitudinal species. Bi-plot overlay of aspect scaled 100%. Final stress of the 2-D ordination = 14.8; Monte Carlo *P* = 0.004. Refer to Table 3.1 for the full list of species names, and to section 3.5.1 for changes in species codes.

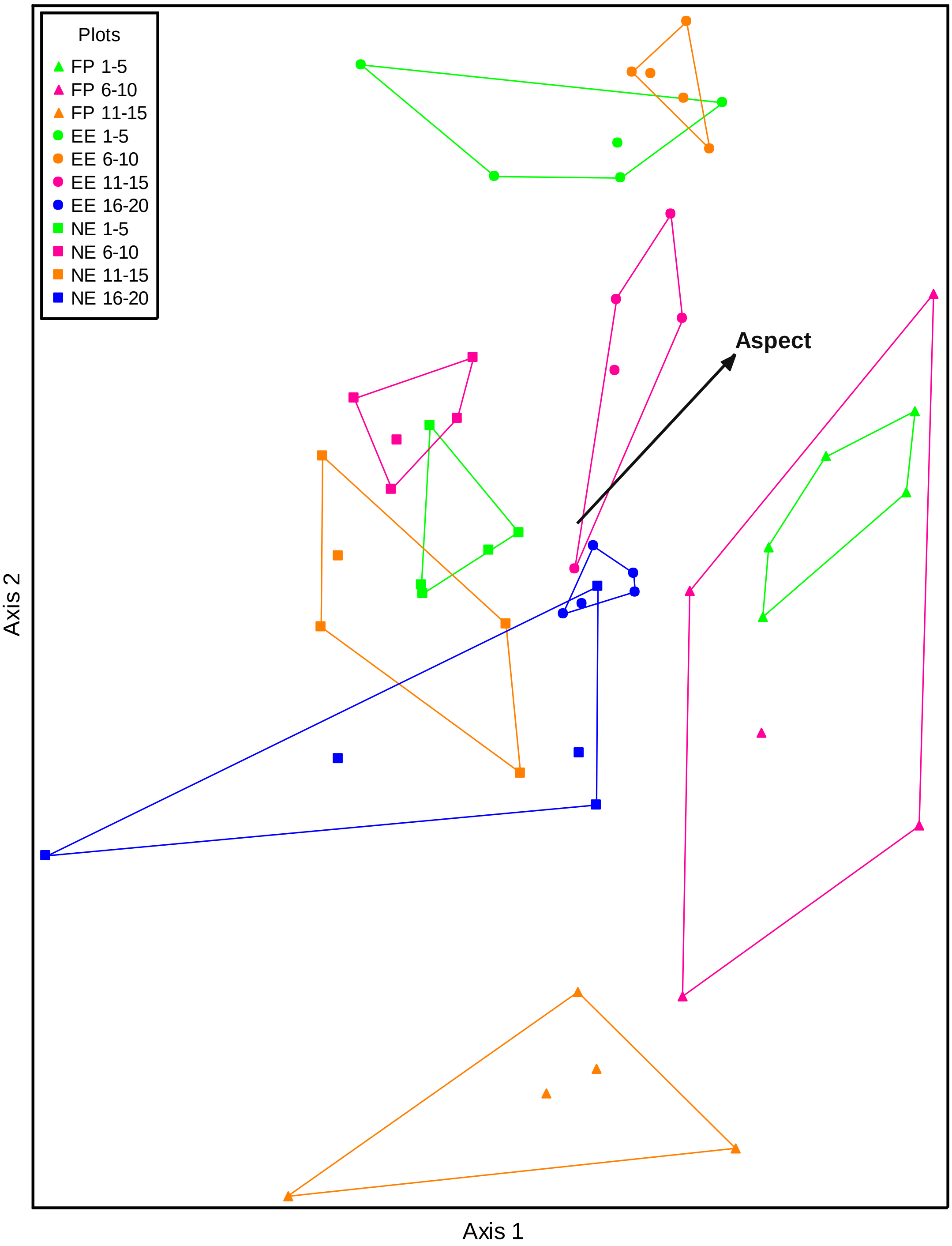

Figure 3.4 Non-metric multidimensional (2-D) scaling of the 55 Mt Taranaki herbfield plots, grouped by transect. FP = Fantham's peak; EE = East Egmont; NE = North Egmont. Plots are numbered per elevation (m) of each transect: 1–5 = 1650–1600; 6–10 = 1600–1550; 11–15 = 1550–1500; 16–20 = 1500–1450. Note that no transect at 1500–1450 m was recorded for Fantham's Peak. The bi-plot overlay of aspect is scaled 100%. Final stress of the 2-D ordination = 14.8; Monte Carlo *P* = 0.004.

Table 3.3 Pearson *r* and Kendall tau correlations of Mt Taranaki herbfield environmental variables with the ordination axes (of ordinations in Figures 3.4 and 3.5). Bold indicates values above the r^2 cut-off (.25) considered to have a significant relationship with the axes.

Axis		**1**			**2**	
	r	***r*²**	**tau**	***r***	***r*²**	**tau**
Altitude	-.155	.024	-.124	.348	.121	.263
Slope	-.380	.145	-.268	-.196	.038	-.143
Aspect	-.521	**.271**	-.385	.537	**.289**	.345

Table 3.4 Results of two-way factorial perMANOVA analysis using Sørensen (Bray-Curtis) dissimilarities between community compositions of 45 plots in the Mt Taranaki herbfield, based on the interaction between plot location and elevation ranges (m). Significant *P* in bold (< 0.05; *P*-values based on 4999 permutations). df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; *F* = pseudo-*F* value by permutation.

Source	**df**	***SS***	***MS***	***F***	***P***
Location	2	1.8756	0.93781	25.072	**0.0002**
Elevation	2	0.67571	0.33786	9.0326	**0.0002**
Interaction	4	0.80676	0.20169	5.3922	**0.0002**
Residual	36	1.3465	0.37404E-01		
Total	44	4.7046			
Comparison*				***t***	***P***
Fantham's peak vs. East Egmont				5.3619	**0.0002**
Fantham's peak vs. North Egmont				4.0933	**0.0002**
East Egmont vs. North Egmont				5.7117	**0.0002**
Comparison*				***t***	***P***
1650–1600 vs. 1600–1550				2.4947	**0.0002**
1650–1600 vs. 1550–1500				3.1212	**0.0002**
1600–1550 vs. 1550–1500				3.2389	**0.0002**

*Pair-wise *a posteriori* tests among sites and elevation ranges (m), significant *P*-values in bold.

3.5.2 Species dominance and diversity

The overall coefficient of variation (CV) totals for the species columns was 164.25%, indicating a high amount of variability within the species data due to the dominance and rarity of some species, which was more apparent as relativisations were not applied prior to analysis (i.e. data was in raw RA form therefore variability was not evened out by first relativising the data). The richness and diversity indices (Table 3.5) and rank-abundance statistics (Table 3.6) show that East Egmont plots contained the fewest species and species evenness and diversity decreased with increasing altitude. Similarly, the alpha diversity of 22.1

suggests species richness was higher in the lowest elevation range plots, and lower (16.5) in the higher elevation plots (Table 3.5). The diversity scores on the Shannon's and Simpson's indices support the observation that diversity was higher in the plots at the lowest elevations, and the North Egmont plots more diverse than the Fantham's Peak or East Egmont (Table 3.5). It is also worth noting that the total number of species increased 35% from the higher altitudes to the lower. *Coprosma* and mosses were most abundant at plots within the highest elevation range, followed by *Celmisia glandulosa* (Table 3.6), both of which had high RA across all elevation ranges. The three fern species were absent from the two highest elevation ranges. *Coriaria pteridoides* had higher RA at the highest elevation range compared to the lower ranges, where it was only present again at 1550–1500 m. The non-natives *Hypochaeris* and *Sagina* were absent from the two higher elevations, yet the third non-native *Cerastium* was present in low abundances across all four.

Fantham's peak

There were 36 species recorded within the 15 plots (60 m^2) at Fantham's Peak. Fantham's Peak had the highest abundance (compared to the other sites) of red tussock *Chionochloa*, and also the highest abundances of *Coriaria plumosa* and larger-leaved *Coriaria pteridoides*. As shown in Table 3.6, the most abundant species were *Celmisia glandulosa* and *Coprosma,* with the lowest RA belonging to *Epilobium pernitens*. The Fantham's Peak plots also contained all three non-native species identified across the entire study: *Cerastium, Hypochaeris* and *Sagina*. Along the elevation gradient, at Fantham's Peak (Figure 3.5) *Celmisia glandulosa* had the greatest RA, which was higher at lower elevations, but decreased again from 1547 m. Moss decreased with decreasing altitude, and *Chionochloa* increased with decreasing altitude. The two *Coriaria* species had varied distributions, but *C. pteridioides* was most abundant at higher elevations.

East Egmont

The East Egmont plots contained the least species with a total of only 28 in 20 plots (80 m^2). East Egmont had higher abundances of mosses and *Gaultheria* than the other sites (Table 3.6), and plots also contained *Lobelia,* which was absent from the other sites. *Coprosma* had the greatest abundance at higher elevations (Figure 3.6), and *Oreobolus* and *Celmisia glandulosa* increased with decreasing altitude. At 1506 m an inverse distribution is observed between *Gaultheria, Poa* and moss (sharp decrease) and *Coprosma, Celmisia glandulosa* (sharp increase) and *Oreobolus* (moderate increase), in what is likely to have been a less well-drained plot.

