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Multi-scale influences of abiotic factors on alpine treelines

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

at
Lincoln University
by
Bradley Stuart Case

Lincoln University
2013

Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy.

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by

Bradley Stuart Case

Globally, the maximum elevations at which treelines are observed to occur coincide with a 6.4 °C soil isotherm. However, when observed at finer scales, treelines display a considerable degree of spatial complexity in their patterns across the landscape and are often found occurring at lower elevations than expected relative to the global-scale pattern. There is still a lack of understanding of how the abiotic environment imposes constraints on treeline patterns, the scales at which different effects are acting, and how these effects vary over large spatial extents. In this thesis, I examined abrupt *Nothofagus* treelines across seven degrees of latitude in New Zealand in order to investigate two broad questions: (1) What is the nature and extent of spatial variability in *Nothofagus* treelines across the country? (2) How is this variation associated with abiotic variation at different spatial scales? A range of GIS, statistical, and atmospheric modelling methods were applied to address these two questions.

First, I characterised *Nothofagus* treeline patterns at a 15x15km scale across New Zealand using a set of seven, GIS-derived, quantitative metrics that describe different aspects of treeline position, shape, spatial configuration, and relationships with adjacent vegetation. Multivariate clustering of these metrics revealed distinct treeline types that showed strong spatial aggregation across the country. This suggests a strong spatial structuring of the abiotic environment which, in turn, drives treeline patterns. About half of the multivariate treeline metric variation was explained by patterns of climate, substrate, topographic and disturbance variability; on the whole, climatic and disturbance factors were most influential.

Second, I developed a conceptual model that describes how treeline elevation may vary at different scales according to three categories of effects: thermal modifying effects, physiological stressors, and disturbance effects. I tested the relevance of this model for *Nothofagus* treelines by investigating treeline elevation variation at five nested scales (regional to local) using a hierarchical design based on nested river catchments. Hierarchical linear modelling revealed that the majority of the variation in treeline elevation resided at the broadest, regional scale, which was best explained by the thermal modifying effects of solar

radiation, mountain mass, and differences in the potential for cold air ponding. Nonetheless, at finer scales, physiological and disturbance effects were important and acted to modify the regional trend at these scales. These results suggest that variation in abrupt treeline elevations are due to both broad-scale temperature-based growth limitation processes and finer-scale stress- and disturbance-related effects on seedling establishment.

Third, I explored the applicability of a meso-scale atmospheric model, The Air Pollution Model (TAPM), for generating 200 m resolution, hourly topoclimatic data for temperature, incoming and outgoing radiation, relative humidity, and wind speeds. Initial assessments of TAPM outputs against data from two climate station locations over seven years showed that the model could generate predictions with a consistent level of accuracy for both sites, and which agreed with other evaluations in the literature. TAPM was then used to generate data at 28, 7x7 km *Nothofagus* treeline zones across New Zealand for January (summer) and July (winter) 2002. Using mixed-effects linear models, I determined that both site-level factors (mean growing season temperature, mountain mass, precipitation, earthquake intensity) and local-level landform (slope and convexity) and topoclimatic factors (solar radiation, photoinhibition index, frost index, desiccation index) were influential in explaining variation in treeline elevation within and among these sites. Treelines were generally closer to their site-level maxima in regions with higher mean growing season temperatures, larger mountains, and lower levels of precipitation. Within sites, higher treelines were associated with higher solar radiation, and lower photoinhibition and desiccation index values, in January, and lower desiccation index values in July. Higher treelines were also significantly associated with steeper, more convex landforms.

Overall, this thesis shows that investigating treelines across extensive areas at multiple study scales enables the development of a more comprehensive understanding of treeline variability and underlying environmental constraints. These results can be used to formulate new hypotheses regarding the mechanisms driving treeline formation and to guide the optimal choice of field sites at which to test these hypotheses.

Keywords: Alpine treelines, *Nothofagus*, spatial pattern, variability, spatial scale, abiotic factors, landscape metrics, hierarchical models, atmospheric models, physiological stress, topoclimate, disturbance

Acknowledgements

While carrying out a PhD project and writing a thesis is largely a personal endeavour, such a large undertaking would not be feasible without the help and contribution of many people. First, a big thanks to my main supervisory team: Richard Duncan and Roddy Hale, who were always available to provide much appreciated help with thinking about treelines at a conceptual level and with reading and reviewing my written work. Thanks to Tim Curran, who stepped in at the end as an associate supervisor and provided comments on the full thesis document. A special thanks to Peyman Zawar-Reza at Canterbury University for providing guidance on, and access to, the TAPM atmospheric model which formed the basis for Chapters 4 and 5 and for providing comments on portions of my thesis document. This thesis has also benefited from many excellent conversations with a range of people: Maaike Bader, Hannah Buckley, Ellen Cieraad, Marie-Josée Fortin, Melanie Harsch, Phil Hulme, Matt McGlone, Janet Wilmshurst, and the Lincoln University Spatial Ecology Group. Thanks also to those who have provided me with the necessary spatial data and analysis advice over the course of the thesis: Andrew Tait (NIWA), David Pairman (Landcare), Stella Belliss (Landcare), James Sheperd (Landcare), Mark Stirling (GNS Science), Stuart Charters (Lincoln University). A big thank you to Lincoln University for providing operational and tuition funding for my thesis work. Last, but certainly not least, this thesis would not have been possible without the support of my family: Hannah and Sam have always been there for me throughout this process even though sometimes I'm sure it seemed it would go on forever! Also, I would like to thank my parents-in-law, Elizabeth and Bob, who have been a solid base of support for the three of us since moving to New Zealand 10 years ago.

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Chapter 1

Introduction

1.1 Overview

Alpine treeline ecotones are transitional zones between forest and alpine plant communities at high elevations. Alpine treelines form at elevations where abiotic conditions become too harsh for trees to establish, survive and grow. Due to their conspicuousness as a global phenomenon, alpine treelines have long been studied by ecologists with the aim of describing their patterns and understanding their underlying causative processes (e.g. Daubenmire 1954, Troll 1973, Tranquillini 1979, Holtmeier 2009, Körner 2012). Despite the considerable legacy of treeline research, both globally and regionally, the mechanisms underpinning treeline formation are still not fully understood (e.g. Piper *et al.* 2005, Sveinbjörnsson *et al.* 2010). Nonetheless, considerable progress has been made and has led to several reviews of treeline research in recent years (Körner 1999, 2012, Sveinbjörnsson 2000, Young and León 2007, Holtmeier 2009, Richardson and Friedland 2009, Malanson *et al.* 2011). What is clear from these syntheses and from individual studies is that treelines display distinctive patterns of spatial variability that are dependent on the scale of observation, the life-history characteristics of the tree species forming the treeline, historical influences of disturbances, and the abiotic context. For instance, while there is undoubtedly a global, temperature-based threshold governing the elevation at which trees can grow (Körner and Paulsen 2004), many treelines are often found at much lower elevations locally due to context-related effects (Sveinbjörnsson 2000). Thus, at finer scales, the abiotic environment provides a complex background against which a range of physical, ecological and physiological processes operate and interact to create treelines of differing patterns. The overall focus of this thesis is on quantifying and understanding the nature of treeline variability, using New Zealand's *Nothofagus* treelines as the system of interest.

1.2 Patterns and processes at treeline

Much of what is currently known about treeline patterns and processes has resulted from research based on two dominant approaches: the 'global' approach and the 'landscape' approach (Malanson *et al.* 2011). The global perspective on treeline research has sought to characterise worldwide patterns of treeline variation with respect to variables such as

temperature and latitude and search for the mechanism underpinning these patterns. There is a hump-shaped, global latitudinal pattern of treeline elevation variation (Troll 1973, Körner 1998), with a clear difference in the maximum treeline elevations reached by continental as compared to oceanic island treeline locations (Figure 1.1). Körner and Paulsen (2004) established that altitudinal tree limits are generally associated with a mean soil temperature of around 6.4°C, indicating that there is an overall temperature-based threshold to the growth of upright trees at high altitudes. Although Körner and Paulsen (2004) found *Nothofagus* treelines in New Zealand to be an exception to the above rule, forming at higher temperatures relative to the global mean trend, the alignment of New Zealand's treelines with the global trend has since been confirmed based on new temperature data collected at treelines across the country (Cieraad 2011). In the search for a physiological mechanism behind this treeline-temperature relationship, evidence suggests that at high elevations, low temperatures limit the ability of trees to utilise carbon for growth processes (e.g. Li *et al.* 2002, Hoch and Körner 2003, Handa *et al.* 2005, Piper *et al.* 2005, Körner and Hoch 2006, Körner 2008, Sveinbjörnsson *et al.* 2010). While this mechanistic explanation is still under some debate (Wiley and Helliker 2012), it is nonetheless generally accepted that treelines will form at elevations related to this temperature-based threshold, in the absence of other local-scale stressors.

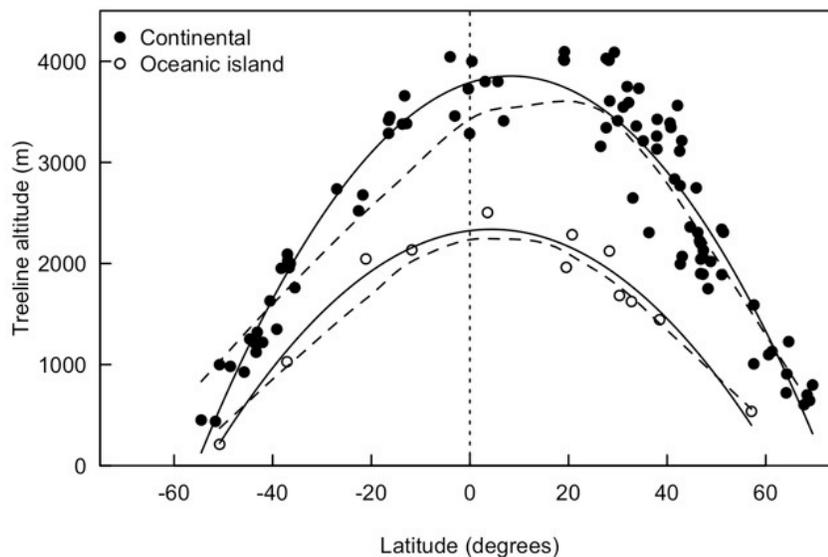


Figure 1.1 The relationship between treeline elevation and latitude for a global sample of 105 continental and oceanic treeline locations (from Berdanier 2010).

The landscape approach to treeline research, on the other hand, aims to disentangle the array of biotic and abiotic influences and interactions that cause different treeline patterns in different locations and at different scales, from regional to local (Figure 1.2). Thus, the focus of the landscape approach is on investigating treeline pattern-process relationships across the full treeline ecotone regardless of whether or not treelines are occurring at their temperature-driven limit. One of the main concerns of the landscape approach is in understanding how and why treelines at these finer scales deviate from their maximum attainable elevation at certain locations across the landscape and how they may respond to climate change (Holtmeier and Broll 2005, 2007, 2012). There have been a range of methods used to investigate treeline patterns and processes at sub-global scales, including: regional comparisons of treeline elevation along precipitation and temperature gradients (e.g. Daniels and Veblen 2004); landscape-scale characterisations of treeline patterns and pattern change using GIS- and remote sensing-based analyses (e.g. Danby and Hik 2007a, Stueve *et al.* 2011, Mathisen *et al.* 2013); site-scale investigations of population dynamics at treelines (e.g. Cuevas 2000, Camarero and Gutiérrez 2004, Hofgaard *et al.* 2009, Harsch 2010, Kullman 2010); dendrochronological analyses at treelines to look at the effects of historical climate on tree growth and population dynamics through time (e.g. Cullen *et al.* 2001a, b, Wang *et al.* 2006); modelling approaches aimed at understanding the relative effects of ecological processes such as facilitation and competition (e.g. Malanson 1997, Wiegand *et al.* 2006, Martínez *et al.* 2011); and microsite-scale approaches investigating physiological processes related to a range of stressors (e.g. Germino *et al.* 2002, Johnson *et al.* 2004, Maher and Germino 2006). Results emerging from these and other studies have shown that treeline patterns and processes are context- and scale-specific (Figure 1.2). At continental-to-regional scales, evidence suggests that that treeline patterns are governed by temperature, in line with global patterns, but these can be modulated by other factors including available soil and atmospheric moisture (Daniels and Veblen 2003), the degree of continentality (Caccianiga *et al.* 2008), the size of surrounding mountains (i.e. the ‘mass-elevation effect’) (Han *et al.* 2012), and geological factors (Butler *et al.* 2007). At landscape-to-local scales, topographic and geomorphologic variability and disturbance exert strong influences (Holtmeier and Broll 2005). All of these factors overlay across scales, ultimately affecting ecological and physiological processes near and within a tree, that lead to the treeline dynamics observed at that location.