North Egmont

North Egmont was the most diverse with 40 species in 20 plots (80 m^2). North Egmont shared its top ranking species with Fantham's Peak (*C. glandulosa* and *Coprosma*, respectively), and also contained all three fern species: *Blechnum*, *Hymenophyllum* and *Polystichum* (Table 3.6). The least abundant species *Dracophyllum* and *Huperzia* were not found at either of the other sites. The altitudinal distribution of *Oreobolus, Celmisia glandulosa* and *Chaerophyllum* decreased sharply at 1547 m and again at 1499 m, with an increase of *Celmisia gracilenta* and *Anaphalioides* at those same altitudes (Figure 3.7). At 1550 and 1544 m there is an increase in *Oreobolus* and a decrease in *Celmisia gracilenta*. These patterns of inverse distribution relationships represent shifts between drainage in the plots.

Overall species dominance

Coprosma was most frequently ranked in the top 2 species across all sites and elevations. This was followed by *Celmisia glandulosa*, mosses and *C. gracilenta*. The least abundant species were *Brachyglottis*, *Dracophyllum, Geranium*, *Lobelia*, *Lycopodium*, *Polystichum* and *Sagina*, all of which were only found at one of the three locations and in low abundance.

Table 3.5 Dominance-diversity summary for the Mt Taranaki herbfield communities at different locations and elevations. N = species total; S = alpha diversity (richness); E = evenness; H’ = Shannon’s diversity index; D’ = inverse of Simpson’s diversity index.

	# plots	***N***	**S**	**E**	**H’**	**D’**
1650–1600 m	15	28	16.5	0.83	2.32	0.87
1600–1550 m	15	30	16.7	0.83	2.28	0.86
1550–1500 m	15	36	18.3	0.81	2.34	0.86
1500–1450 m	10	38	22.1	0.83	2.57	0.89
Fantham’s Peak	15	36	19.1	0.79	2.32	0.85
East Egmont	20	28	15.9	0.82	2.26	0.86
North Egmont	20	40	19.5	0.84	2.50	0.89

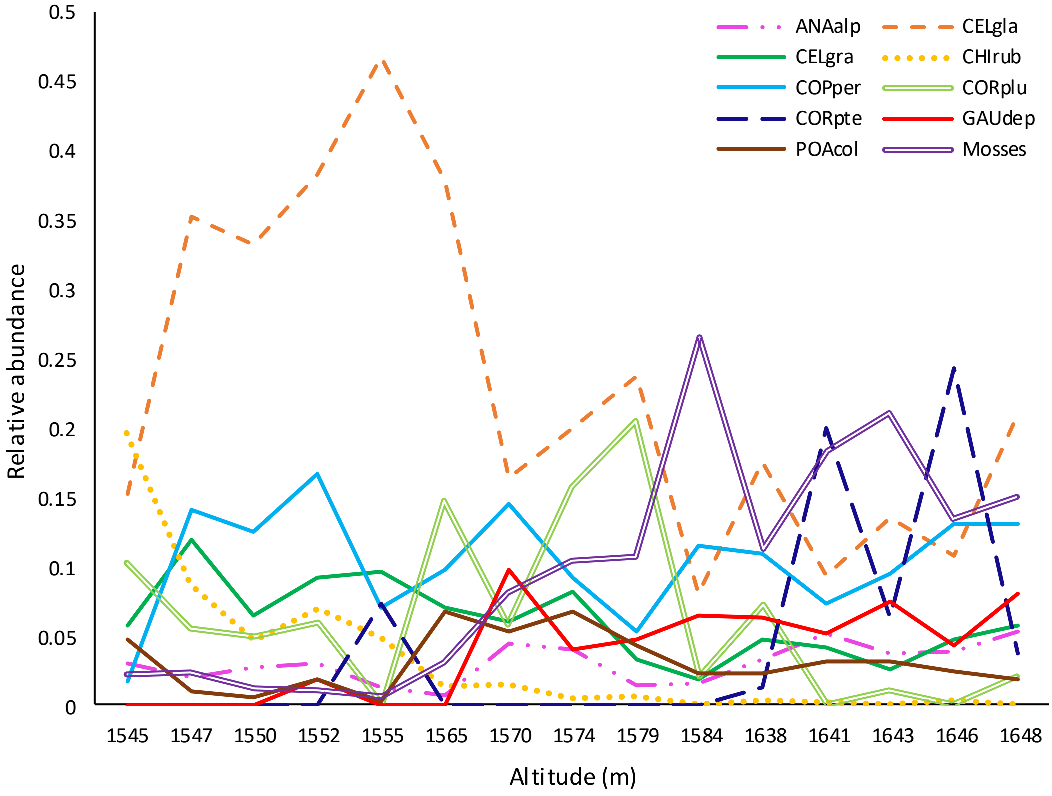

Figure 3.5 Distribution of the 10 most abundant species along the elevation gradient at Fantham’s Peak.

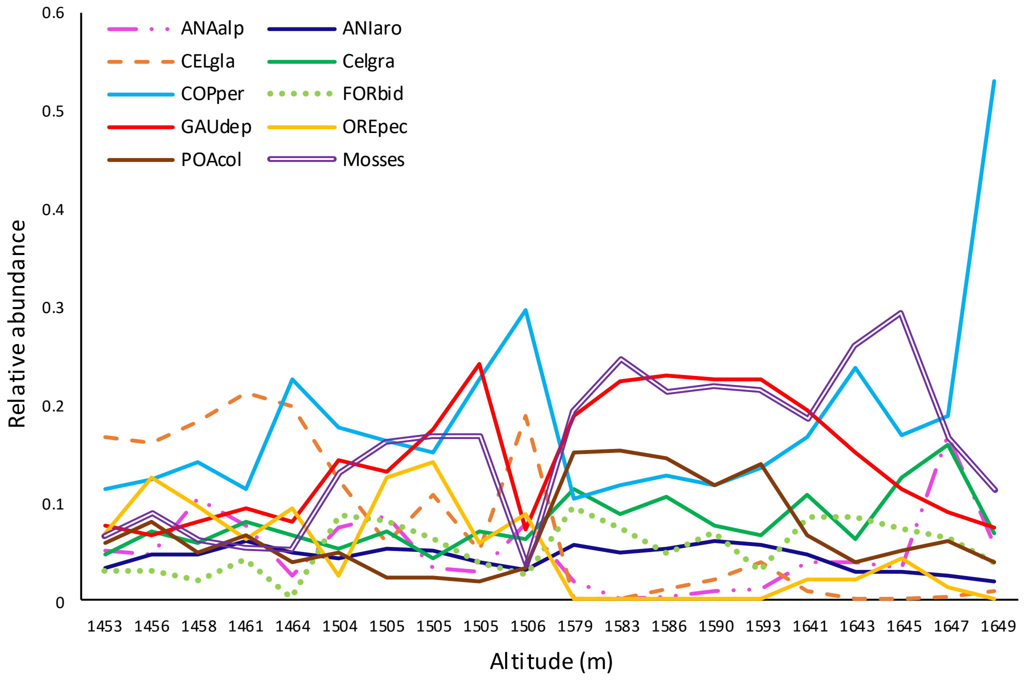

Figure 3.6 Distribution of the 10 most abundant species along the elevation gradient at East Egmont.

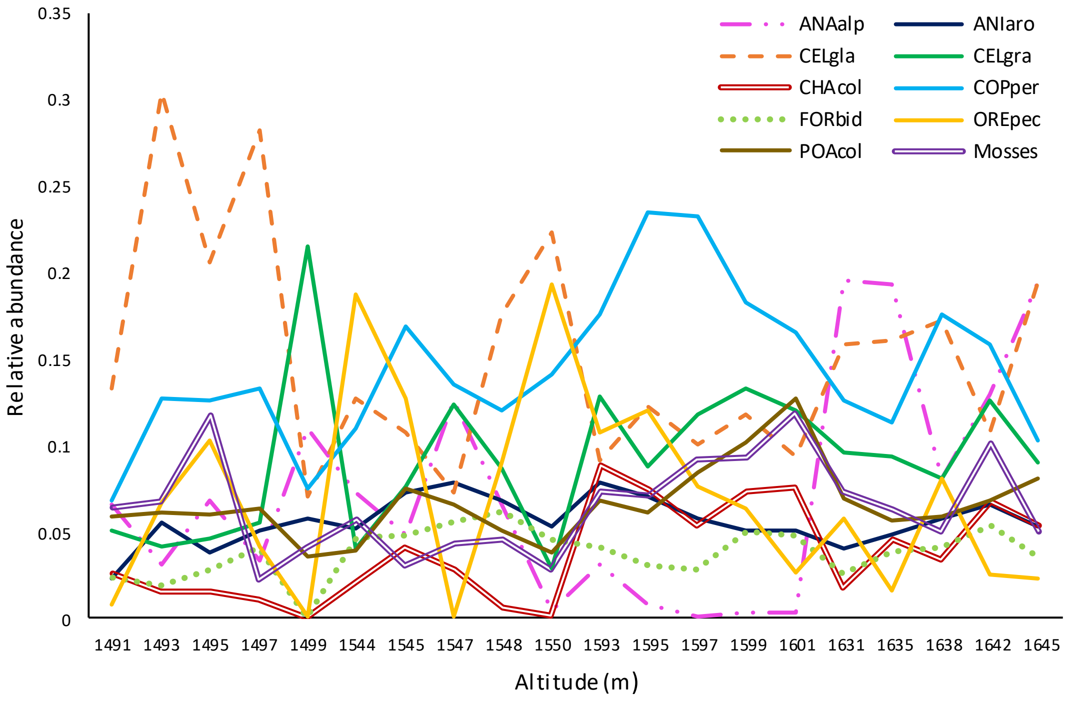

Figure 3.7 Distribution of the 10 most abundant species along the elevation gradient at North Egmont.

Table 3.6 Species ranked abundances for each site and elevation range (metres) on Mt Taranaki. Bold indicates species ranked within the top five most abundant at each site and elevation range. Dash (-) indicates species absence from that site. FP = Fantham's Peak; EE = East Egmont; NE = North Egmont. Elevation ranges 1650–1600; 1600–1550; 1550–1500; 1500–1450 m.