1.3 Scale: the tie that binds

Many ecological patterns and processes are scale-dependent (Levin 1992) and hierarchically structured (Allen and Starr 1982), and it is clear that treelines display these properties (Malanson *et al.* 2011). For instance, it is well-recognised that spatial and temporal patterns of tree establishment in many treeline ecotones are contingent on the influence of factors across multiple scales (Camarero and Gutiérrez 2004, Malanson *et al.* 2007, Elliott 2011). However, there have been relatively few multi-scale investigations of treeline (but see Daniels and Veblen 2003, 2004, Danby and Hik 2007, Malanson *et al.* 2007, Harsch *et al.* 2009, Elliott and Kipfmüller 2010, Elliott 2011). Indeed, much of the research on alpine treeline patterns and their drivers have either been based on a relatively few observations at a global scale or intensive observations at relatively few, small study sites, and have generally focussed on one or two influential factors per study. The high-elevation environment places limitations on the ability to collect relevant data regarding treeline patterns and multiple abiotic influences across extensive areas, thus limiting the investigation of scale-related effects. However, the use of remote-sensing and GIS-based analyses and datasets and hierarchical statistical modelling methods can be combined to provide ways to address this limitation (Malanson *et al.* 2011). Nonetheless, the literature provides only a few examples where GIS and remote sensing-based approaches have been used to characterise and model treeline patterns in relation to abiotic variability (Allen and Walsh 1996, Rees 2007, Bader and Ruijten 2008). Further, hierarchical statistical models (e.g. McMahon and Diez 2007) have yet to be employed to address scale-dependencies in treeline patterns. Such modelling approaches, for example, might provide a useful way to partition variation in treeline characteristics across scales, enabling the identification of the critical scales at which treeline variation is occurring. Thus, there is a clear need for the novel application of spatially-explicit and quantitative methods to characterise treeline ecotone patterns over extensive areas and to more completely model the determinants of these patterns at different scales (Malanson *et al.* 2011). Such analyses will help bridge the gap between the global and landscape approaches to treeline research, by applying methodologies that are explicitly multi-scale (Harsch 2010, Malanson *et al.* 2011).

		Indicative Scales					
		Global	Continental/ Country-wide	Regional	Landscape	Local	Site/Microsite
Example of abiotic context	Bioclimatic zones	Mountain chains, climatic regions	Mountain ranges	Valley features	Spur vs. gully landforms	Frost hollow, vegetated mound	
Typical abiotic influences	Temperature						
	Precipitation						
	Continentality (degree of coastal vs. continental climate regime)						
	Mass-elevation effect						
	Solar radiation						
	Soil property variation						
	Disturbances						
	Topoclimate (wind, radiation, temperature)						
	Snow depth and distribution						
	Topography and landform						
Microclimate							
Neighbourhood effects							

Figure 1.2 Conceptual diagram of abiotic factors that influence treeline patterns across a range of spatial scales. Modified from Holtmeier and Broll (2005).

1.4 New Zealand's treelines and abiotic environment

From a New Zealand perspective, there are two types of alpine treelines: 1) abrupt treelines comprising two evergreen angiosperm species of the genus *Nothofagus* (*N. solandri* var. *cliffortioides* (Hook. f.) and *N. menziesii* (Hook. f.)), and 2) gradual, mixed-species treelines comprising both angiosperm and gymnosperm tree and tall shrub species (Wardle 2008). The former dominate the majority of alpine areas across New Zealand, covering a range of seven degrees of latitude, while the latter occur in the absence of *Nothofagus*, predominately along a 200 km stretch of the South Island's Southern Alps west of the main divide, known as the 'Westland Beech Gap' (Figure 1.3). This thesis focusses on *Nothofagus*-dominated treelines. *Nothofagus* treelines, in contrast to the majority of alpine treelines worldwide, are abrupt (Wardle 2008), with the ecotone essentially being characterised as a line. Although wind-stunted 'krummholz' *Nothofagus* trees and established seedlings and saplings have been observed above the *Nothofagus* treeline in New Zealand, evidence indicates that they are few and generally within a relatively short distance (< 15 m) of the forest limit (Wardle 1985a, 2008, Wardle and Coleman 1992). Much of the existing characterisation of New Zealand treeline ecotones derive from a handful of relatively fine-scale studies at a few *Nothofagus* treeline sites (Wardle 1981a, 1985a, b, c, Wardle and Coleman 1992, Harsch *et al.* 2012), while other broader descriptions of treelines in New Zealand have largely been anecdotal in form (Wardle 1964, Norton and Schönenberger 1984, Wardle *et al.* 2001). Quantitative data describing treelines in New Zealand have been mainly collected using transect sampling at small scales (Wardle and Coleman 1992, Harsch *et al.* 2012), usually less than 500 metres in spatial extent, and therefore lack spatially-extensive information about the altitudinal location and spatial variability of treeline.

From the perspective of environmental variability, there is a stark difference in precipitation between the west and east sides of New Zealand's axial mountain ranges and a clear north-south temperature gradient across the country (Sturman and Tapper 2006). There are regional complexities to these trends: for example, east of New Zealand's main divide, inland basins within larger mountain ranges have a more continental climate with greater seasonal variability in precipitation and temperatures, while treelines in more subdued terrain and closer to the coast display less climatic variability (Sturman and Tapper 2006). Further, at local scales across the country, terrain at treeline is complex, inducing a high level of variability in sun and wind exposure and in slope gradient, soil composition, and snow

deposition (Leathwick *et al.* 2003). Local mass disturbances (avalanches, rock slides, landslips) are also quite frequently observed along treelines (Cullen *et al.* 2001b, Wardle 2008) and will act to artificially depress treelines below their physiologically-based altitudinal limits. There is also likely an historical component to treeline elevation variability related to past large-scale disturbances due to earthquakes and fires (Wardle 2008) and volcanoes (McGlone *et al.* 1996), for which the geographic pattern of occurrences and intensities are not well documented. Thus, the New Zealand environment provides a rich context within which to investigate associations between treeline patterns and the abiotic environment.

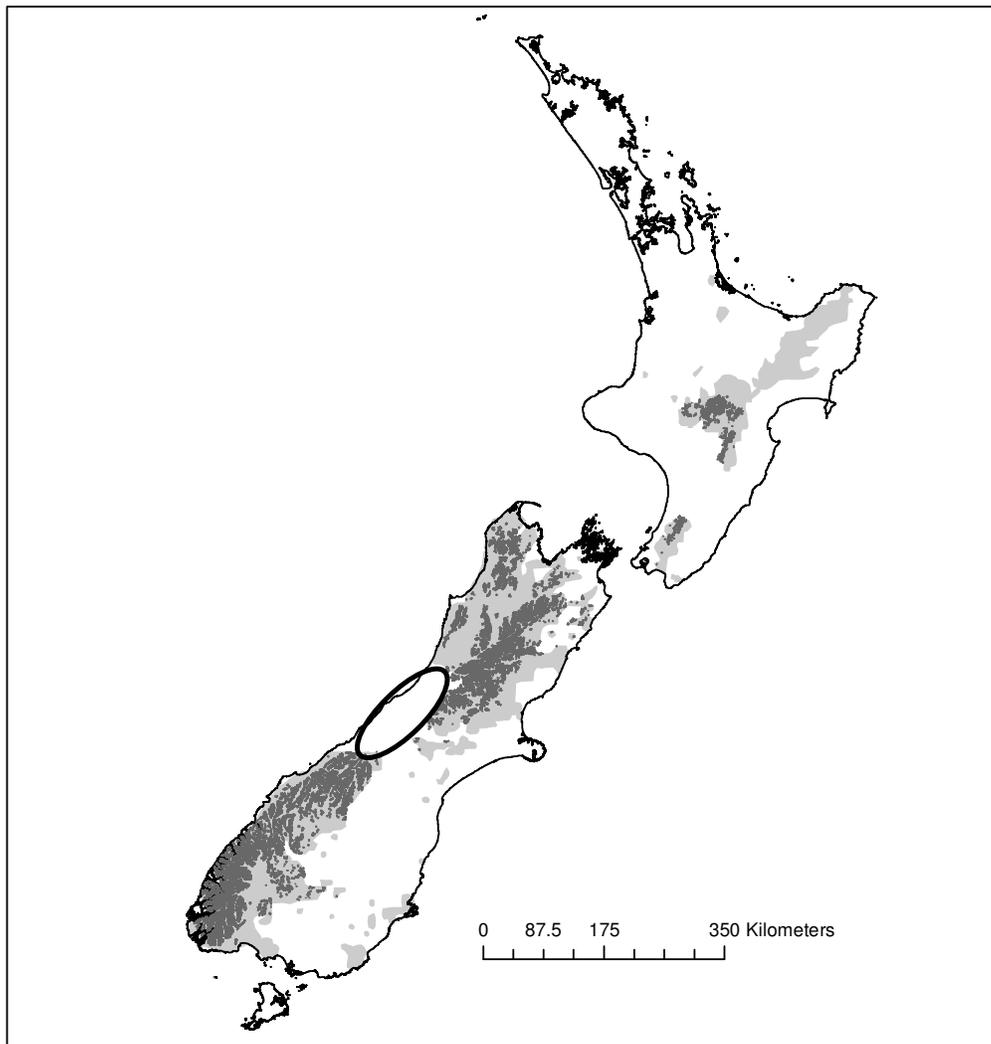


Figure 1.3 Distribution of *Nothofagus* species across New Zealand (light grey) and *Nothofagus*-dominated treelines (dark grey). The oval outlined area indicates the ‘Westland Beech Gap’ on the west coast of the South Island, where *Nothofagus* is absent.

1.5 Research questions

The main research questions of this study are:

1. How do *Nothofagus* treelines vary spatially across New Zealand in relation to abiotic conditions?
2. How does spatial scale mediate the influence of abiotic factors on treeline elevation variation?
3. By quantifying associations between treeline pattern and abiotic variability, what insights can be gained regarding the possible processes structuring treelines across scales?

To answer these questions, I apply a range of spatial and statistical approaches that enables the:

1. Characterisation of treeline patterns and abiotic variability across the full extent of *Nothofagus* treelines in New Zealand.
2. Statistical quantification of the direction and strength of influences of different abiotic factors on treeline elevation at multiple nested scales, from regional to local.
3. Characterisation of topoclimatic variability at treelines across New Zealand.
4. Quantification of the effect of topography, in terms of landform variability and topoclimate, on fine scale treeline elevation variability.

1.6 Thesis outline

To address the above research questions, the remainder of this thesis will cover the following topics:

In **Chapter 2**, I quantify abrupt *Nothofagus* treeline variability at a landscape scale using a set of GIS-based metrics describing treeline shapes, orientations, elevations, spatial configurations, and relationships with adjacent vegetation. Using these metrics, I investigate whether or not *Nothofagus* treelines in New Zealand are characterised by distinct spatial patterns that are associated with broad gradients in climate, substrate, topography, and

disturbance that are found across the country. Results from this analysis constitute the first comprehensive spatial overview of these treelines and their abiotic environments across their full extent.

In **Chapter 3**, I lay out a conceptual framework for how observed variability in treeline position can be explained by three categories of abiotic factors: *thermal modifiers*, *physiological stressors*, or *disturbance factors*. I then use a novel statistical approach for applying this framework to *Nothofagus* treelines across New Zealand at five spatial scales. The aim of this chapter is to provide a general framework for teasing apart the influences of multiple abiotic factors on treeline elevation variation at different spatial scales. This chapter has been accepted with revisions for publication in the journal *Ecography*, co-authored with Richard Duncan.

Topographic complexity in mountainous areas has a major impact on local climates, inducing *topoclimatic* effects such as aspect-related variation in insolation, valley and slope winds, and cold air drainage and ponding. Topoclimatic variation can therefore have critical influences on treelines in terms of inducing local stresses due to frost, drought, and extreme light conditions. However, these effects are virtually impossible to account for using the spatially-explicit, long-term climatic datasets that are typically available. In **Chapter 4**, I therefore explore the novel application of a mesoscale, numerical atmospheric model (TAPM) to generate high resolution (200m) hourly meteorological data in treeline areas. This chapter applies the model at two weather station locations near treeline, one in the North Island of New Zealand, and one in the South Island, in order to test the model's performance against observed data.

In **Chapter 5**, I then extend the use of TAPM to 28, 7x7km treeline study sites across the country. I use hourly data generated from TAPM for January and July 2002 to characterise five topoclimatic indices at over 2100 treeline locations: insolation, temperature variation, an index of frost potential, and index of photoinhibition potential, and an index of desiccation potential. Using these data, and those for two landform variables, slope gradient and curvature, I explore whether topoclimate and landform variation exert a measurable effect on treeline variability across the country.

Chapter 6 concludes the thesis with a general discussion of the results emerging from the previous four chapters, along with some suggestions for possible directions of future treeline research.

Chapter 2

Quantifying landscape-scale treeline patterns: New Zealand's abrupt *Nothofagus* treelines and their abiotic environments

2.1 Introduction

Alpine treelines are highly spatially variable. Treeline ecotones can vary in terms of their floristic composition, their altitudinal positions, and whether they display gradual, abrupt, or wind-stunted 'krummholz' transitions (Holtmeier 2009). For example, in New Zealand treelines vary considerably in elevation and display both floristically-diverse, gradual ecotones on the west coast of the South Island and abrupt *Nothofagus*-dominated treelines elsewhere (Wardle 2008). Within gradual treelines, treeline patterns can be further described by the size, shape, and structural characteristics of the treed patches comprising the ecotone, as well as their spatial relationships. These characteristics can vary considerably in different locations (e.g. Bekker *et al.* 2009). Likewise, the shapes and spatial arrangements of more abrupt treeline boundaries can also vary, as well as their associations with adjacent, above-treeline landcover types. For instance, treeline boundaries range from sinuous to straight, can be densely concentrated in the landscape or relatively spread out, and may be juxtaposed with grasslands, woody shrublands, or non-vegetated landcover types above the treeline. On the whole, such treeline patterns can be indicative of important abiotic factors and underlying processes that drive treeline variability (Wiegand *et al.* 2006). Thus, research aimed at quantifying and analysing treeline patterns across the landscape may provide insight into the possible underlying drivers of treeline variability. This information is critical for understanding the response of alpine areas to anticipated global change (Holtmeier and Broll 2005).

Previous landscape-scale treeline studies have highlighted how different aspects of the abiotic environment, in terms of climate, geology/substrate, topography, and disturbance, influence treeline patterns (Malanson *et al.* 2011). Thermal factors, for example, have been shown to moderate abiotic-biotic interactions at treeline, resulting in differing demographic patterns in different regions (Elliott and Kipfmueller 2010, Stueve *et al.* 2011). In certain landscapes, thermal factors combine with other climatic variables such as precipitation (rain and snow) and wind to cause distinct treeline patterns (Holtmeier 2009). For example Daniels and Veblen (2003) observed that patterns of treeline elevation, tree density, and vegetation cover for *Nothofagus pumilio* treelines in northern Patagonia depended on differences in

climatic regimes between sites on the east and west side of the Andes. Variability in the shapes, sizes, and spatial configurations of mountain ranges, can also greatly affect treeline patterns (Butler *et al.* 2007) by, for example, modifying regional climatic regimes (Caccianiga *et al.* 2008). In addition, variation in geological substrate (e.g. soils and parent materials) affects the availability of moisture and nutrients, deficiencies in which can be apparent at treeline (Loomis *et al.* 2006) and can affect tree physiological function (Gieger and Leuschner 2004). Topographic variability, too, has a strong influence on treeline patterns, largely by modulating the abiotic environment experienced by trees (Butler *et al.* 2009). For instance, slope aspect modifies the amount of solar radiation experienced at treeline which can lead to higher elevation treelines due to increased thermal input (e.g. Danby and Hik 2007; Stueve *et al.* 2011), or cause lower treelines when combined with cold morning temperatures, impairing photosynthesis (Bader and Ruijten 2008). Finally, natural and human disturbances can often play a large role in determining contemporary treeline patterns in some regions (e.g. Daniels and Veblen 2003, Humphries *et al.* 2008), by lowering treelines below limits imposed by other abiotic stressors. While much has been learned about different types of treeline patterns and their causes, studies to date have been diverse in terms of the types of patterns examined and the spatial domains over which investigations were carried out (Malanson *et al.* 2011). Treeline research would thus benefit from approaches that can characterise treeline patterns over large, continuous areas, as well as quantify the relative roles of climate, substrate, topography and disturbance in generating those patterns.

Remote sensing and GIS-based analyses and datasets are critical to mapping treeline patterns in a systematic manner over such large areas. Several previous investigations have explored remote sensing approaches for mapping the transition of land cover types across gradual treeline ecotones (Brown 1994, Baker and Weisberg 1995, Resler *et al.* 2004, Hill *et al.* 2007, Rees 2007, Král 2009). Few studies have extended this type of mapping exercise to characterising treeline patterns quantitatively, and then relating these patterns to abiotic variation with the aim of identifying potential drivers of treeline dynamics. For example, Allen and Walsh (1996) identified six gradual treeline forms using spatial and compositional pattern metrics and then tested for differences in abiotic factors among these forms. Their results suggested that the different treeline patterns arose at least in part due to topoclimatic gradients and differences in natural disturbances and substrate. Similarly, Bekker *et al.* (2009) used patch- and landscape-scale metrics to characterise distinct forest features within Rocky Mountains treeline ecotones; ribbon-shaped patches were identified within the ecotone that reflected the influence of the prevailing wind and microtopographic variation on tree

establishment and development. Such studies indicate that pattern metrics that describe aspects of treeline structure and variability can provide a useful means to examine the interplay between treeline pattern and underlying abiotic variability.

The majority of previous research on treeline pattern to date has focussed on the spatial structure and drivers of gradual treelines, which are more prevalent across treelines globally. Therefore, there is a need for a closer examination of abrupt treeline patterns, particularly as gradual and abrupt treelines are thought to differ with respect to underlying formative processes (Harsch and Bader 2011). In this chapter, a GIS-based approach will be used to develop a range of quantitative metrics to describe patterns of *Nothofagus* treeline variation across New Zealand. Relationships between these patterns and underlying abiotic variation are investigated with the aim of gaining a better understanding of the abiotic conditions structuring variation in these treelines. New Zealand's *Nothofagus*-dominated treelines span seven degrees of latitude, cover a large elevational range, and display considerable local variability that is ostensibly attributable to the vast range of environmental conditions found across the country. This situation thus provides an ideal setting for examining treeline variation in association with abiotic variability. This study addresses the following questions: 1) How do *Nothofagus* treelines vary spatially across New Zealand?; 2) Are there characteristic types of *Nothofagus* treeline patterns?; and 3) What are the relative influences of climate, substrate, topography, and disturbance in structuring these treeline patterns?

2.2 Methods

To address the above study questions, a range of spatial analysis methods, spatial datasets, and statistical analyses were carried out and are described in detail in the following sections. In summary, a range of treeline pattern metrics were used to characterise different aspects of abrupt treelines and their derivation at a landscape scale is described. These landscape-scale treeline metrics formed the basis for the subsequent characterisation of treeline patterns. Secondly, datasets used to define abiotic conditions across *Nothofagus* treeline areas are described. Finally, the statistical analyses for characterising *Nothofagus* treeline patterns and for quantifying relationships with abiotic factors are described.

2.2.1 Description of treeline pattern metrics

Seven metrics for characterising *Nothofagus* treeline pattern across New Zealand were used (Table 2.1). Of these seven, treeline elevation is the only metric previously used in published studies to describe abrupt treeline variation.

Treeline elevation (ELEVATION) – Treeline elevation is defined as the altitude above sea level at which the treeline boundary occurs at a given landscape location. This metric provides an index of the position of a treeline in the landscape relative to other treelines in other locations.

Horizontal and vertical sinuosity (HSIN and VSIN) – Horizontal sinuosity (HSIN) is a metric describing complexity in the shape (degree of curviness) of *Nothofagus* treeline boundaries, as viewed in the horizontal plane. That is, how much does the treeline curve when viewed from above (i.e. a bird’s-eye view). Vertical sinuosity (VSIN) describes complexity in the shape of treelines when viewed from the side.

Adjacent vegetation index (VEGETATION) – This metric is an index of the spatial relationship of *Nothofagus* forest at treeline with adjacent vegetation/landcover types above the treeline. Specifically, the metric is based on the relative proportion of treelines that abut the ‘tussock grassland’ landcover class. Tussock grassland is the dominant vegetated landcover type above the *Nothofagus* treeline across New Zealand, although it is frequently interspersed to varying degrees with four other main landcover types (sub-alpine shrubs, alpine grass/herbfield, alpine gravel and rock) that abut *Nothofagus* forest above treeline in certain areas. Thus, higher proportions of tussock grassland adjacent to *Nothofagus* treelines in a given regions indicates less landcover/vegetation complexity.

Contiguity index (CONTIGUITY) – The contiguity index characterises the relative connectedness of treeline boundaries within a specified neighbourhood zone in the landscape. The contiguity of the *Nothofagus* treeline boundary can be disrupted for a number of reasons. First, species other than *Nothofagus* can form treelines in certain areas where there has been historical disturbance due to anthropogenic (e.g. land clearing for farming) and natural (e.g. landslides) factors. An example of this would be the presence of small patches of mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea ericoides*) trees in dry treeline areas that had been historically cleared or burned for high country farming. Similarly, patches of broad-leaved trees such as *Hoheria sp.* may be found in wetter treeline areas as a pioneer species after natural disturbance such as landslides. Second, gaps in the *Nothofagus* treeline can also

occur in the heads of broad, inland mountain valleys where cold-air ponding and early-morning frosts can limit *Nothofagus* growth and give way instead to subalpine shrubland (Wardle 2008). Thus, large, complex mountain systems with broad valleys might display more treeline gaps than in, for example, coastal valleys that are smaller and where cold air ponding is not evident.

Treeline orientation, relative to slope direction (ORIENTATION) – This index is defined as the direction (azimuth) of treelines relative to the direction of the dominant slope aspect in a region of a specified size. Therefore, this metric describes the overall degree of shift in direction of treelines away from the main ridgeline. At local scales, such shifts in direction may occur where treelines boundaries may be modified by disturbances such as landslides and avalanche chutes, or where there is a high degree landform complexity, such as spur-gully features.

Treeline compactness (COMPACTNESS) – Treeline compactness is defined as the total density of treelines found within a neighbourhood zone of a specified size, and therefore is an index of spatial proximity among treelines in a given landscape. Variation in this index would reflect landscape-scale variation in the size, shape, and configuration of the mountain ranges found in that area. For instance, lower levels of treeline compactness might be indicative of areas where treelines are more widely dispersed along taller, more massive, and less spatially complex mountain ranges, or where disturbance has fragmented treelines. Alternatively, higher treeline compactness might occur in areas where mountains are smaller, less convoluted, and less disturbed.

Table 2.1 A description of the seven pattern metrics developed to characterise spatial variability in abrupt *Nothofagus* treelines.

Treeline pattern metric	Derivation	Descriptor of:
Treeline elevation (ELEVATION)	Mean treeline elevation across all treelines within a landscape zone	Treeline position relative to sea level
Horizontal sinuosity (HSIN)	Mean sinuosity of treeline segments in the horizontal plane within a landscape zone	Treeline edge shape
Vertical sinuosity (VSIN)	Mean sinuosity of treeline segments in the vertical plane within a landscape zone	Treeline edge shape
Adjacent vegetation index (VEGETATION)	The length of tussock grassland edge adjacent to treelines relative to total treeline length within a landscape zone	Spatial relationships of treelines with adjacent vegetation
Contiguity index (CONTIGUITY)	Total length of contiguous (ie connected) treeline segments relative to the total treeline length within a landscape zone	Treeline continuity in the landscape
Orientation index (ORIENTATION)	Total length of treeline edge oriented in ridge direction relative to slope direction within a landscape zone	Complexity of treeline landscape orientation
Treeline compactness (COMPACTNESS)	Treeline line density within a 5km neighbourhood of all treeline segments averaged within a landscape zone	Landscape arrangement and proximity of treelines

2.2.2 Computation of treeline pattern metrics

Nothofagus treelines were delineated across the entire country using the New Zealand Landcover Database 2 (LCDB2), which provides a complete spatial representation of landcover types across New Zealand at the *c.* 1:50,000 scale derived from Landsat satellite imagery (<http://www.mfe.govt.nz/issues/land/land-cover-dbase/>). Using the LCDB2 dataset within a GIS (ArcGIS 9.3), treelines were identified as lines demarcating the polygon boundaries between ‘indigenous forest’ and four subalpine/alpine non-forest landcover classes occurring within the known range of *Nothofagus* species in New Zealand. Only the indigenous forest class was used to define forest; this meant that treelines formed by other possible forest cover types (e.g. mānuka/kānuka, deciduous forest, etc.) were not considered to be treelines for the purpose of this research and these areas essentially became gaps in the *Nothofagus* treeline. As mentioned in the treeline metrics descriptions above, the formation of treeline by non-*Nothofagus* species was relatively uncommon and was generally indicative of situations where past disturbance had removed the pre-existing *Nothofagus* forest. The treeline dataset derived using these methods formed the basis for computing the above-mentioned treeline pattern metrics.

Of the seven treeline pattern metrics used, the two sinuosity metrics (HSIN and VSIN) are fundamentally ‘treeline-segment-level’ metrics: they require fixed-length treeline segments for their computation. HSIN was computed as the ratio of the total length along a treeline line segment in the horizontal plane to the direct Euclidean distance between the start and end points of the line. An HSIN value of 1 would therefore indicate that a line segment is perfectly straight, with progressively larger HSIN values indicating an increasingly sinuous line in the horizontal plane. VSIN was computed in a similar way to HSIN, with the exception that the numerator of the ratio is now the total length of the line segment in the vertical plane. Thus, VSIN = 1 indicates a completely level treeline and progressively larger values of VSIN > 1 indicate an increasingly sinuous line in the vertical plane. These metrics were calculated for three treeline datasets split into 1km, 2.5km, and 5km segment lengths to determine if sinuosity was sensitive to segment length

As a way of computing all seven metrics at a consistent scale across the country, a standard ‘landscape zone’ of a fixed area was used. As a basis for choosing the size of this zone, spatial correlograms for HSIN and VSIN were computed to get an indication of the distances in the landscape at which values for these two metrics become relatively uncorrelated. Correlogram analyses indicated that the two indices become spatially

uncorrelated at distances greater than about 20 kilometres (Appendix A.1). This suggests that, within a distance of 20km, these segment-level metrics are more similar in their values than they are to values to segments more than 20km away. Thus, metrics computed at distances below 20km should be relatively representative of treeline patterns within the local landscape. Based on this, a landscape zone size of 15 km x 15 km was deemed a reasonable area within which to compute all seven treeline metrics in a consistent manner across New Zealand.

A grid of 230, 15 x 15 km square landscape zones was generated in ArcGIS to cover all *Nothofagus* treelines in New Zealand (Figure 2.1). A mean treeline ELEVATION was computed for treelines comprising each landscape zone based on elevation data from a 25 m resolution digital elevation model (DEM) data for New Zealand (Barringer *et al.* 2002). Mean values of HSIN and VSIN for the three segment lengths were calculated from all segments within the landscape zones. The strong correlation for both HSIN and VSIN among the three segment lengths within landscape zones indicated that these metrics were relatively insensitive to segment length. Therefore, HSIN and VSIN values at only the 1km segment length were used for subsequent analyses. The VEGETATION index was computed for each landscape zone by totalling the length of treeline adjacent to tussock landcover polygons and dividing this length by the total treeline length in each landscape. Treeline CONTIGUITY was determined by distinguishing among 1km treeline segments that were connected to two other segments at both ends (i.e. 'contiguous') relative to those that were not connected to other segments at either one or both ends (i.e. 'non-contiguous'). To compute the CONTIGUITY index for each landscape, the number of contiguous segments was summed and divided by the total number of segments within each landscape zone. To compute the ORIENTATION index, an index presented by Dorner *et al.* (2003) was adapted for describing relative patch orientations. First, the angle between the azimuth of each 1km treeline segment and the mean slope azimuth (i.e. the direction of the main ridgeline) at the location of that segment was calculated. Subsequently, the total length of treelines with angles less than 30 degrees (i.e. roughly oriented parallel to slope direction) was divided by the total length of treelines in each landscape zone with angles greater than 60 degrees (i.e. roughly oriented perpendicular to slope direction). To compute COMPACTNESS for each landscape zone, the Line Density tool in ArcGIS 10 was first used to calculate the density of lines within a 5km radius moving window along treelines, producing a line density surface. These density values were then averaged by 15 x 15 km landscape zone.