	FP	**EE**	**NE**	**1650**	**1600**	**1550**	**1500**
ANAalp	10	9	**4**	**4**	13	7	6
ANIaro	15	10	8	11	7	8	9
BLEpen	18	26	25	-	-	20	20
BRAele	35	-	-	-	-	33	-
CARdru	14	27	21	28	18	14	17
CELgla	**1**	**5**	**1**	**3**	**3**	**1**	**1**
CELgra	**5**	**4**	**3**	**5**	6	**3**	**3**
CERfon	28	-	32	23	27	34	32
CHAcol	20	-	10	14	12	17	21
CHIrub	8	14	14	24	22	9	10
COLcan	34	-	36	27	29	36	-
COPper	**2**	**1**	**2**	**1**	**2**	**2**	**2**
CORplu	**4**	-	16	18	9	13	11
CORpte	6	-	34	10	-	24	-
DRAfil	-	-	39	-	-	-	37
EPIgla	31	-	29	-	-	26	33
EPIper	36	24	28	-	26	27	34
EUPcun	17	25	31	17	20	28	28
FORten	16	7	9	9	8	10	12
GAUdep	7	**3**	11	6	**4**	**5**	8
GERsp.	-	-	30	-	-	35	29
GUNmon	24	18	24	21	-	-	15
HUPaus	-	-	40	-	-	-	38
HYMmul	-	23	27	-	-	32	26
HYPrad	22	-	19	-	-	16	30
KELdie	25	16	17	16	19	21	19
LOBang	-	19	-	-	-	-	22
LUZban	11	11	13	12	10	15	16
LUZcol	29	22	22	19	21	-	-
LYCfas	13	13	15	13	14	12	14
OREpec	12	8	**5**	8	11	**4**	**4**
OURmac	23	17	18	26	24	22	13
PENpum	32	-	12	20	15	18	24
POAcol	9	6	6	7	**5**	11	7
POLcys	-	-	35	-	-	-	35
PRAcol	33	21	33	-	28	30	31
RANniv	19	15	20	22	17	19	18
SAGpro	30	-	-	-	-	29	-
VERodo	-	28	26	-	30	31	25
VIOcun	21	-	37	-	25	25	36
WAHpyg	26	20	38	25	23	-	27
Lichens	27	12	23	15	16	23	23
Mosses	**3**	**2**	7	**2**	**1**	6	**5**

3.5.3 Comparison of percent cover and point intercept methods

The comparison of the two sampling methods (percent cover and point intercept) showed the point intercept method failed to account for rarer species (Figure 3.8). The point intercept method also underestimated species that are small of stature, such as *Prasophyllum*, a leek orchid not usually taller than 30 cm that grows erect and solitary; or *Luzula colensoi*, a dwarf woodrush that can form patches but was often found as a single individual in this study; and *Kelleria* that forms dense patches, with prostrate stems but erect foliage, yet was also frequently found as a solitary individual in the Mount Taranaki plots.

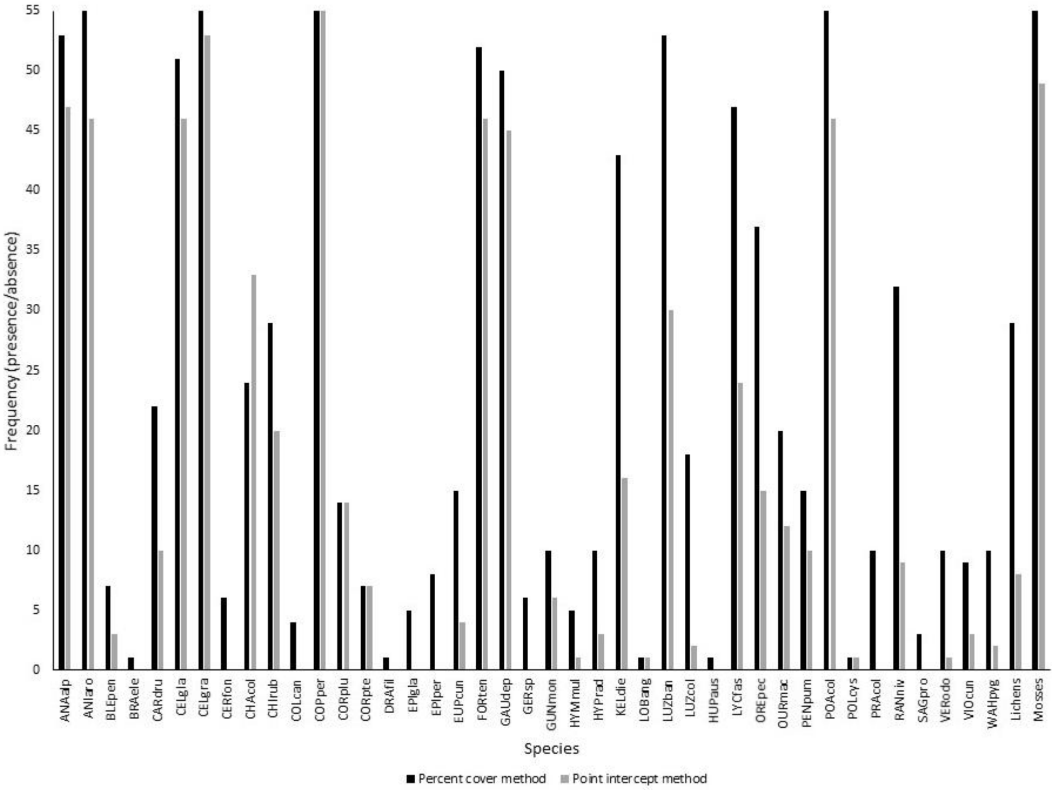

Figure 3.8 Bar plot of frequency of species occurrence across all sites and plots in the Mt Taranaki herbfield, using the percent cover (black lines) and line-point intercept (yellow lines) methods. Results were converted to presence/absence for comparison of the two sampling methods. A full species list is provided in Table 3.1.

3.6 Discussion

The differences observed in community composition, attributed to plot location and elevation range, shows the herbfield vegetation across the mountain has been affected by different historic events, and different stages of community development explain the variations in species distributions and abundances. Although aspect had some relationship with several of the East Egmont plots, the association was weak, and altitude and slope did not appear correlated with community composition. However, because aspect is the result of where the study sites were located, we can infer that its correlation with the axes is due to the differences in species composition between the sites. Altitude is an indirect variable and only accounts for change in species composition on a larger scale. Other studies have indicated site-specific variables such as soil moisture and temperature account for more variation than altitude alone, and serve as better predictors of species distribution (i.e. Lookingbill & Urban 2005).

The increase in species diversity with decreasing altitude observed in the herbfield vegetation supports the ecological theory of altitudinal diversity gradients (Kraft et al. 2011). del Moral and Grishin (1999) noted that volcanic disturbance has varying effects on vegetation, for example, shallow tephra deposits may not always destroy vegetation, and recovery can be swift following such eruptions, but vegetation recovery is determined by the severity of the eruption. Fantham’s Peak has had a longer period of volcanic stability than the other two sites, with the last eruptions from this secondary vent occurring somewhere between 3300 and 2500 years before present (Downey et al. 1994). The lower species evenness and dissimilarity of composition observed between the Fantham’s Peak plots suggests the Fantham’s Peak communities are in later stages of development, as species have had longer to colonise the area following the last volcanic disturbance.

Known for being pioneers in ecological succession, it is unsurprising that moss should be among the dominant plants within the herbfield. Even though transect sites were selected to contain less than 50% moss cover, the two genera (*Racomitrium* and *Polytrichum*) were widespread throughout the three study locations. Mosses are hardy and regenerate quickly following desiccation, and can form large, dense mats in alpine regions (Mark 2012). *Coprosma perpusilla* is a dwarf shrub that is widespread in alpine to sub-alpine regions in New Zealand, forming dense patches of creeping, rooting stems (Mark 2012). The thick leaves of *Coprosma* may help it to withstand alpine environments, and the creeping stems probably anchor it to the substrate, thereby increasing tolerance to disturbance, as it was prolific in the herbfield plots. *Celmisia glandulosa*, also widespread in all but the driest alpine regions of New Zealand (Mark 2012), develops roots or stolons that occur either just above or below ground. The variety of *Celmisia glandulosa* found on Mount Taranaki, *C. glandulosa* var. *latifolia*, has broader leaves than *C. glandulosa* (Mark 2012). *Celmisia glandulosa* prefers sites that are less well-drained (Mark 2012), and the extremely high mean annual rainfall on Mount Taranaki (NIWA 2014) provides an ideal habitat. The species ordination produced an interesting diagram from an ecological perspective, as species are represented as points that show their similarities in composition across the plots. The groups highlighted in the diagram shift from fertile, less well-drained sites in the middle to the drier, less-fertile upper altitudinal slopes. *Oreobolus* and *Ranunculus* are at the lower portion of group 1, closer to group 3, as they also have a preference for sites with less drainage.

The heterogeneity of the North Egmont lower elevation plots can be attributed to patchiness in the vegetation as the lowest transect lay within the boulder-filled gully of Hongi’s Valley. The transport of boulders through erosion of underlying material or through transport with snowmelt may have caused diffuse disturbance (sensu Pickett et al. 1999) within the communities of Hongi’s Valley. The remaining three transects at North Egmont displayed relatively similar compositions to each other, suggesting communities there are in similar stages of succession following the last eruptions that occurred over 260–700 years before present. The most recent eruption at North Egmont was the minor c. AD 1755 Tahurangi eruption which did not cause extensive damage to vegetation as it appears to have produced only fine ash, found extensively over the entire mountain but lacking lapilli (tephra 2–64 mm in diameter), so plants on the upper slopes may have been buried but are likely to have recovered quickly (Druce 1966; Platz et al. 2011).

The AD 1655 Burrell Lapilli eruption, the largest recent eruption, distributed approximately 30 cm of tephra over the east-northeast and east-southeast flanks of the mountain (Druce 1966; Topping 1972). A succession of eruptions first distributed tephra to the southeast, the second larger and lengthier eruption force was directed toward Manganui and Stratford Plateau at East Egmont, and the final eruption sent tephra northeast (Topping 1972). Consequently, it appears much of the herbfield vegetation at East Egmont is still in relatively early stages of development, as it had the lowest number of species identified and a higher total relative abundance of moss of the three study sites. The Burrell eruption has also had a substantial impact on vegetation at lower altitudes on the mountain, particularly large, emergent tree species (Efford 2012; Efford et al. 2014). Although Burrell Ashes were deposited via wind to the east-northeast (Druce 1966) and would have covered the northeast flanks of the mountain (North Egmont study sites), this ash was coarse to fine (2 mm to < 0.063 mm) and therefore unlikely to have substantially affected the North Egmont herbfield vegetation in the long-term. However, observations on Mount Ruapehu following the AD 1995 and 1996 eruptions showed some plant species suffered extensive damage. Between 1500–1760 m, a mean ash depth range of 65–25 mm resulted in up to 60% defoliation of *Gaultheria colensoi*, and *Luzula colensoi* was completely removed from those sites (Clarkson et al. 1997). Up to 50% of defoliation occurred at the higher altitudes, and up to 34% at the lower altitudes (Clarkson et al. 1997). It was noted that *Anisotome aromatica* had produced new growth when surveyed eight months following the 1996 eruption, and *Gaultheria colensoi* had re-sprouted from below-ground biomass, indicating fast recovery (Clarkson et al. 1997). The research of Clarkson et al. (1997) of the vegetation re-growth on Mount Ruapehu represents the only study in New Zealand measuring very recent effects of volcanic eruptions in an alpine herbfield. In the c. 400 years since the Burrell eruption, plants at both North Egmont and Fantham’s Peak seem to have recovered, but the low species diversity at East Egmont indicates those sites are still showing effects of the eruption. The Burrell eruption may have caused more extensive damage than is evident today, and some species may have been removed entirely following deposition of ash.

Interestingly, Fantham’s Peak had a high abundance of the toxic mountain tutu *Coriaria pteridoides,* which is frequently an early colonist following disturbance (Clarkson 1986), yet it was entirely absent from the East Egmont plots and had a very low abundance at North Egmont. This appears to contradict the theory that Fantham’s Peak has remained free from disturbance for a longer period than the other sites. One explanation for the presence of *C. pteridoides* at Fantham’s Peak is that it has managed to colonise disturbed ground following erosion of the upper slopes, as it is known to readily establish upon unconsolidated substrate (Rogers 1989). As the highest elevation transect at Fantham's Peak had the steepest slope angle of any of the transects across the study, it suggests debris flow may have contributed to the community composition there on a smaller scale than was detected in the ordination, and the abundance of *C. pteridioides* at higher elevations supports this theory. *Coriaria* is known to be a nitrogen fixing genus offering excellent facilitative properties for other plants in low nutrient soil (McQueen et al. 2006), which may also explain the lack of diversity in the East Egmont plots in its absence. It must be noted that *C. pteridoides* is found at East Egmont, and may simply have been excluded from the plots due to the nature of the sampling methods.

Because the study sites were located along the northeast to southeast sides of the mountain, exposure to prevailing salt-laden westerly winds was minimal. Fantham's Peak and East Egmont are more exposed to southerly winds that flow across the Cook Straight (Marcus & Moore 1983), which may influence communities at those sites, but probably has had less influence than volcanic events have. The compositional differences between sites is unlikely to be the result of dispersal limitations between sites, as many of the herbfield species on Mount Taranaki are well-adapted to wind dispersal, and have successfully colonised the mountain from the other alpine regions of New Zealand. Chapter Four contains a more detailed account of dispersal mechanisms of the herbfield species. A final observation here is that volcanic disturbance aside, the compositional irregularities observed between sites may simply be the result of these communities at altitude being more exposed to abiotic stress than lowland sites, so are subsequently in varied stages of colonisation and assembly.

3.7 Conclusions

Previous studies concerning the effect of eruptions on vegetation (e.g. McGlone et al. 1986; Clarkson 1990; Lees & Neall 1993; Efford et al. 2014) have focused extensively on lower montane forest and the wider reaches of Egmont National Park. The research of Clarkson (1977, 1981) included direct gradient analysis of change in community composition with altitude and compositional changes around the volcanic cones, but did not specifically examine compositional changes within the herbfield belt at different locations around the mountain. The variation observed within the alpine herbfield communities at three different sites on Mount Taranaki is most likely related to the volcanic eruptions that have occurred in the last 500 years. In particular, the AD 1655 Burrell Eruption appears to have greatly affected the vegetation at East Egmont, with low species diversity suggesting that East Egmont is only in the early stages of community assembly and is therefore still recovering from the eruption. This was also observed by Efford et al. (2014) at lower altitudes, where the upper montane forest displayed inconsistent assemblages when compared to sites at similar altitudes, indicating a lack of convergence in composition. Additional research incorporating more plots and transect so as to compile a more comprehensive data set is advised, in order to examine the extent of the eruption effects within the herbfield on a larger scale.

3.8 References

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Chapter Four: Colonisation and evolutionary priority effects in the Mount Taranaki alpine herbfield

4.1 Abstract

Priority effects can impact community assembly by excluding later arriving species via niche pre-emption, and this can drive clade radiation over millions of years. In order to determine when priority effects become apparent in communities, comparison was made of two New Zealand alpine regions. Evolutionary priority effects have been found in the Murchison Mountains of the South Island, where the most dominant species in that alpine community belonged to older evolutionary lineages. The present research tested for priority effects in the Mount Taranaki alpine herbfield, geologically much younger than the Murchison Mountains, and the site of frequent volcanic disturbance. The priority effects analysis compared abundances of genera located in the herbfield plots with estimated ages of clade divergence using simple and multiple linear regression. The results indicated priority effects are not yet evident in the Mount Taranaki alpine communities, as the genera belonging to older evolutionary lineages were not more abundant in the communities. Instead, the composition of the Taranaki herbfield is strongly influenced by the frequency of disturbances and isolation from seed sources, as many species in the North and South Island alpine regions have failed to colonise Mount Taranaki.

4.2 Introduction

Priority effects are yet to be widely studied in terrestrial ecosystems. To date, most priority effects studies have focused on aquatic ecosystems, both freshwater (e.g. Wilbur & Alford 1985; Lawler & Morin 1993; Blaustein & Margalit 1996) and marine (e.g. Shulman et al. 1983; Almany 2003; Irving et al. 2007). Testing priority effects in natural systems, particularly over long time scales, is challenging, as colonisation history is often difficult to determine (Fukami 2015). Frameworks with which to test priority effects are also scarce within the literature (Fukami et al. 2016), but recent studies are slowly contributing to improved methodologies (e.g. Sarneel et al. 2016).

Silvertown (2004) hypothesised that niche pre-emption, a priority effect, of early-arriving colonists was responsible for the high rates of endemism of plant genera found on the islands throughout Macaronesia. This brought to light the role of priority effects in shaping not only community assemblages in the ecological sense, but also within an evolutionary context. Unlike the archipelagos of Hawai'i and the Galapagos where the level of endemism appears to be the product of extreme isolation, Silvertown noted that the Canary Islands of Macaronesia were not faced with the same dispersal barriers. An alternative hypothesis for assembly of species in the Canary Islands was that niche pre-emption led to colonisation success, as older genera were more diverse, yet diversity decreased with the number of colonisation events. Silvertown suggested a test for this alternative hypothesis would be to examine detailed molecular phylogenies of clades to see if speciation decreased with time as adaptive radiation caused a reduction in niche space. If early colonists gain priority for niche space, the ensuing diversification and radiation results in a large clade that diminishes ecological availability, limiting the establishment of closely related species later on (Silvertown 2004; Silvertown et al. 2005; Tanentzap et al. 2015).

Evidence for evolutionary priority effects has been found in the alpine floral communities of the Murchison Mountains (Fiordland National Park, New Zealand). Community assembly there appears to have been influenced by colonisation timing, as older lineages had greater cover per unit area, and congeneric associations occurred frequently in older genera (Lee et al. 2012; Leopold et al. 2015; Tanentzap et al. 2015). The Murchison Mountains are part of the Southern Alps, a mountain range extending almost the length of the South Island. The Southern Alps offer an ideal site in which to test evolutionary priority effects, as the endemism and diversity observed in the New Zealand alpine flora belies the geological age of habitat availability. The uplift of the Southern Alps commenced during the late Miocene and accelerated during the Pliocene (5–2 Ma), and periods of glaciation throughout the Plio-Pleistocene further modified these alpine habitats (McGlone et al. 2001; Winkworth et al. 2005). The New Zealand alpine flora has therefore undergone rapid radiation within just a short evolutionary period. As priority effects appear to have influenced community assembly in the Murchison Mountains in the form of niche pre-emption (Lee et al.

2012; Tanentzap et al. 2015), it is likely they also contributed to diversification of some clades (Tanentzap et al. 2015).

If priority effects have been detected in the Murchison Mountain communities, a system with an age of c. 5–2 Ma, then when do such effects become apparent? The youngest alpine zone in New Zealand, Mount Taranaki, began forming c. 135,000 years ago, and, following a series of catastrophic eruptions, the present volcanic cone is estimated to be less than 10,000 years old (Zernack et al. 2011). Frequent eruptions have influenced the pattern of vegetation across the mountain (Druce 1966; McGlone et al. 1988; Lees & Neall 1993), resulting in a much more recent assemblage of species when compared to the well-established communities studied in the Murchison Mountains. In addition to the disturbance history of Mount Taranaki, its age also means species have had less time in which to colonise the mountain. This is evident by the number of species that are present in other North Island alpine zones, but have failed to colonise Mount Taranaki, which may be the result of the distance from seed sources (Clarkson 1986).