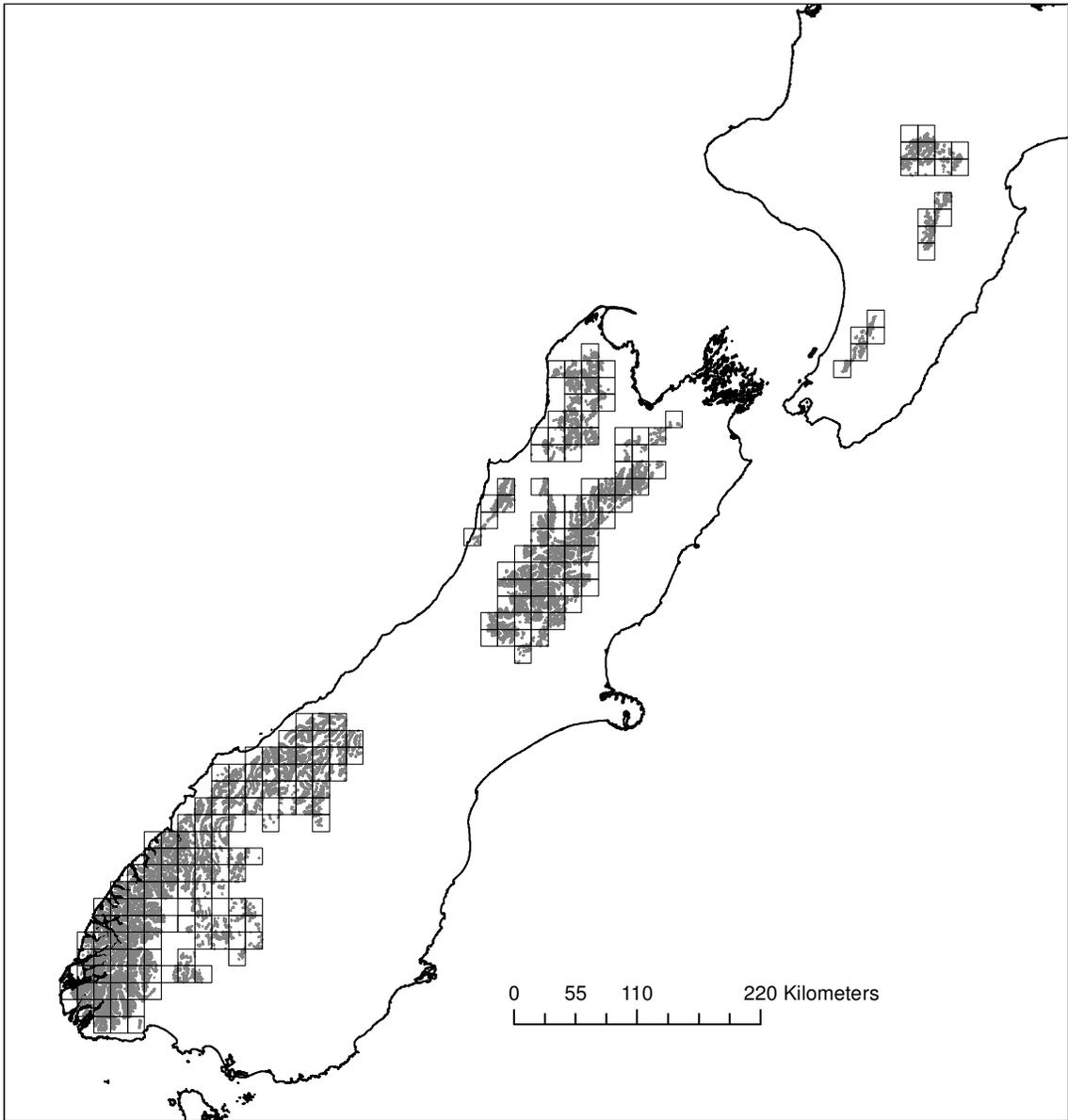


Figure 2.1 Map of 230, 15 x 15km landscape zones (black grid cells) within which spatial patterns of *Nothofagus* treelines (grey areas) were quantified.

2.2.3 Description of abiotic data

A suite of variables representing broad-scale patterns of climate, substrate, topographic variability, and disturbance prevalence was extracted for each of the 230 landscape zones (Table 2.2, and Appendix A.2). These data formed the basis for subsequent analyses of relationships between treeline pattern and abiotic variation.

Climate data – The climate data consisted of landscape zone mean values for factors describing the main climatic gradients across the study area: mean annual temperature (MAT), mean annual global solar radiation (SOLRAD), the number of frost days per year (FROST), mean annual wind speed (WIND), and mean October vapour pressure deficit (VPD). These data were extracted from spatially-explicit, long-term climate data grids for New Zealand (Leathwick *et al.* 2002a, Wratt *et al.* 2006).

Substrate data – The substrate data consisted of landscape zone mean values for factors related to broad gradients in dominant rock and surface material variability and soil types. Two diversity indices, rock type diversity (ROCK_DIV) and soil type diversity (SOIL_DIV), were computed. To do this, areal proportions of the different rock and soil types occurring within each landscape zone were extracted in the GIS from the New Zealand Land Resource Inventory dataset (NZLRI; Newsome *et al.* 2000) and the Shannon diversity index was then computed using the ‘diversity’ function within the package ‘Vegan’ in R (Oksanen *et al.* 2013). Next, landscape zone means of data for four ordinal variables representing coarse spatial patterns of soil parent material variability: soil particle size (PSIZE), soil drainage (DRAINAGE), calcium availability (CALC), and phosphorous availability (PHOS) were extracted in the GIS from the Land Environments of New Zealand (LENZ) dataset. Data for these factors were based on coarse-level information regarding the distribution of dominant soil parent materials occurring across the country (Leathwick *et al.* 2002b). Data for these four factors were the best available for representing overall broad patterns of substrate variation occurring across the study area and their use was therefore not directed at investigating the importance of a particular soil property (e.g. particle size) or nutrient (e.g. calcium).

Topography data – Four variables were used to characterise topographic shape and variability within landscape zones. An index of ‘mountain mass’ (M_MASS) was computed in the GIS as the total area of land occurring above 1200m within each landscape zone. Within each

landscape zone, elevation range (ELEV_RANGE) was computed using the New Zealand 25m resolution DEM as the difference between the maximum and minimum elevation in each zone. A raster dataset characterising different landform types (e.g. ridge, spur, backslope, footslope etc.) across New Zealand (Barringer *et al.* 2008) was used to compute a mean landform diversity index (LF_DIV) for each landscape zone, using the same method as for rock and soil type diversity described previously. Further, the ratio of the total area of divergent landform elements to that of convergent landform elements (DIV_CONV) within each landscape zone was computed.

Disturbance data – The relative amount of disturbance in each landscape zone was characterised using three factors: erosion severity (EROSION), the variety of landcover types (LC_VAR), and relative earthquake intensity (EQ_INTENS). The mean degree of erosion severity was extracted from the NZLRI dataset, where erosion severity is an ordinal ranking from 0 (negligible) to 5 (very severe), and includes a range of erosion types such as debris avalanches, earth flows and slips, scree slopes, and mudflows, which are all indicative of the prevalence of historical natural, and possibly anthropogenic, disturbance. The variety of landcover types within each landscape zone was extracted from the LCDB2 dataset. This factor is particularly indicative of human disturbance, as more landcover types occur, on average, in areas where humans have modified the landscape, such as along the outside edges of *Nothofagus* treeline areas (see map in Appendix B). Mean earthquake intensity for each landscape zone was extracted from a spatially-explicit grid of the expected mean peak ground acceleration (PGA) within a 150 year return interval across New Zealand, expressed as the proportion of the acceleration due to gravity (Stirling *et al.* 2002). Earthquake intensity is an indication of the likelihood of major catastrophic disturbances such as landslides.

Table 2.2 A summary of the 20 abiotic factors extracted for each of the 230 treeline landscape zones.

Acronym	Factor category	Factor description
MAT	Climate	Mean annual temperature
SOLRAD	Climate	Annual global solar radiation
VPD	Climate	Mean October vapour pressure deficit
FROST	Climate	Number of annual frost days
WIND	Climate	Average annual wind speed
M_MASS	Topography	Index of mountain mass
DIV_CONV	Topography	Ratio of divergent to convergent
ELEV_RANGE	Topography	Total elevation range
LF_DIVERSITY	Topography	Landform diversity
ROCK_DIV	Substrate	Diversity of rock types
SOIL_DIV	Substrate	Diversity of soil types
PHOS	Substrate	Index of phosphorous availability
CALC	Substrate	Index of calcium availability
P_SIZE	Substrate	Index of particle size
DRAIN	Substrate	Index of soil drainage
EQ_INTENS	Disturbance	Earthquake intensity
EROSION	Disturbance	Erosion severity index
LC_VAR	Disturbance	Landcover variety

2.2.4 Data analysis

A number of data analyses were carried out to address the research questions. First, I used ordination and clustering of the seven treeline pattern metrics to investigate treeline pattern spatial variability across New Zealand. The aim of this analysis was to determine whether these metrics together define different treeline types in multivariate space. The clustered treeline types were then mapped spatially to determine the nature of their spatial patterns across the country. Second, I used spatial regression and multivariate RDA techniques to look at how variability in treeline pattern metrics were related to abiotic variation across the 230 treeline landscapes. Overall, a ‘typology’ of *Nothofagus* treelines across New Zealand was described for New Zealand, interpreted using information gathered from the above analyses. All data analyses were carried out using R statistical software version 2.15.2 (R Core Team 2012).

Cluster analysis of treeline pattern metrics into treeline ‘types’

To create a typology of *Nothofagus* treelines across New Zealand, a cluster analysis of treeline pattern metrics computed for the 230 landscape was carried out. An agglomerative hierarchical clustering procedure was employed (“hclust” function in R), using Euclidean distances as a measure of dissimilarity among metrics in multivariate space and using Ward’s linkage algorithm for cluster creation. In an agglomerative hierarchical clustering analysis, a cluster “tree” or dendrogram is produced based on the dissimilarity among observations in multivariate space, whose branches are the clusters produced by the clustering algorithm employed. Observations grouped on different branches of the tree are more dissimilar than those on other branches of the tree. Branch lengths indicate the degree of dissimilarity of observations on a given branch relative to those on the neighbouring branch below a given split on the dendrogram. A dendrogram contains as many clusters as there are observations on the lowest branches of the tree and a decision is therefore required on how many clusters best describe the natural groupings inherent in the dataset and, thus, where to cut the dendrogram to obtain informative groupings or clusters of observations. To determine the optimal cluster size at which to cut the dendrogram, I examined how variation in two statistics measuring the strength of cluster membership (average silhouette width and Pearson’s gamma) varied with cluster size, from five to 12 clusters. Average silhouette width is a statistic that indicates the overall degree of membership of all observations to their assigned clusters, and is computed as the average distances between each observation and all observations of a given cluster, compared to the same measure computed for the next closest

cluster, averaged over all observations (Borcard *et al.* 2011). Pearson's gamma is based on a Mantel correlation between the original distance matrix and binary matrices computed from the dendrogram cut at different levels (Borcard *et al.* 2011). For both analyses, the number of clusters producing the highest test statistic was used to determine the most appropriate cut level.

To determine if the final cluster groups after cutting could be considered "distinct" from each other (i.e. well-separated), observations comprising each cluster group were labelled on PCA reduced space bi-plots of the treeline metrics dataset. These plots provide an indication of how the different clusters show separation in PCA multivariate space and thus how well the metrics that best define particular PCA axes were able to differentiate among clusters. Univariate statistical distributions of each of the metrics comprising each cluster group were then plotted using boxplot diagrams to provide a means to determine which metrics best-differentiated each cluster group. To examine the pattern of spatial aggregation of the cluster groups, clusters were plotted spatially by linking each observation back to its original treeline landscape zone in the GIS. Ultimately, the box plot summaries, the GIS-based maps of clusters, and GLS model results for the different pattern metrics, were used to interpret clusters and develop a descriptive typology of *Nothofagus* treelines in New Zealand.

Associations among abiotic factors and treeline pattern metrics

Generalised least squares (GLS) regression (R package "nlme"; Pinheiro *et al.* 2009) was used to look at the relationship between each of the seven individual treeline pattern metrics and the four sets of abiotic factors representing the effects of climate, substrate, topography, and disturbance. Given the spatially contiguous nature of many of the 230 treeline landscapes, GLS models incorporating five different spatial covariance structures (linear, spherical, Gaussian, exponential, and ratio) were run to account for possible spatial autocorrelation issues in computing regression parameters (Crawley 2007). The five models including a correlation structure were compared against a GLS model that did not include a spatial correlation structure, to determine which of the six model structures provided the best fit to the data. The best-fit model for each pattern metric was then compared among the four abiotic factor sets (i.e. climate, substrate, geomorphology, and disturbance) to infer the relative importance of these four influences in describing variability in the seven metrics. An intercept-only model was also included for comparison to indicate whether the four abiotic factor models were informative relative to a null scenario. Model comparisons were carried

out using the AICcmodavg R package (Mazerolle 2011) based on AIC_c values and Akaike weights (AIC_cWt) for each model. Models with lower AIC_c and higher AIC_cWt values were considered as having relatively more support (Anderson 2008).