The first aim of the present research is to test if priority effects are evident in the alpine herbfield communities of Mount Taranaki, using the relative abundance cover data from Chapter Three. If priority effects exist in the Mount Taranaki herbfield, it is hypothesised that genera belonging to older evolutionary lineages will be more abundant, as observed by Lee et al. (2012) in the Murchison Mountains. The second aim of this research is to examine how dispersal barriers have contributed to community composition in the herbfield by comparing species abundances to dispersal mechanisms. The final aim of this research is to evaluate which species are ‘missing’ from the herbfield communities of Mount Taranaki by comparing species distributions across the alpine regions of New Zealand. Description of the methods used to test for priority effects, dispersal mechanisms and depauperate species in the Mount Taranaki herbfield communities will be included in the methods section. This will be followed by presentation of the results, discussion of the findings and concluding statements.

4.3 Methods

4.3.1 Age estimates and plant genera

In order to determine the presence of priority effects within the Mount Taranaki herbfield species, ages of genera were required. These were provided by Landcare Research (Dunedin, New Zealand), having been compiled and corrected since the initial study by Lee et al. (2012). The ages are based on estimates of time-calibrated molecular phylogenies from various publications, and used as a proxy for immigration timing of the arrival of the clade to New Zealand. The age itself represents 'stem' age, which is an estimate of years since divergence of a clade from its most recent extant relative that exists outside of New Zealand (Lee et al. 2012). The ages and error estimates provided by Landcare Research are included in the species list in the Appendix (Table A2). Genera for which estimated ages were not available were excluded from the following analyses, and the genera used for analysis are listed in Table 4.1. Averages were taken if multiple ages were available (i.e. from different publications).

The data used in the following analyses is the relative abundance (RA) data collected from the Mount Taranaki herbfield plots, as in Chapter Three. Where multiple species from one genus were identified, their relative abundances were summed together to compile RA data for that genus. As the focus of this research was priority effects among New Zealand native species, non-native genera were removed from the data set. Non-vascular genera were also excluded as ages for these genera were not known. Subspecies were included as individual species but taxonomic ranks lower than subspecies (variety or form) were not counted as individuals[2]. As in Lee et al. (2012) genera used for analysis (known hereafter as 'focal genera') were those with evolutionary ages less than 10 Ma, as alpine habitats did not exist in the New Zealand landmass prior to then. The focal genera all belong to monophyletic clades, and age estimates included species found within the Mount Taranaki plots, with the exception of *Brachyglottis* and *Celmisia*, for which published ages only included *Brachyglottis greyi* and *Celmisia mackaui.* Some estimates also included clades with species not indigenous to New Zealand, these were *Euphrasia*, *Poa*, *Ranunculus* and *Wahlenbergia*.

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[2] Nomenclature follows the New Zealand Plant Conservation Network (February 2017).

Table 4.1 List of genera in the Mt Taranaki herbfield plots, with number of species (in plots and in New Zealand) and estimated ages (Ma) of clade divergence. N_T = number of species in genus identified in the Mt Taranaki plots; N_{NZ} = total number of native species in genus in New Zealand; % plots = percentage of plots in which the genus occurred. Bold indicates focal genera (ages < 10 Ma).

Genus	Family	N_T	N_{NZ}	Age
Anisotome	**Apiaceae**	**1**	**16**	**3.9**
Blechnum	Blechnaceae	1	23	12.43
Brachyglottis	**Asteraceae**	**1**	**29**	**3.4**
Celmisia	**Asteraceae**	**2**	**68**	**5**
Chaerophyllum	**Apiaceae**	**1**	**5**	**1.6**
Chionochloa	Poaceae	1	34	19.95
Coprosma	Rubiaceae	1	56	12.13
Coriaria	Coriariaceae	2	8	61.05
Dracophyllum	**Ericaceae**	**1**	**34**	**6.8**
Euphrasia	**Orobanchaceae**	**1**	**16**	**5.7**
Forstera	**Stylidiaceae**	**1**	**7**	**6.32**
Gaultheria	Ericaceae	1	10	14.46
Gunnera	Gunneraceae	1	6	27.3
Huperzia	**Lycopodiaceae**	**1**	**1**	**4**
Hymenophyllum	Hymenophyllaceae	1	24	32.77
Lobelia	Campanulaceae	1	14	14.2
Lycopodium	**Lycopodiaceae**	**2**	**4**	**4.6**
Oreobolus	**Cyperaceae**	**1**	**3**	**5.1**
Pentachondra	**Ericaceae**	**1**	**1**	**8.75**
Poa	**Poaceae**	**1**	**42**	**3.55**
Polystichum	Dryopteridaceae	1	7	15.3
Ranunculus	**Ranunculaceae**	**1**	**45**	**5.05**
Veronica	Plantaginaceae	1	130	10.21
Wahlenbergia	**Campanulaceae**	**1**	**15**	**4.8**

4.3.2 Statistical analyses

Data analysis was performed using STATISTICA (Version 12, Statsoft). Pearson correlation was performed to test if any relationship existed between species richness and clade age, to determine if the older clades were more diverse, as in Lee et al. (2012). Species diversity of all genera listed in Table 4.1 (N_{NZ}) was transformed (log x+1) and compared to stem ages. As the present study featured much lower species diversity than the study by Lee et al. (2012), correlation was performed for the diversity of the genera across New Zealand and not for diversity observed within the Mount Taranaki communities.

Due to the low diversity in the Mount Taranaki genera, the analyses focused on RA (as a measure of dominance) rather than the occurrence of congeneric species, therefore testing if RA was related to age. To achieve linearity, the RA values were transformed by taking the natural log (ln) of mean RA of all focal genera, before observing the relationships between RA and stem age using linear regression. Linear regression analysis was performed for:

- Log-transformed mean RA of focal genera present for which ages were available (as listed in Table 4.1) across all plots, with age as the predictor.
- Log-transformed mean RA for focal genera at each site (Fantham's Peak, East Egmont, North Egmont), with age as the predictor.
- Log-transformed mean RA for focal genera at each elevation range (1650–1600, 1600–1550, 1550–1500, 1500–1450 m), with age as the predictor.
- Log-transformed mean RA for focal genera across all plots, with richness (N_{NZ}) as the predictor.

Multiple linear regression was performed to test the relationship between log-transformed mean RA of focal genera across all plots, with both age and richness as predictors. Residual analysis was performed to test the assumptions of the multiple regression.

4.3.3 Comparison of dispersal and species abundances

The summary of the dispersal mechanisms of the plants identified in the Mount Taranaki herbfield plots was compiled using the publication by Thorsen et al. (2009). The classification system used by Thorsen et al. for description of dispersal mechanisms was aneomochory (wind), hydrochory (water), endo- and epi-zoochory (animal), ballistic (explosive), invertebrates, barochory (gravity) and geocarpy (subterranean fruiting). In the present study, zoochory and invertebrates were combined as 'animals'. The total RA data for each species was summed together with genera of the same family, then converted to percent cover of each family over the study area, to compare dispersal mechanisms of each family and their percent cover.

4.4 Results

4.4.1 Priority effects

The Pearson correlation showed no relationship between diversity of the New Zealand genera and clade age ($r = .03$, $P = 0.9$). The regression analyses revealed no statistically significant relationship between the effects of age on RA, at either the site or elevation level (Figures 4.1a-h). No relationship was observed for richness as a predictor of relative abundance (Figure 4.2), so richness of genera as a whole (sum of total New Zealand species within the focal genus/genera) does not have an effect on relative abundances within the Mount Taranaki herbfield plots. The multiple regression results presented in Table 4.2 further detail the lack of relationship observed between RA and richness and age, as shown by the low values of B and β coefficients (negative B and β for age, low positive B and β for richness). Inspection of the residual plot (Figure 4.3) shows a random distribution of residuals, indicating a good fit to the linear model.

Table 4.2 Multiple regression results for log-transformed (ln) mean relative abundance of focal genera across all plots with age (Ma) of divergence and richness (N_{NZ}) as predictors. $r = .151$; $r^2 = .023$; $F(2,11) = .123$; standard error of estimate = 3.06. B = B coefficient (unstandardised); β = beta coefficient (standardised); SE = standard error. *P* significant at < 0.05.

	B	**SE B**	**β**	**SE β**	***t*(11)**	***P***
Intercept			-5.61	2.755	-2.04	0.066
Age	-0.011	0.299	-0.02	0.497	-0.04	0.971
Richness	0.150	0.299	0.02	0.042	0.50	0.626

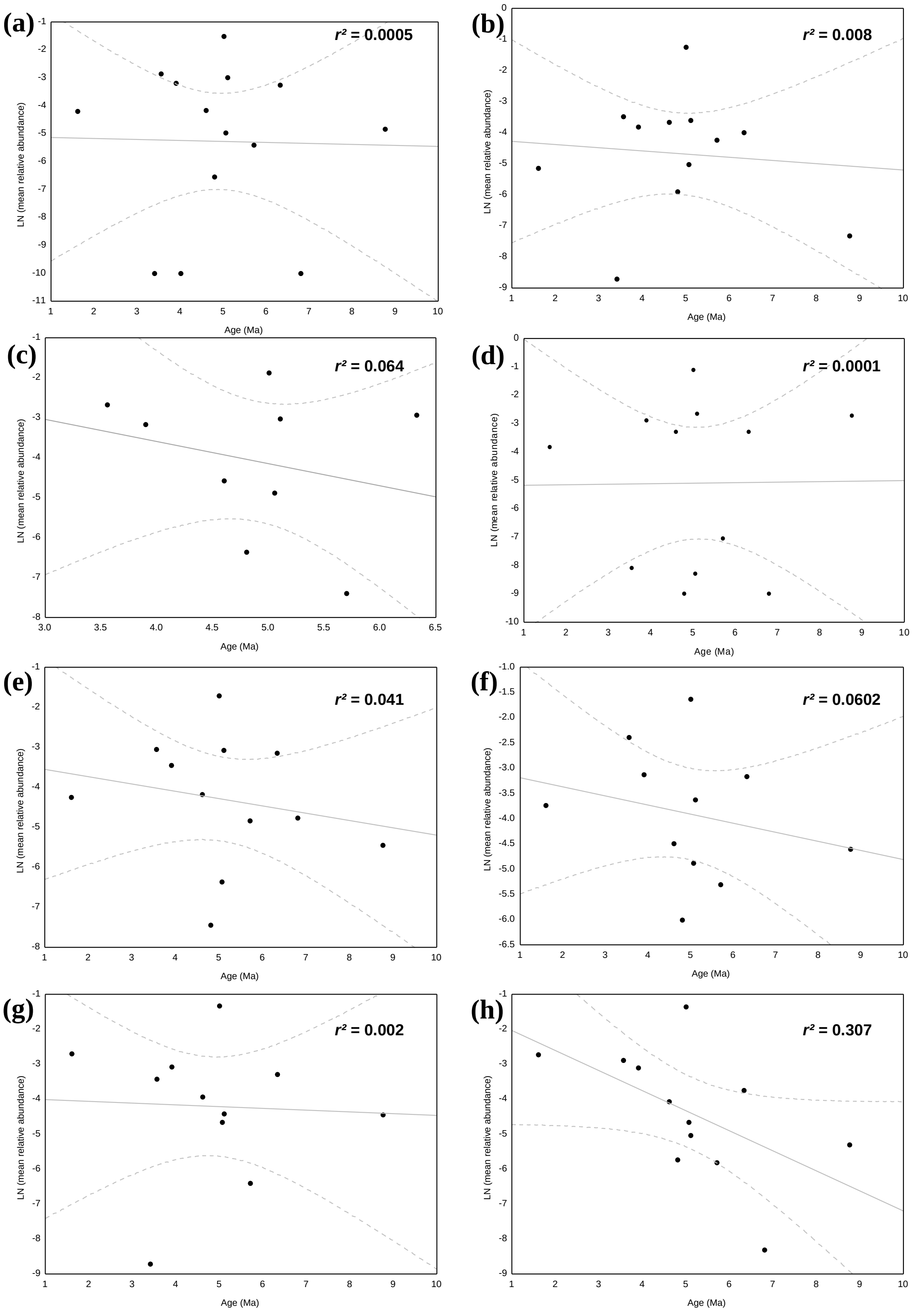

Figure 4.1 Linear regression showing the relationship between log-transformed (ln) mean RA (y axis; LN mean relative abundance) and estimated clade ages of focal genera in the Mt Taranaki herbfield, across all plots **(a)**, and by site and elevation range: **(b)** Fantham's Peak; **(c)** East Egmont; **(d)** North Egmont; **(e)** 1650–1600 m; **(f)** 1600–1550 m; **(g)** 1550–1500 m; **(h)** 1500–1450 m. Coefficients of determination (r^2) are included for each graph. Graphs presented with 95% confidence intervals, solid line represents the model mean.

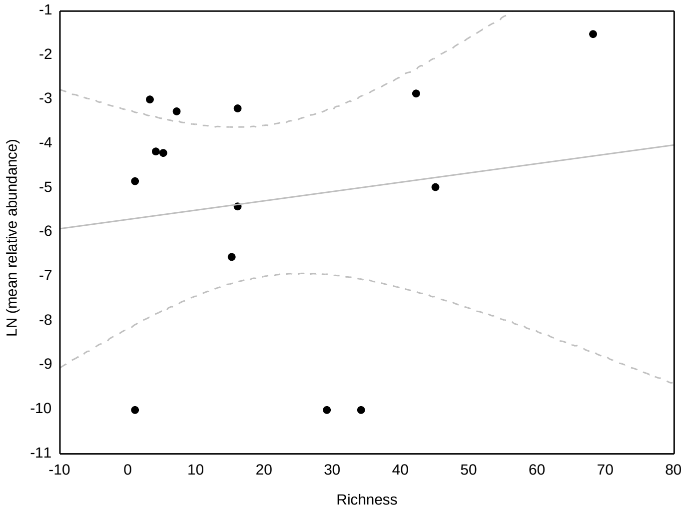

Figure 4.2 Linear regression showing the relationship between log-transformed (ln) mean RA (y axis; LN mean relative abundance) and richness (N_{NZ}) of focal genera across all plots. Graph presented with a 95% confidence interval, solid line represents model mean. r^2 = 0.023.

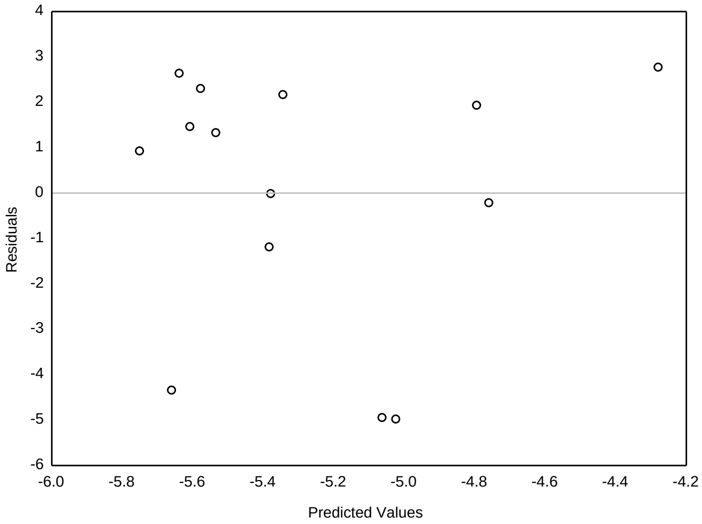

Figure 4.3 Residual plot showing the distribution of raw residuals for observations and predicted values of the multiple regression model presented in Table 4.2.

4.4.2 Dispersal and species distribution

The families that covered more than 5% of the study area each used two or more dispersal mechanisms, and of those, wind and animal dispersal were included each time (Table 4.3). However, Caryophyllaceae, Plantaginaceae and Ranunculaceae had four dispersal mechanisms, including wind and bird, yet had low cover in the study area.

Table 4.3 Seed dispersal mechanisms used (+) by families and genera in the Mt Taranaki herbfield plots. % cover = total cover of family across study site.

Family/subfamily	**Genera included**	**% cover**	**Wind**	**Water**	**Animal**	**Ballistic**	**Gravity**	**Geocarpy**
Apiaceae	*Anisotome* *Chaerophyllum*	8.4	+	+	+			
Asteraceae	*Anaphalioides* *Brachyglottis* *Celmisia* *Hypochaeris*	14.6	+	+	+			
Blechnaceae	*Blechnum*	0.6	+					
Campanulaceae	*Wahlenbergia*	0.2	+			+		
Caryophyllaceae	*Cerastium* *Colobanthus* *Sagina*	0.2	+	+	+	+		
Coriariaceae	*Coriaria*	5.0	+		+			
Cyperaceae	*Carex* *Oreobolus*	8.8	+	+	+			
Dryopteridaceae	*Polystichum*	0.01	+					
Ericaceae	*Dracophyllum* *Gaultheria* *Pentachondra*	11.9	+		+			
Geraniaceae	*Geranium*	0.1	+		+	+		
Gunneraceae	*Gunnera*	0.6	+					
Hymenophyllaceae	*Hymenophyllum*	0.1	+					
Juncaceae	*Luzula*	3.9		+	+			
Lobeliaceae*	*Lobelia*	0.2	+	+	+			
Lycopodiaceae	*Huperzia* *Lycopodium*	2.4	+					
Onagraceae	*Epilobium*	0.2	+		+			
Orchidaceae	*Prasophyllum*	0.1	+	+				
Orobanchaceae	*Euphrasia*	0.7	+	+		+		
Plantaginaceae	*Ourisia* *Veronica*	1.0	+	+	+	+		
Poaceae	*Chionochloa* *Poa*	11.1	+	+	+			
Ranunculaceae	*Ranunculus*	1.0	+	+	+		+	
Rubiaceae	*Coprosma*	21.7	+		+			
Stylidiaceae	*Forstera*	5.7	+		+			
Thymelaeaceae	*Kelleria*	1.2	+		+			
Violaceae	*Viola*	0.2	+			+		+

* Sub-family

4.5 Discussion

4.5.1 Priority effects

As highlighted earlier in this chapter, evolutionary priority effects are difficult to test. Several caveats need be taken into consideration when interpreting the results of this study. Because the Mount Taranaki data was not fitted to a Bayesian model that can account for the uncertainty of age estimates, it must be stressed that the results of these analyses should be treated as preliminary results only. Further research fitting the data to a model that enables increased error estimates may provide more definitive evidence for priority effects. Models using age estimates as proxies for immigration of focal genera produce results that may not be highly accurate, as immigration timing can never be precisely determined (Tanentzap et al. 2015), so cautionary interpretation is advised.