Variance partitioning of abiotic influences on treeline pattern metrics

To investigate the overall relative amounts of variation explained by climate, substrate, topography, and disturbance in the multivariate spatial patterns of treeline pattern metrics, a canonical redundancy analysis (RDA) and variance partitioning using the ‘varpart.MEM’ function in R, as described by Legendre *et al.* (2012). In essence, the RDA method combines multiple regression and principle component analysis (Borcard *et al.* 2011), whereby the method seeks a series of linear combinations (ie axes) of the explanatory factors that best describe variation in the response matrix (Borcard *et al.* 2011). The varpart.MEM function allows this multivariate regression to be constrained by two to four different matrices of explanatory factors and, hence, can be considered a partial, multivariate regression (Borcard *et al.* 2011). The output from this analysis is a breakdown of how much total variation in the response variable is explained by each of the explanatory matrices alone, as well as for each matrix while holding the effects of the other explanatory matrices constant (Legendre *et al.* 2012). This enables the computation of the individual amounts of variation explained by each explanatory matrix, as well as amount of explained variation shared among all of the explanatory matrices (Legendre *et al.* 2012). As a further step, I used Principle Coordinates of Neighbour Matrices (PCNM) within the varpart.MEM function to investigate the extent to which variation in treeline metrics across the landscape zones is spatially-structured (Borcard *et al.* 2011). The PCNM analysis deconstructs the matrix of geographic distances among all pairs of landscapes into orthogonal eigenvectors, via principal coordinates analysis (PCoA), that describe all possible scales of spatial variation present in the distance matrix (Borcard and Legendre 2002). This matrix of eigenvectors can then be used in the RDA variance partitioning framework to describe spatially-structured variance in the response matrix.

RDA and variance partitioning of the treeline pattern metrics as the response matrix against the four multivariate matrices of explanatory factors (i.e. the climate, substrate, topography, and disturbance factor matrices) was carried out. This procedure was then repeated using two explanatory matrices: one with all of the combined abiotic variables and another containing the PCNMs representing the effect of ‘space’, using only the PCNMs that were found to be significantly related to the response matrix based on a forward variable

selection procedure (Blanchet *et al.* 2008).

2.3 Results

2.3.1 Treeline pattern metric variability

There was considerable variation in the seven treeline pattern metrics across the 230 treeline landscape zones (Table 2.3). Horizontal sinuosity (HSIN) varied from 1.5 to 3, indicating that treeline segments are 50% to 300% more curvy relative to a straight line. Vertical sinuosity (VSIN) varied from 1.02 to 1.2 across the study area, meaning that treeline segments in some areas display as little as 2% vertical variation relative to a straight horizontal line, while other areas display up to 20% variation from a straight treeline. Mean treeline elevation was highly variable across the 230 landscapes, ranging from a low of about 560 metres above sea level (masl) to a high of almost 1400 masl. Treeline densities range from less than 200m of treeline length per 1km² area up to almost 1500m of treeline per 1km² area. The proportion of adjacent tall tussock grassland, as an index of variability in adjacent vegetation along treelines, varied from no tussock grassland in some landscape zones up to 99% adjacent tussock vegetation. Treeline contiguity varied from under 50% of 1km treeline segments being connected on both ends to other treeline segments in some landscape zones to perfect contiguity of all treeline segments in others. Lastly, landscape zones varied in the degree to which treeline segments were oriented in the direction of the ridgeline versus the slope direction; values ranged from a high degree of orientation in the slope direction (low index values) for a few landscapes to landscapes primarily oriented in the direction of the main ridgeline (high index values). Further, there were differing patterns of spatial variation in the treeline metrics across the study area (Figure 2.2).

Table 2.3 Descriptive statistics of the seven treeline pattern metrics across the 230 treeline landscapes in New Zealand.

Treeline metric	Minimum	Maximum	Mean	S.D.
Treeline elevation	563.5	1385.4	1032.0	183.6
Horizontal sinuosity	1.510	3.024	2.118	0.352
Vertical sinuosity	1.017	1.232	1.111	0.033
Adjacent vegetation index	0.000	0.989	0.553	0.212
Contiguity index	0.439	1.000	0.836	0.122
Orientation index	0.670	24.000	4.905	3.310
Treeline compactness	0.137	1.462	0.756	0.258

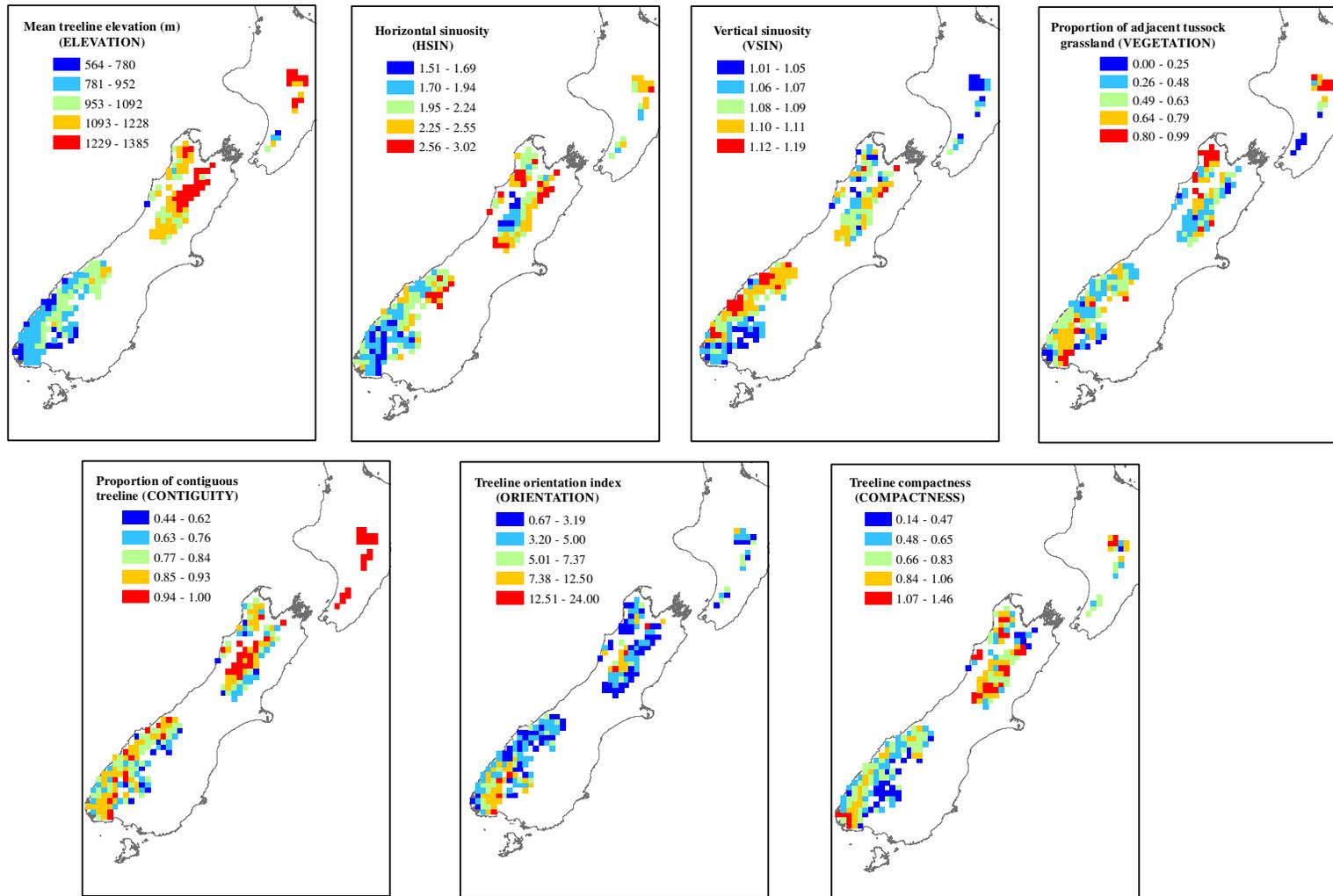


Figure 2.2 Maps showing the spatial distribution of mean treeline metric values for 230, 15x15km treeline ‘landscapes’ across New Zealand. Values range from low (blue colours) to moderate (light green) to high (orange/red colours).

2.3.2 Cluster analysis of *Nothofagus* treeline pattern metrics

The dendrogram produced based on a cluster analysis of the seven treeline metrics indicated that there were approximately five to twelve distinct cluster groupings separated by relatively-long branch lengths (Figure 2.3). Plots of average silhouette width and Pearson's gamma statistics against the number of clusters (Figure 2.4) suggested that a seven cluster solution was an appropriate cut-off threshold for producing relatively distinct clusters (Figure 2.3). Plotting the seven clusters back onto a reduced-space PCA biplot verified that there was clear among-cluster separation (Figure 2.5). This suggests that the seven clusters can be reasonably-well differentiated by metrics that define different portions of the multivariate space. Boxplots of each treeline pattern metric by cluster group showed that strong differences existed among most of the clusters for different metrics, such that there was typically at least one metric, or a combination of two or three metrics, that best-differentiated a given cluster relative to the other clusters (Figure 2.6). Spatial mapping of the observations comprising different cluster groups indicated that clusters were distinctly spatially aggregated across the study area (Figure 2.7). An overall descriptive typology for New Zealand's *Nothofagus* treelines is presented in Table 2.4.

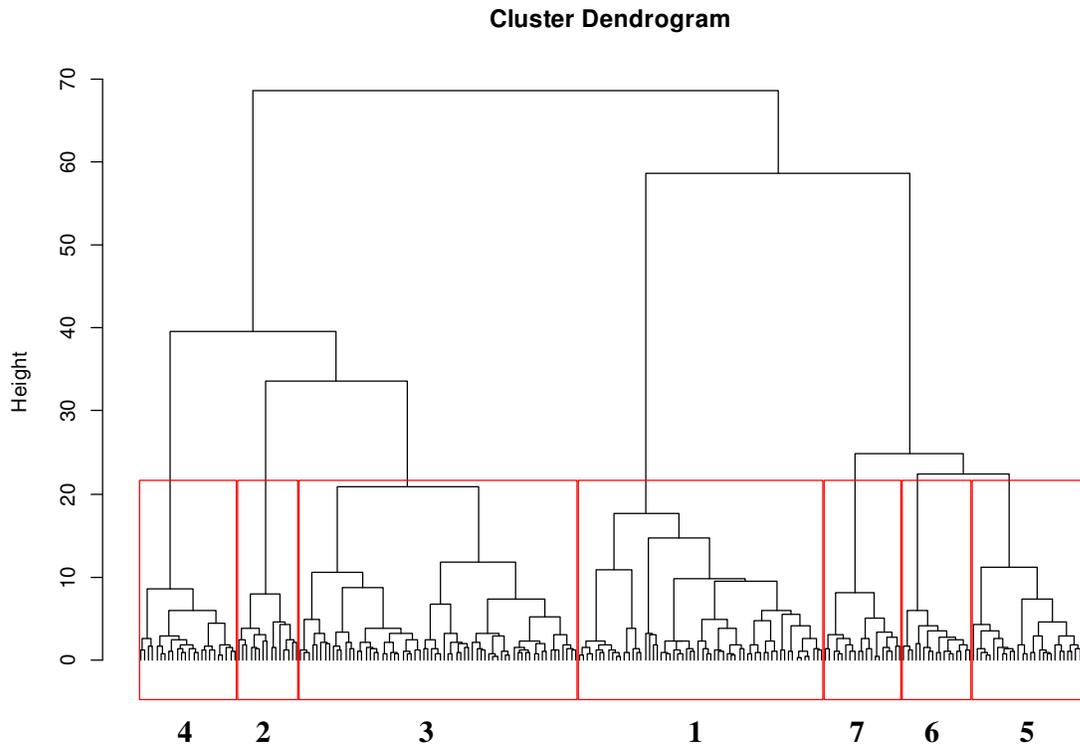


Figure 2.3 Cluster dendrogram for cluster analysis of the 230 treeline landscape zones using Euclidean distances and Ward’s linkage method. Rectangles delimit the seven clusters deemed to characterise relatively distinct *Nothofagus* treeline types in New Zealand. Numbers refer to the different treeline cluster types, as described in Table 2.4.