The Pearson correlation result is consistent with the findings of Lee et al. (2012), where they observed no relationship between clade age and species richness for New Zealand genera within their study. They noted some older genera had high species richness but others of the same age were species poor, and the same can be said for the present study. In contrast, some of the more recently colonised genera in the Mount Taranaki plots had high species richness, notably *Poa, Ranunculus* and *Celmisia*. The lack of relationship between community dominance (RA) and age, as shown by the regression analyses, suggests there is no evidence for evolutionary priority effects within the Mount Taranaki herbfield communities. Lee et al. found that the Murchison Mountain plots were dominated by focal genera belonging to older lineages, which supported the theory of priority effects. However, their study included use of a Bayesian framework fitted to linear regression models, thereby accounting for uncertainty of clade age estimates. Another notable difference between the present study and that of Lee et al. is the lack of species diversity and congeneric associations present within the Mount Taranaki alpine flora, with 72 species included in their priority effects analysis and only 16 in this study. Lee et al. had a much larger sample area (6550 m^2 compared to 220 m^2), and a geologically older and more stable study site in which well-established communities have had time to develop.

Unlike the Murchison Mountains that belong to an extensive alpine range, Mount Taranaki is isolated from other New Zealand alpine regions by approximately 130 km. Evolutionary priority effects can shape community composition over millions of years (Leopold et al. 2015), a time frame during which the alpine habitats of Mount Taranaki were still forming. The communities of the Southern Alps have had 5–2 Ma to assemble (Batt et al. 2000), drawing from a species pool of paleoendemics and recent arrivals that were able to quickly disperse and adapt to the newly formed alpine habitats (McGlone et al. 2001). Because the age estimates of clades used by Lee et al. focused on their arrival into New Zealand with formation of the first alpine habitats (i.e. the Southern Alps), analysis of evolutionary priority effects becomes problematic when applying clade ages to Mount Taranaki, as many of those clades had established in the New Zealand alpine habitats before Mount Taranaki (in its present state) was formed. Although there is evidence the original volcanoes of the Taranaki Volcanic Succession reached alpine altitudes, during the sequential build and collapse of the original volcanoes (Lees & Neall 1993; Alloway et al. 1995) much of the alpine vegetation would likely have been destroyed, so it is not known if plants belonging to older lineages had managed to colonise the earlier volcanoes. Niche conservatism, in which species retain ancestral traits such as competitive ability (Wiens et al. 2010), could enable clade age to still be a predictor in younger communities. The traits that allowed a species to induce priority effects at initial colonisation may be passed on to make them superior competitors, thus retaining the ability to induce priority effects regardless of when they colonised. However, the lack of age related effects in the Taranaki alpine communities does not support niche conservatism conferred priority effects. The low diversity and infrequent congeneric associations suggest initial community assembly is still occurring on Mount Taranaki, so effects relating to colonisation timing are yet to be observed. In this respect, it appears unlikely the use of clade age as a proxy for immigration timing of the Mount Taranaki species is a suitable measure for priority effects there.

4.5.2 Dispersal and species diversity

As none of the Taranaki alpine herbfield flora are endemic to Mount Taranaki at the species level, we know that multiple independent colonisation events have occurred following recent eruptions. There are several species that are found on the older Pouakai Ranges, part of the earlier Taranaki Volcanic Succession, that have yet to colonise Mount Taranaki, and conversely, there are several species found within the alpine zone of Mount Taranaki that do not occur within the Pouakai ranges (Clarkson 1981). The latter is the result of the lower altitude of Pouakai not supporting the high alpine species, and the species missing from Mount Taranaki that occur on Pouakai is likely due to the combination of colonisation timing, the preference for substrate and the frequency of eruption events that have periodically disturbed vegetation on the mountain (Clarkson 1981, 1986).

Ecosystem colonists are usually wind dispersed, followed by animal dispersal, although species employing animal dispersal can be rare in volcanically disturbed sites (Wood & del Moral 1988). The absence of native land mammals has enabled the New Zealand flora to adapt well to bird dispersal, and birds are therefore the most common animal dispersers in New Zealand (Clout & Hay 1989). Seed dispersal by both wind and animals is an important factor in colonisation on Mount Taranaki, as the more abundant families use both of those dispersal mechanisms. Although there were families that used bird and animal dispersal but had low abundances, those with high abundances contained very widespread, common genera including *Anisotome, Celmisia, Chionochloa*, *Coprosma*, *Coriaria*, and *Gaultheria*, so it is unsurprising they have managed to disperse and establish in such abundance from other areas. However, the more abundant families on Mount Taranaki are missing several notable species that are known to occur within the central North Island alpine regions. *Dracophyllum recurvum*, *Celmisia spectabilis*, and *Gaultheria colensoi* are abundant at 1370–1700 m on Mount Ruapehu (Gibbs 1966), but are not known from the Taranaki flora. Several species of *Raoulia* (Asteraceae), *Euphrasia*, *Epilobium*, *Ranunculus, Myosotis* (Boraginaceae; wind, water and animal dispersal) and *Ourisia* (Druce 1973) are easily dispersed and widespread throughout the North Island mountains, yet are missing from the Taranaki alpine communities.

As observed by Efford et al. (2014) in their study of the effects of the AD 1655 Burrell eruption at the Mount Taranaki treeline observed persistent damage to emergent trees in areas where the eruption was directed. They also noted a lack of species convergence, suggesting a slow recovery following the Burrell eruption, as species composition in those disturbed areas was inconsistent with surrounding, unaffected areas. This same absence of convergence is present in the higher altitudinal communities of the alpine herbfield, where compositional differences between sites were related to eruption history, as discussed in Chapter Three. The alpine species missing from Mount Taranaki that are present on the Pouakai ranges further demonstrates the lack of convergence. That species common in other North Island mountains are absent from Mount Taranaki is a direct result of age, isolation and recent volcanism.

4.6 Conclusions

This study provides the first analysis of evolutionary priority effects in the alpine herbfield communities of Mount Taranaki, and the first priority effects study of plant communities in the North Island of New Zealand. Although the results indicate an absence of priority effects within the Mount Taranaki plots, caution is advised due to the uncertainty of clade age estimates and the manner in which the data was fitted to the regression model. However, although the priority effects analyses were not entirely reliable due to uncertainty of age estimates, it is still unlikely that evolutionary priority effects are influencing assembly in the Taranaki alpine communities. The low species diversity and lack of convergence in the Mount Taranaki alpine flora is the result of eruption events and distance from seed sources, indicating assembly is still occurring, so evidence for priority effects is unlikely to be observed in the communities there for some time yet. Still, this represents a first step in determining when evolutionary or ecological priority effects become evident, as Mount Taranaki contains communities that have only recently established in comparison to the long-established communities of the Murchison Mountains.

4.7 References

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Synthesis

5.1 Discussion

The research presented in this thesis has shown that the AD 1655 Burrell eruption has greatly influenced the composition within the alpine herbfield of Mount Taranaki. This is supported by the low species diversity observed in the East Egmont plots, which is where the main axis of debris blast from the Burrell eruption was directed. Furthermore, there appears to be a lack of community convergence at North Egmont, East Egmont and Fantham's Peak, the result of frequent eruptions spanning the last 500 years. The lack of species convergence was also observed at the upper montane treeline by Efford et al. (2014), and the present research represents the first study focused on the compositional differences resulting from the effects of eruptions at higher elevations on Mount Taranaki.

The research of Lee et al. (2012) indicated the priority effect of niche pre-emption among early colonising plant genera contributed to community assembly in the alpine flora of the Murchison Mountains. Colonisation sequence is yet to have an effect on the communities of the Taranaki alpine herbfield, and instead the pattern of assembly is currently the result of dispersal and establishment of species following various eruptions and erosion events, rather than priority effects. That the Taranaki alpine flora is significantly depauperate compared to the North and South Island alpine communities, including volcanic landscapes, also indicates community assembly is still occurring on Mount Taranaki.

Although the present research has not provided evidence for priority effects in the Taranaki alpine communities, it has given an indication of when priority effects are unlikely to be present in communities. In undisturbed communities lacking significant dispersal barriers, priority effects may be observed, as in the Murchison Mountains. Community assembly pressures leading to clade diversification in the South Island alpine flora have been observed in the geologically older Southern Alps, but these pressures on radiation and diversification are not yet established in the Mount Taranaki assemblages.

5.2 Recommendations for future research

It may be useful in future studies of the Mount Taranaki herbfield to include environmental measures of soil chemistry, soil moisture content, rainfall, and temperature regimes specific to each site. This additional data would enable researchers to rule out the influence of these variables on community composition in a robust manner, rather than using regional data and altitude as proxies (Lookingbill & Urban 2005). I would also recommend that a greater number of plots and transects be sampled to construct an ample dataset of the herbfield vegetation, to draw comparisons across a larger study area. In addition, if point intercept is used to sample herbfield sites, it is recommended that a greater intensity of sampling be employed (i.e. smaller intervals between points), to account for rare or small species.

Following the recommendation of Efford (2012) of re-measuring the treeline composition on Mount Taranaki, I also suggest re-measuring the herbfield vegetation to determine how the communities are developing. This would enable researchers to see when or if species convergence is occurring. However, if we use the frequency of past eruptions as a predictor of future eruptions, then it is highly likely that volcanic disturbance may again impact vegetation on the mountain. The erosion that occurs naturally at higher altitudes and exposed areas on the mountain may also affect the herbfield communities, so convergence is unlikely to be observed until long after the volcano is extinct.

Evidence for priority effects in the alpine flora of New Zealand is still yet to be widely researched, and although several studies have shown support for evolutionary priority effects as a potential mechanism for diversification of the New Zealand alpine flora (Lee et al. 2012; Leopold et al. 2015), it is not yet known how long it takes for these effects to strongly impact community composition. Mount Taranaki is the most newly formed alpine region in New Zealand, with frequent eruptions, and therefore does not support the likelihood of priority effects. A test of priority effects in older systems in the North Island may prove profitable, such as Mount Hikurangi in the Raukumara Range.

Although priority effects analysis remains a relatively novel branch of community ecology, studies are emerging that show the applications of priority effects theory to the field of restoration ecology (e.g. Trowbridge 2007;

Wainwright et al. 2012; Young et al. 2016). Any research concerning priority effects, either evolutionary or ecological, will contribute to improving our understanding of how communities assemble, from which practical applications can be developed.

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Appendices

Appendix 1

Post hoc analysis of species variation

One-way factorial analysis of variance (ANOVA) was performed to test for variations in mean distribution of the herbfield species. Post hoc analyses of those species found to differ significantly (ANOVA *t*-test resulting in *P*-values < 0.05) using Duncan's new multiple range test showed that 25 of the total 43 species identified had significantly different mean relative abundances between sites, presented in Appendices A1.1 and A1.2.

Table A1.1 Duncan's new multiple range test showing differences in mean relative abundances of species between sites in the Mt Taranaki herbfield. Only species with significant *P* in a prior ANOVA were tested and shown here. Significant (< 0.05) *P*-values in bold. FP = Fantham's Peak; EE = East Egmont; NE = North Egmont.

	FP vs EE	**FP vs NE**	**NE vs EE**
ANAalp	0.262	**0.013**	0.124
ANIaro	**<0.001**	**<0.001**	**0.004**
CARdru	**0.001**	**0.004**	0.467
CELgla	**<0.001**	**0.009**	**0.015**
CELgra	0.128	**0.016**	0.298
CHAcol	0.315	**0.000**	**<0.001**
CHIrub	**0.033**	0.072	0.651
COPper	**0.002**	0.089	0.103
CORplu	**<0.001**	**<0.001**	0.372
CORpte	**0.004**	**0.003**	0.978
EUPcun	**<0.001**	**<0.001**	0.924
FORten	**<0.001**	**0.004**	**0.012**
GAUdep	**<0.001**	0.403	**<0.001**
GERsp.	1.000	**0.012**	**0.015**
KELdie	0.067	**<0.001**	**0.023**
LUZban	0.284	**0.044**	0.282
LUZcol	0.755	**0.032**	**0.020**
LYCfas	**<0.001**	**0.005**	0.375
OREpec	0.226	**0.022**	0.217
PENpum	0.911	**0.001**	**0.001**
POAcol	**0.001**	**0.002**	0.750
SAGpro	**0.033**	**0.025**	1.000
VIOcun	**0.004**	**0.004**	0.864
Lichens	**<0.001**	0.550	**<0.001**
Mosses	**0.012**	0.136	**<0.001**

Table A1.2 Duncan’s new multiple range test showing differences in mean relative abundances of species between elevations in the Mt. Taranaki herbfield. Only species with significant *P*-values in a prior ANOVA were tested and shown here. Values shown are *P*-values, significant (< 0.05) *P*-values are in bold. 1650 = plots 1650–1600 m; 1600 = plots 1600–1550 m; 1550 = plots 1550–1500 m; 1500 = plots 1500–1450 m.

Elevation comparison	**1500 1550**	**1500 1600**	**1500 1650**	**1550 1600**	**1550 1650**	**1600 1650**
ANAalp	0.472	**0.007**	0.079	**0.034**	**0.020**	**<0.001**
CELgla	0.926	**0.043**	**0.034**	**0.044**	**0.032**	0.833
CHIrub	0.325	**0.015**	**0.012**	**0.001**	**0.001**	0.841
CORpte	0.756	1.000	**0.039**	0.740	0.056	**0.034**
FORten	0.125	0.061	**0.046**	0.649	0.541	0.844
GERsp.	**<0.001**	**<0.001**	**<0.001**	0.865	0.874	1.000
GUNmon	**<0.001**	**<0.001**	**0.003**	1.000	0.350	0.320
HYMmul	**0.002**	**0.001**	**0.001**	0.635	0.657	1.000
HYPrad	**0.012**	0.562	0.587	**0.004**	**0.004**	1.000
LUZban	0.962	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.914
LUZcol	1.000	**0.034**	**0.001**	**0.027**	**<0.001**	0.112
OURmac	**0.005**	**<0.001**	**<0.001**	0.248	0.136	0.664
POAcol	**0.041**	**0.001**	0.407	**<0.001**	0.178	**<0.001**
PRAcol	0.069	0.054	**0.008**	0.828	0.310	0.386
RANniv	0.995	0.584	**0.049**	0.604	0.056	0.122
VERodo	**0.016**	**0.008**	**0.008**	0.705	0.686	0.957
Mosses	0.998	**0.004**	**0.004**	**0.003**	**0.003**	0.936

Table A2 List of species found in the Mount Taranaki herbfield plots, with the age estimates and either standard deviation (SD) or upper and lower confidence intervals (CI) of age estimates, as provided by Landcare Research in Dunedin.

Binomial	**Common name**	**Family**	**Age**	**SD**	**Upper CI**	**Lower CI**
Vascular						
Anaphalioides alpina		Asteraceae	missing			
Anisotome aromatica	kopoti, common aniseed	Apiaceae	3.9		7	1.4
Blechnum penna-marina subsp. *alpina*	alpine hard-fern	Blechnaceae	12.43	5.23		
Brachyglottis elaeagnifolia		Asteraceae	3.4		5.7	1.3
Carex drucei	Druce's hook sedge	Cyperaceae	missing			
Celmisia glandulosa var. *latifolia*	Egmont bog mountain daisy	Asteraceae	5		9	2.4
Celmisia gracilenta	pekapeka, mountain daisy	Asteraceae	5		9	2.4
Cerastium fontanum subsp. *vulgare*	mouse-ear chickweed	Caryophyllaceae	non-native			
Chaerophyllum colensoi var.	mountain myrrh	Apiaceae	1.6		2.6	0.8
Chionochloa rubra subsp. *rubra* var. *inermis*	red tussock	Poaceae	19.95		23.6	16.65
Colobanthus canaliculatus		Caryophyllaceae	missing			
Coprosma perpusilla subsp. *perpusilla*		Rubiaceae	12.13		17.41	7.44
Coriaria plumosa	mountain tutu	Coriariaceae	61.05	12.2		
Coriaria pteridioides	small-leaved tutu	Coriariaceae	61.05	12.2		
Dracophyllum filifolium		Ericaceae	6.8		9.68	5.77
Epilobium glabellum	willowherb	Onagraceae	missing			
Epilobium pernitens	willowherb	Onagraceae	missing			
Euphrasia cuneata	North Island eyebright	Orobanchaceae	5.7		7.05	4.37
Forstera tenella		Stylidiaceae	6.32	1.1		
Gaultheria depressa var. *novae-zelandiae*	snowberry	Ericaceae	14.46		22.4	6.89
Geranium sp.		Geraniaceae	missing			
Gunnera monoica		Gunneraceae	27.3	9.8		
Huperzia australiana	clubmoss	Lycopodiaceae	4	3		
Hymenophyllum multifidum	filmy fern	Hymenophyllaceae	32.77	8.93		
Hypochaeris radicata	cats ear	Asteraceae	non-native			

Binomial	Common name	Family	Age	SD	Upper CI	Lower CI
Kelleria dieffenbachii		Thymelaeaceae	missing			
Lobelia angulata	Pratia	Campanulaceae	14.2	missing		
Luzula banksiana var.	woodrush	Juncaceae	missing			
Luzula colensoi	dwarf alpine woodrush	Juncaceae	missing			
Lycopodium fastigiatum	alpine clubmoss	Lycopodiaceae	4.6	4.97		
Oreobolus pectinatus	comb or cushion sedge	Cyperaceae	5.1	0.9		
Ourisia macrophylla subsp. *macrophylla*	mountain foxglove	Plantaginaceae	missing			
Pentachondra pumila		Ericaceae	missing			
Poa colensoi	blue tussock	Poaceae	3.55		5.5	1.8
Polystichum cystostegium	alpine shield fern	Dryopteridaceae	15.3	0.9		
Prasophyllum colensoi	leek orchid	Orchidaceae	missing			
Ranunculus nivicola	mountain buttercup	Ranunculaceae	5.05	0.84		
Sagina procumbens	pearlwort	Caryophyllaceae	non-native			
Veronica odora		Plantaginaceae	10.26	5.29		
Viola cunninghamii	mountain violet	Violaceae	missing			
Wahlenbergia pygmaea subsp. *drucei*	North Island harebell	Campanulaceae	4.8		7.67	3.13
Non-vascular						
Lichen spp.						
Polytrichum spp.						
Racomitrium cripsulum						
Racomitrium lanuginosum var. *pruinosm*						
Racomitrium sp.						

Table A3 Attributes of the Mount Taranaki study sites. Altitude (Alt.; m) and GPS start/end refers to altitudes and coordinates recorded at the start and end of each transect.

Site	**Plots**	**Slope**	**Aspect**	**Alt. start**	**Alt. end**	**GPS start**	**GPS end**
Fantham's Peak	1–5	34°	120°	1648	1636	E 1692654 N 5648206	E 1692670 N 5648205
	6–10	27°	130°	1584	1560	E 1692752 N 5648134	E 1692785 N 5648127
	11–15	27°	75°	1555	1542	E 1692788 N 5648068	E 1692804 N 5648065
East Egmont	1–5	20°	165°	1649	1639	E 1693119 N 5649502	E 1693134 N 5649493
	6–10	31°	135°	1593	1576	E 1693221 N 5649426	E 1693231 N 5649416
	11–-15	17°	105°	1506	1504	E 1693366 N 5649337	E 1693383 N 5649324
	16–20	32°	135°	1464	1450	E 1693343 N 5649081	E 1693351 N 5649070
North Egmont	1–5	23°	65°	1645	1628	E 1692985 N 5650659	E 1693004 N 5650661
	6–10	18°	75°	1601	1591	E 1693090 N 5650663	E 1693109 N 5650659
	11–15	28°	75°	1550	1542	E 1693198 N 5650677	E 1693216 N 5650674
	16–20	25°	75°	1499	1489	E 1693283 N 5650620	E 1693297 N 5650622