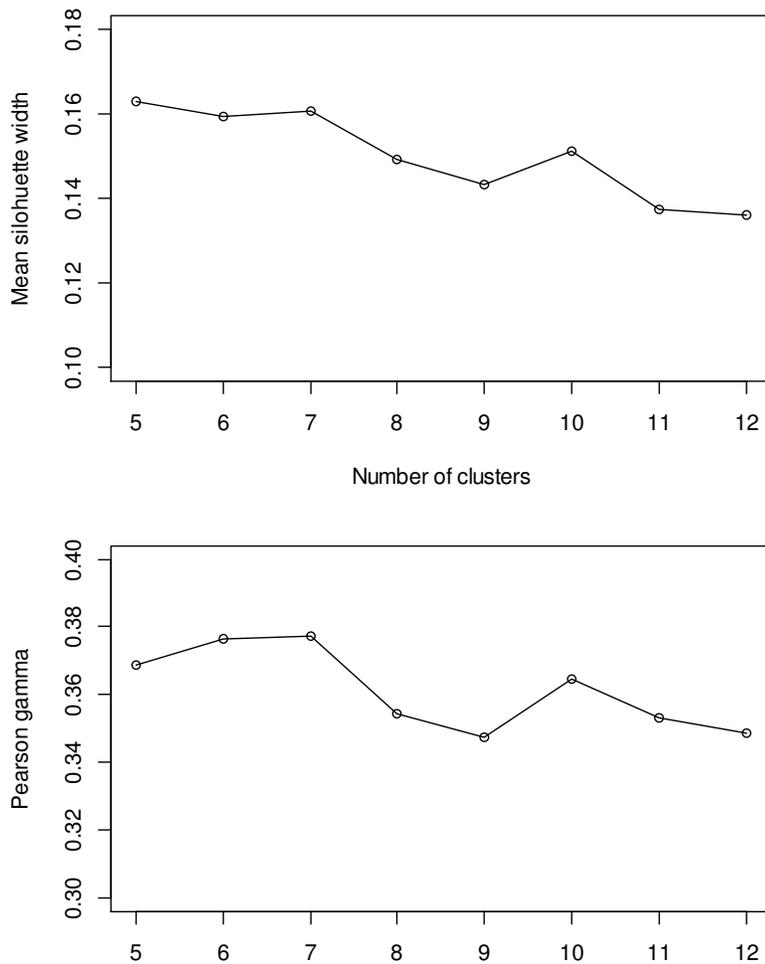


Figure 2.4 Change in two cluster separation metrics, mean silhouette width and Pearson's gamma, plotted against a range of possible cluster groupings. Higher values for both metrics indicate higher within-cluster homogeneity and between-cluster differences. Therefore, seven clusters provide the best partitioning solution.

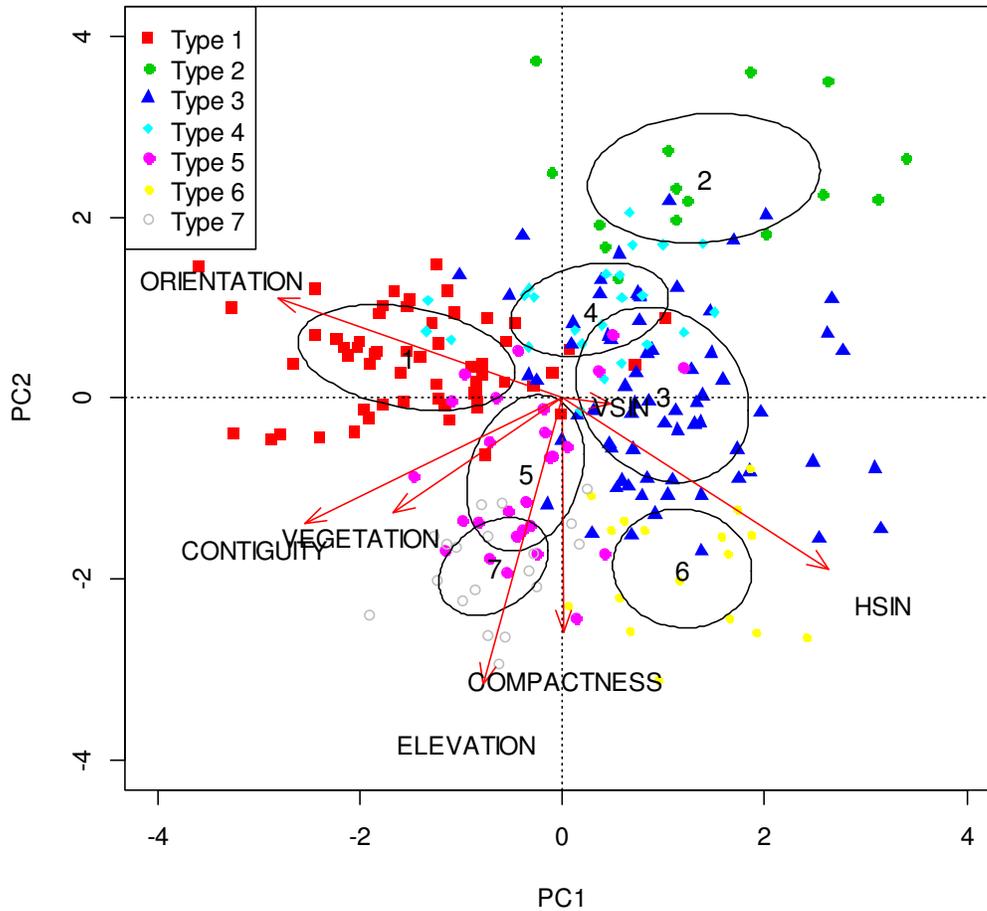


Figure 2.5 The seven cluster groups plotted on a principal component reduced space biplot of treeline metrics for the first two principal component axes. Observations (i.e. landscapes, $n = 230$) are coloured based on membership in one of the seven treeline type clusters. Also overlaid are standard deviation dispersion ellipses based on PCA site scores for each cluster.

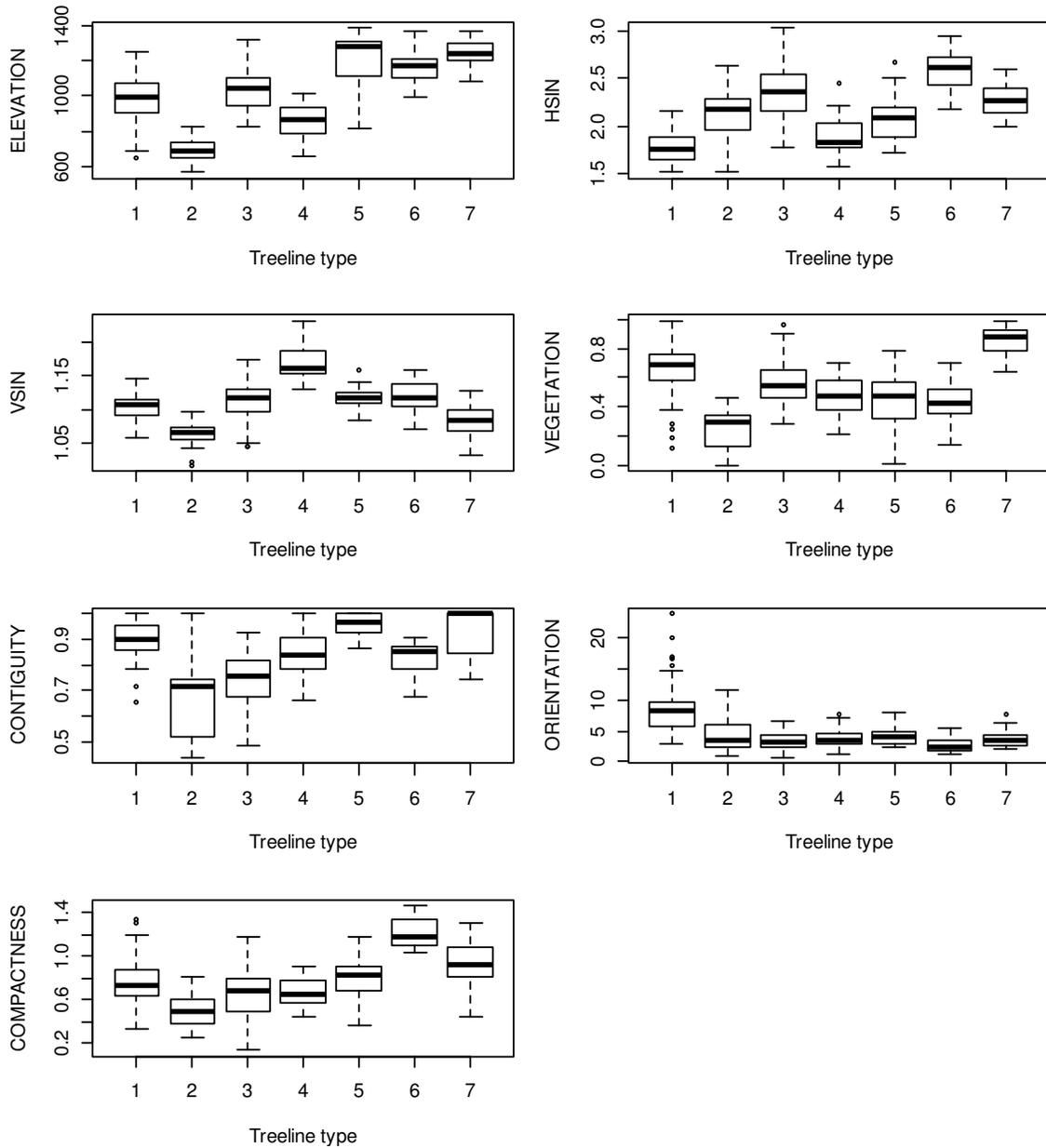


Figure 2.6 Boxplots showing the statistical distributions of the 12 treeline metrics by treeline cluster types.

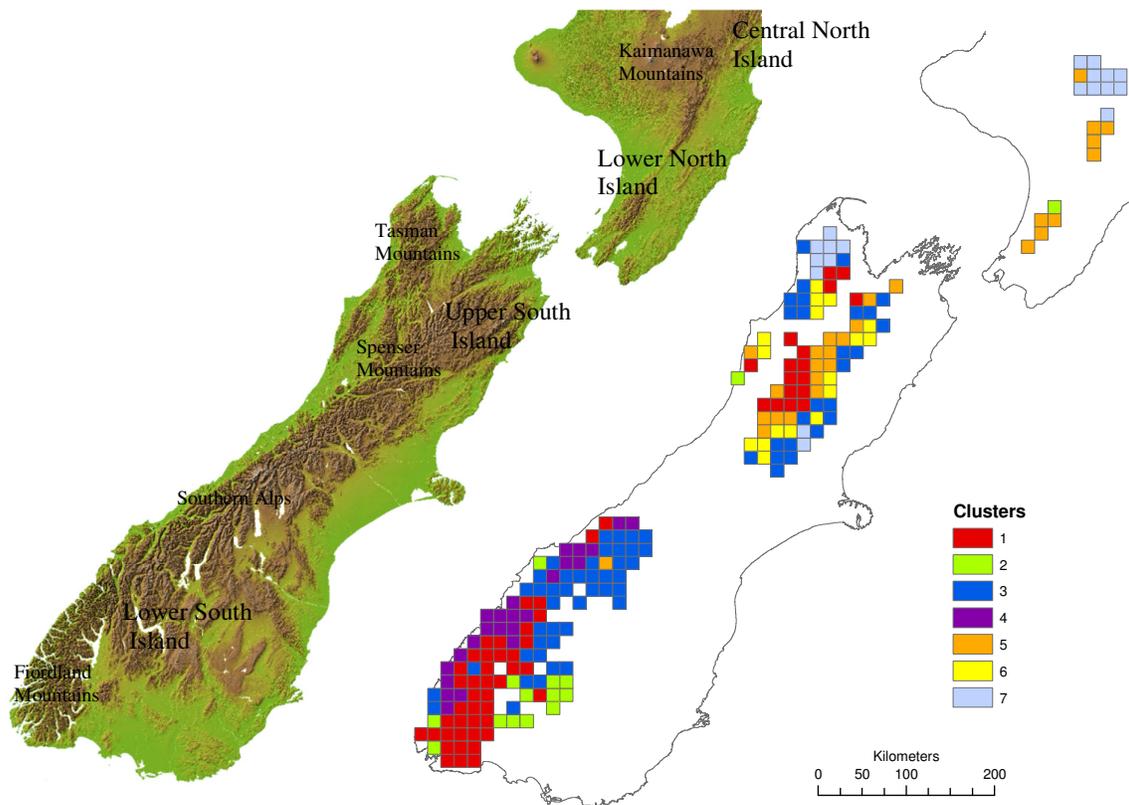


Figure 2.7 On the left is a context map highlighting the main mountain ranges and regions within the study area. The map on the right displays the spatial distributions of the seven treeline clusters across the study area. Due to the proximity of treelines to the coastline in some areas, portions of several grid cells extend beyond the coastline, although this portion of the cell area was removed from analyses. Refer to Table 2.4 for a description of the different treeline types.

Table 2.4 Description of *Nothofagus* treeline types across New Zealand (see Figure 2.7 for a map of these types).

Type	Key pattern metrics	Interpretation
1 <i>n</i> = 60	Mean ELEVATION: 997 m Lowest HSIN Highest ORIENTATION High VEGETATION, CONTIGUITY	Type 1 treelines are located across the main Fiordland mountain ranges. The dominant characteristics of these treelines are indicative of a cool thermal regime, a low degree of geomorphologic complexity of these mountains, and low levels of local disturbance.
2 <i>n</i> = 15	Mean elevation: 697 m Lowest VSIN, COMPACTNESS, VEGETATION, CONTIGUITY High: ORIENTATION	Type 2 treelines are located mainly along the eastern mountains of the lower South Island. This type largely consists of small treeline fragments in lower-elevation ranges that have largely been affected by clearing of vegetation for high-country farming.
3 <i>n</i> = 68	Mean ELEVATION: 1035 m High VSIN Low CONTIGUITY, ORIENTATION	Type 3 treelines make up a large portion of the Southern Alps region and are also found along the outer edges of the mountains of the upper South Island. Dominant characteristics of these treelines suggest an important influence of complex local topography and disturbance.
4 <i>n</i> = 24	Mean ELEVATION: 857 m Low HSIN Highest VSIN	Type 4 treelines are located along lower-lying mountains of western Fiordland and the western Southern Alps. The dominant characteristics of these treelines are similar to Type 1 treelines but suggest greater local topographic complexity and disturbance.
5 <i>n</i> = 27	Mean ELEVATION: 1203 m Highest CONTIGUITY High VSIN	Type 5 treelines are found in the tall central mountain ranges of the upper South Island and lower North Island. Dominant characteristics indicate continental thermal regime, low levels of local disturbance, yet variable local topography.
6 <i>n</i> = 17	Mean ELEVATION: 1177 m Lowest ORIENTATION Highest HSIN, COMPACTNESS High VSIN	Type 6 treelines are found scattered throughout parts of the upper South Island mountains. Dominant characteristics of these treelines suggest the influence of large, structurally-complex mountain ranges with variable local topography and potentially high levels of local disturbance.
7 <i>n</i> = 19	Mean ELEVATION: 1241 m Low VSIN High HSIN, CONTIGUITY, COMPACTNESS Highest VEGETATION	Type 7 treelines are located in the Tasman Mountains region of the northwest South Island and the Kaimanawa Range of the central North Island. Dominant characteristics of these treelines suggest the influence of large, warm mountain ranges with relatively low topographic variability.

2.3.3 Abiotic influences on treeline pattern

For each treeline pattern metric, GLS models incorporating a spatial correlation structure consistently ranked more highly, based on AIC_c , than models without a spatial correlation structure (Appendix A.3), indicating the presence of substantial spatial autocorrelation in the landscape-scale data. There was no evidence of trends in the residuals of the best-ranked regressions for each pattern metric, suggesting that the correlation structures effectively accounted for the effect of spatial autocorrelation in the models.

Based on AIC_c model comparisons, models including abiotic factors as explanatory variables strongly out-ranked the intercept-only models for all treeline metrics (Table 2.5). On the whole, disturbance factors were the most informative in terms of describing spatial variation in the treeline metrics, comprising the top-ranked model for four out of seven metrics (HSIN, VEGETATION, CONTIGUITY, ORIENTATION). For ELEVATION and COMPACTNESS, the climate model ranked the highest, while the topography model was the most informative for describing variation in VSIN.

The canonical redundancy analysis with variance partitioning indicated that 47% of the total variance in a multivariate matrix of the seven treeline metrics could be explained based on the climate, substrate, topography, and disturbance datasets (Figure 2.8a). Individually, each of the explanatory factor datasets explained between 26 and 38% of the variance in the response data. The amount of ‘pure’ variation explained by the climate dataset alone, after accounting for the effects of the other three explanatory datasets, was 9%, while the pure effects of the substrate, topography, and disturbance datasets were 2%, 3%, and 3%, respectively (Figure 2.8A). There was a considerable amount of shared variation among all datasets (17%). The inclusion of significant PCNM eigenvectors into the variance partitioning indicated that 30% of the 47% of variance in treeline metrics explained by the abiotic factors is spatially structured, while 17% is not spatially structured. An additional 9% of the variance in treeline metrics can be explained by spatial structure unaccounted for by the explanatory variables (Figure 2.8B). In total, abiotic and spatial factors could together explain 56% of the variation in the multivariate treeline metric dataset.

Table 2.5 Comparison of five alternative models describing variability in each of seven treeline pattern metrics across 230, 15x15 km landscape zones. Modelling used generalised least squares (GLS) regressions incorporating autocorrelation structures to account for spatial autocorrelation. ΔAIC_c and Aikaike weight ($AIC_c Wt$) values indicate the contribution of each model towards describing variability in a given pattern metric, with higher ranked models displaying lower ΔAIC_c and higher $AIC_c Wt$ values. K is the number of model parameters.

Response	Model	K	AIC_c	ΔAIC_c	$AIC_c Wt$
Treeline elevation	Climate	9	2673.557	0	0.814
	Substrate	10	2676.559	3.002	0.181
	Topography	9	2683.99	7.43	0.015
	Disturbance	7	2702.69	26.13	0
	Intercept-only	2	3046.72	370.16	0
Horizontal sinuosity	Disturbance	7	10.59	0	0.702
	Climate	9	12.37	1.78	0.289
	Topography	9	19.33	8.73	0.009
	Substrate	10	30.98	20.38	0
	Intercept-only	2	181.22	170.63	0
Vertical sinuosity	Topography	9	-1071.17	0	0.999
	Disturbance	7	-1057.51	13.66	0.001
	Climate	9	-1045.05	26.12	0
	Substrate	10	-1019.67	51.50	0
	Intercept-only	2	-898.29	172.88	0
Adjacent vegetation index	Disturbance	7	-155.19	0	0.978
	Climate	9	-146.61	8.58	0.013
	Substrate	10	-144.89	10.30	0.006
	Topography	9	-143.39	11.79	0.003
	Intercept-only	2	-50.41	104.78	0
Contiguity index	Disturbance	7	-371.65	0	0.988
	Climate	9	-362.64	9.01	0.011
	Topography	9	-357.80	13.85	0.001
	Substrate	10	-339.10	32.55	0
	Intercept-only	2	-305.04	66.61	0
Orientation index	Disturbance	7	1156.32	0	0.92
	Substrate	10	1162.02	5.70	0.053
	Climate	9	1163.69	7.37	0.023
	Topography	9	1167.16	10.8	0.004
	Intercept-only	2	1207.62	51.30	0
Treeline compactness	Climate	9	-66.42	0	0.972
	Disturbance	7	-59.30	7.11	0.028
	Topography	9	-51.16	15.26	0
	Substrate	10	-36.44	29.97	0
	Intercept-only	2	38.23	104.65	0

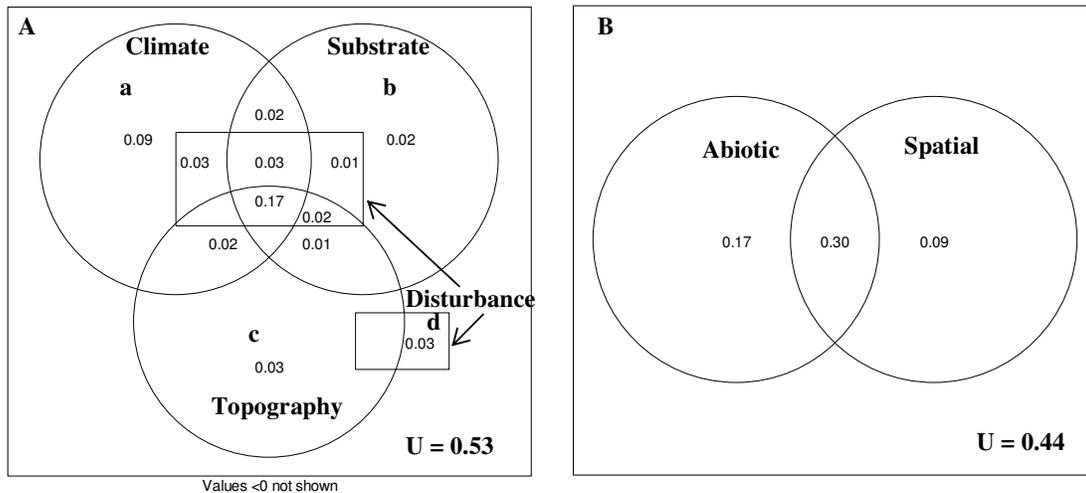


Figure 2.8 (A) Variance explained by a redundancy analysis (RDA) relating variation in a matrix of the seven treeline metrics to four matrices of abiotic factors: climatic, geologic, topographic and disturbance (as detailed in Table 4). U is the unexplained variance; a-d relate to the pure effects of each set of abiotic factors. The total of each circle represents the portion of variance explained for a given factor. The overlapping portions of the circles/rectangles indicate the amounts of shared variation amongst different combinations of the four sets of abiotic factors. (B) Variation explained by an RDA relating variation in the seven treeline metrics to two explanatory matrices: a matrix of all abiotic factors from A combined (Abiotic variation), as well as a matrix of significant spatial eigenvectors derived from a principle coordinates of neighbour matrices (PCNM) analysis of the 230 treeline landscapes (Spatial variation). See Methods text for further information.

2.4 Discussion

This chapter offers three unique contributions to the growing body of research on landscape-scale treeline variation: (1) the use of novel metrics to describe abrupt treeline patterns across large spatial extents, (2) the classification of New Zealand's *Nothofagus* treelines, and (3) an extensive, nation-wide analysis of landscape-scale *Nothofagus* treeline patterns in relation to abiotic variability.

A GIS-based approach was used to describe landscape-scale spatial patterns in *Nothofagus* treelines across the full extent of these treelines in New Zealand. This was achieved through the derivation and use of seven metrics describing landscape-scale variation in treeline shape, treeline orientation, treeline elevation, spatial relationships among treelines, and spatial relationships between treelines and adjacent vegetation. Results show that the seven treeline metrics produce different patterns of *Nothofagus* treeline variation across New Zealand (Figure 2.2) and, together, result in distinctive treeline types that are spatially clustered across the country (Figure 2.7). Further, treeline patterns are evidently associated with abiotic variation (Table 2.5 and Figure 2.8). Overall, results suggest that: 1) these metrics are useful for characterising differing facets of *Nothofagus* treeline variability, and 2) treeline variability is structured by different aspects of the abiotic environment across New Zealand.

Nothofagus treeline patterns are the result of complex and interacting abiotic influences. Results from redundancy analyses followed by variance partitioning show that explained variability in the seven pattern metrics, together, is largely shared amongst climate, substrate, topographic, and disturbance factors (Figure 2.8). This outcome is corroborated by the GLS regressions (Table 2.5); climate, disturbance, topography, and substrate models were each most highly ranked for at least one pattern metric and, for the treeline elevation and horizontal sinuosity metrics, the top two models were informative based on Akaike weights. It is widely recognised that treelines have highly spatially-variable and that this variability is also dependent on the underlying abiotic template (Malanson *et al.* 2007). Indeed, treeline patterns can be generated by different processes, the relative roles of which are modulated by characteristics of the local mountain environment (Holtmeier and Broll 2005). Regional geologic history and past and present geomorphological processes largely drive mountain structure which, in turn, provides the template for landscape-scale climatic, topographic and disturbance variability (Butler *et al.* 2007). For instance, in New Zealand's lower South Island, there is a clear difference in the mountain structure of the Fiordland mountain ranges

and those of the eastern Southern Alps. The highly-glaciated Fiordland mountains are underlain by erosion-resistant rocks such as gneiss and granite (Wood 1962), while those in the Southern Alps region are mainly composed of greywacke that is undergoing continual uplift and erosion processes (Graham 2008). These different underlying geologies result in considerable differences in the abiotic environment of these two areas, ultimately producing distinctive treeline patterns. While treelines in these two zones are of a similar mean elevation, the Fiordland region (treeline Type 1) is characterised by relatively straight, contiguous, and undisturbed treelines, as compared to the sinuous and more discontinuous treelines characteristic of the Southern Alps (treeline Type 3). Thus, the seven *Nothofagus* treeline types described in this study are associated with distinct mountain environments characterised by differing abiotic factors. Treeline pattern metrics may therefore provide a synthetic description of treelines and their abiotic environments that could be used to infer the possible processes that may drive treeline variability in different landscapes (Allen and Walsh 1996).

Climate exerts well-recognised broad-scale influences on treeline patterns, influencing treeline position (Körner and Paulsen 2004) and treeline ecotone dynamics and form (Harsch *et al.* 2009). Results from the present study are consistent with the importance of climatic influences on treeline; climate variables accounted for the largest portion of independent variance explained in the multivariate analysis and ranked highly in GLS regressions in terms of explaining patterns of treeline elevation, horizontal sinuosity, and treeline compactness. Considerable importance was also attributed to the effect of disturbance on *Nothofagus* treeline variability; disturbance factors comprised the top-ranking explanatory models for four of seven metrics. The impact of past disturbance on treeline is often localised in nature, manifesting as lowered treeline positions due to avalanches, earthquake-induced landslides, erosion, and human-based disturbances such as the clearing and burning of forests for farming (Holtmeier 2009). Results from this study indicate that there is a strong, emergent landscape-scale signal of these types of historical disturbance effects on different aspects of *Nothofagus* treeline variability, including the shape, orientation, and contiguity of treelines, as well as the prevalence of tussock grassland as the dominant adjacent vegetation type. Indeed, this effect coincides with different treeline cluster types, such as those situated on the eastern edges of the main South Island mountain ranges that interface with high-country farming lands (e.g. treeline Type 2) or comprise steep mountains of weathered greywacke (e.g. treeline Type 3) that are known for their susceptibility to mass movement disturbances (Crozier 1986). The relative importance attributed to disturbance in this study is consistent with evidence from

other studies indicating that present-day patterns of many treelines around the world are the result of legacy disturbance effects rather than, or additional to, contemporary climatic effects (Sarmiento and Frolich 2002, Holtmeier and Broll 2007).

Topography and substrate factors were not highly ranked, on the whole, for their ability to explain variation in the individual pattern metrics (Table 2.5). Topographic factors comprised the top-ranked model for one pattern metric, vertical sinuosity. Treelines that display high vertical variability are therefore likely to be found in regions with high local topographic variation (treeline Types 3, 4, and 5). The substrate model was not highly-ranked for any of the seven pattern metrics. Substrate variables used in this study describe broad scale variation in rock and soil conditions across the study, and the relatively weak association of these variables with treeline pattern may simply indicate that these factors are not highly influential on *Nothofagus* treelines, or that other substrate-related variables not included in the analyses may be more important. Nonetheless, although not ranked as highly as climate and disturbance, substrate and topographic variables contributed to the overall explanation of multivariate treeline pattern variation (Figure 2.8). Substrate-related influences have been shown to be highly important in driving treeline patterns elsewhere at local scales (Resler 2006, Butler *et al.* 2009, Holtmeier and Broll 2012), and it may be that these effects are less distinct at the relatively large spatial resolution and extent at which analyses were carried out in this study.

There have been very few spatially-extensive analyses of landscape-scale treeline pattern that have employed descriptive metrics (Baker and Weisberg 1995, Allen and Walsh 1996, Weiss 2009, Bekker *et al.* 2009), and this present study represents the first to describe abrupt treelines using landscape analysis approaches. The use of multiple pattern metrics across a wide range of abiotic variation enables the development of a more comprehensive picture of treeline variation across the landscape than would be possible with data collected at small, disparate sites. Thus, the GIS-based, landscape-scale approach used in this study fills a gap that exists in the treeline literature between the information offered by data-sparse, global-scale investigations of treeline elevation, and that offered by a range of intensive, site-specific studies of local treeline dynamics (see Malanson *et al.* 2011 for a review of these). In New Zealand, for example, much of what has been published about *Nothofagus* treelines comprises studies at a few sites by relatively few people ((Wardle 1985a, b, c, 2008, Wardle and Coleman 1992, Harsch 2010, Cieraad 2011, Harsch *et al.* 2012) or general descriptions of New Zealand vegetation (e.g. Wardle 1964). Results from this study could be used to

generate new hypotheses regarding possible causes of treeline formation and to direct site-scale research at appropriate treeline locations in order to best address these hypotheses.

Gaining insights into the linkages among ecological patterns, environmental heterogeneity, and underlying processes is one of the driving aims of landscape ecology (Turner 2005). However, possible insights gained through the examination of pattern-environment relationships at treeline ecotones are highly contingent on the analytical approaches used (Bowersox and Brown 2001). In this study, different results may have emerged by computing the treeline pattern metrics in a different way, by using different or additional pattern metrics to describe treeline variability, by choosing different or additional abiotic variables to explain treeline patterns, or indeed via all of the above. Nonetheless, the fact that treeline pattern metrics clustered into logical treeline types that were spatially distinct, and that 50% of the variance in multivariate treeline pattern could be explained by abiotic factors, suggests that the methods used are enabling meaningful descriptions of these treelines to be made. One additional issue relates to the scale at which analyses were carried out: although spatial autocorrelation analyses indicated that the 15 x 15km landscape was an appropriate scale at which to investigate treeline patterns, inferences from this study are nonetheless limited to this one scale. It is well-recognised that treeline variability results from the influence of abiotic variation at multiple spatial scales (Malanson *et al.* 2007); therefore, analyses that can tease apart these scale-dependent effects on treeline pattern are merited.

Chapter 3

A framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline position

3.1 Introduction

Introduction

The alpine treeline can be defined as the transition zone between upright trees greater than 2m in height (Wardle 1974) and low-statured alpine vegetation that form where environmental stress levels surpass the ecological tolerances of the local tree species (Tranquillini 1979). The elevational position at which the treeline boundary occurs varies spatially at multiple scales ranging from broad-scale latitudinal gradients, where treeline elevation declines with increasing latitude (Körner 1998), to fine-scale variation over distances of tens of metres (Holtmeier 2009). This variation in treeline elevation depends upon the relative importance of processes causing growth limitation in trees, those affecting tree population dynamics, particularly the establishment and survival of seedlings, as well as historical influences such as past disturbances (Sveinbjörnsson 2000). Thus, treeline elevation represents an integrative metric of how different processes have together acted to cause the formation of the treeline boundary at specific locations. While multiple processes may induce treeline formation, the relative influence of each of the processes in causing the formation of the treeline boundary at a given treeline location is ultimately governed by a range of abiotic factors whose effects are scale dependent (Holtmeier and Broll 2005, Malanson *et al.* 2007, Elliott 2011).

Different approaches to studying variation in treeline position have focussed on processes operating at a variety of spatial scales. At very broad-scales the focus has been on the role of temperature in determining the uppermost treeline position (Körner and Paulsen 2004, Randin *et al.* 2013). At finer, landscape scales the focus has been on understanding patterns of variation in treeline structure and dynamics in relation to a range of biotic or abiotic factors (Malanson *et al.* 2011). The broad scale approach tends to ignore finer-scale variability and its causes (Holtmeier and Broll 2005). The landscape approach, while well suited to understanding the fine-scale mechanisms of treeline formation at a site of interest, is usually limited in site replication and the generality of inferences that can be drawn. A theoretical reconciliation of these different approaches might be achieved using methods that

can distinguish the scales at which different factors exert a controlling influence (Malanson *et al.* 2011).

It is generally accepted that there must be an upper limit to the survival or growth of upright trees that is set by a physiological threshold linked to low temperatures. Three lines of evidence support this. First, uppermost treeline elevations globally tend to coincide with a mean growing season air temperature in the range of 5.5 to 7.5°C (Körner 1998) and a mean root-zone soil temperature of 6.7°C (Körner and Paulsen 2004). At higher latitudes these critical isotherms occur at progressively lower elevations due to decreasing solar thermal input, leading to a strong negative relationship between latitude and mean treeline elevation (Körner 1998). Second, consistent with temperature limitation, treeline elevation has increased at many sites globally in response to recent climate warming (Grace 2002, Harsch *et al.* 2009, Holtmeier 2009). Third, there is a physiological basis for low temperature limitation as a predominant cause of treelines. Quantities of photoassimilates in trees at treeline are typically higher than in those at lower elevations, suggesting that photosynthetic functioning is not diminished with decreasing temperature (Hoch and Körner 2012); instead, it appears that cold temperatures prevent trees from allocating available carbon stores to meristem growth (eg. cell division and differentiation) (Rossi *et al.* 2008) thus limiting their stature. Hence, both biogeographic and physiological evidence strongly points to low-temperature growth limitation as the dominant mechanism controlling the upper limit of treeline formation.

While a decline in treeline elevation at higher latitudes due to lower thermal input is the best-documented and understood pattern in treeline variation, there is considerable finer-scale variation around this broad trend, with treeline elevation often varying quite markedly over scales ranging from tens of meters to several hundreds of kilometres (Holtmeier and Broll 2005). Understanding this finer-scale variation is challenging because many factors, in addition to temperature, can locally influence treeline elevation. Gradients in precipitation, for example, can cause lower treeline elevations regionally if the critical threshold for tree growth set by moisture availability occurs below that set by temperature limitation (e.g. Ohse *et al.* 2012), or if the interaction between high temperature and low precipitation causes drought stress (e.g. Daniels and Veblen 2004). At local scales, such as those pertaining to particular mountain valleys or hillsides, topographic variability strongly influences factors such as wind exposure and local soil properties. This, in turn, can push the critical limit for tree growth below the elevation set by temperature alone, causing local variability in treeline elevation (Holtmeier 2009).

The aim in this chapter is to provide a general framework for quantifying variation in treeline elevation, and understanding the role of abiotic factors in causing this variation, at multiple spatial scales. I first propose a conceptual model for understanding the way in which different abiotic factors act to influence treeline elevation and at what spatial scales their effects might be evident. Next, I develop an analytical framework that enables the partitioning of variation in both treeline elevation and abiotic factors by spatial scale and to examine the relationships between these at specific spatial scales. Finally, I apply the conceptual model and analytical framework to a case study aimed at understanding the causes of variation in the elevation of abrupt *Nothofagus* treelines across New Zealand. These treelines are highly variable, and previous work has indicated that they can reach temperature-driven maximum elevations at some locations (Cieraad 2011), while being considerably lower than this limit at other locations, ostensibly due to the effects of physiological stress and local disturbances (Wardle 2008). Therefore, this system is ideal for investigating how different effects manifest at different scales to cause observed patterns of treeline elevation variation.

3.2 Conceptual model

Given the strong correlation between treeline elevation and temperature at broad scales, I assume that, in the absence of other limiting factors, treeline for a given species occurs at the elevation corresponding to the critical temperature threshold below which tree growth is no longer possible (the ‘climatic treeline’ *sensu* Körner 2007). In an idealised situation, where perfectly smooth mountainsides are subjected to the same climate regime, treeline would therefore be a straight line coinciding with this critical temperature isotherm. In reality treelines deviate from this straight line in many locations and I conceptualise how this variation in treeline elevation is influenced by different abiotic factors by grouping these into three categories: thermal modifiers, physiological stressors, and disturbances.

Initially, I aimed to use available temperature data to directly characterise the thermal environment at treeline. However, gridded, GIS-based temperature data in New Zealand were unsuitable for this purpose, because the interpolation procedures used to spatially estimate temperature from weather station data incorporated elevation as a lapse rate correction variable. Elevation and temperature in the treeline zone were therefore strongly correlated across the country ($r = -0.60$, Appendix B.1), but it was not possible to isolate the true temperature-elevation relationship due to the inclusion of elevation to predict temperature in the spatial interpolation model. In lieu of independent temperature data at treeline, I use an

alternate set of factors, termed ‘thermal modifiers’, to account for variability in the thermal environment at treeline locations. Thermal modifiers are factors that act to alter thermal regimes and thus to raise or lower the elevation at which the critical temperature isotherm occurs, thus raising or lowering treeline elevation accordingly. For example, a key thermal modifier is variation in the amount of solar radiation reaching the earth’s surface. At the same elevation, lower latitude sites receive on average more radiant energy per unit area, and thus tend to be warmer than higher latitude sites, causing treeline elevation to decrease with latitude. At finer spatial scales, sites on more sun-exposed aspects receive more radiant energy and are warmer than sites on less sun-exposed aspects, and would be expected to have higher treelines (Danby and Hik 2007). Alpine thermal regimes, and thus treeline elevations, may also be modified by factors such as continentality (Caccianiga *et al.* 2008), mountain mass effects (Han *et al.* 2012) and topography-induced thermal effects such as cold air ponding in valleys (Wardle 2008).

I define physiological stressors as factors additional to temperature that can impair physiological processes and limit tree growth locally. For treeline species growing at elevations close to the critical temperature threshold or that are particularly physiologically sensitive, it is likely that additional stresses, such as limited moisture or nutrient availability, will further impair physiological processes such as carbon assimilation and allocation and lower the elevation at which tree growth is possible (Figure 3.1). Physiological stressors include factors such as wind, frost, drought or limited nutrient availability. For example, the fact that Andean treelines occur at lower elevations on east-facing slopes has been attributed to low-temperature photoinhibition caused by a combination early-morning cold temperatures and high insolation on these slopes (Bader and Ruijten 2008), which disrupts photosynthesis and can substantially lower carbon assimilation at treeline (Germino *et al.* 2002).

Finally, abrupt disturbances such as landslides, fire, severe wind storms and snow avalanches can kill trees and temporarily push the treeline below the limit imposed by temperature and physiological stressors. While some disturbances could also be considered physiological stressors (such as wind), we define disturbances as infrequent catastrophic events that lower treeline by killing or removing trees from which recovery to the former treeline position can occur but may take years or decades.

I hypothesise that spatial variability in treeline elevation can be understood with reference to these three categories of factors and their effects, with the critical caveat that different factors are likely to have effects at different spatial scales.

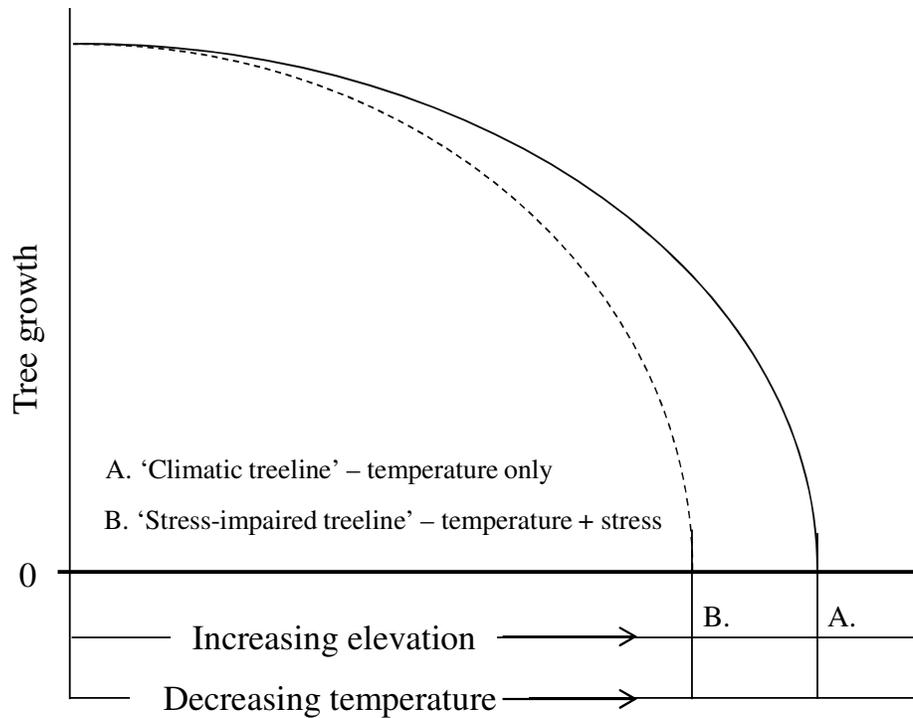


Figure 3.1 Conceptual diagram of effects of temperature and physiological stress on tree growth and treeline elevation. As temperature decreases with increasing elevation (lapse rate) in mountain areas, metabolic processes associated with tree growth (solid black line) are impaired and then cease when a critical physiological threshold is surpassed, causing treeline formation (A. – ‘climatic treeline’). With the additional influence of stress (e.g. drought conditions) on tree physiological functioning, the critical threshold occurs at higher temperatures causing treeline to occur at lower elevations (B – ‘stress-impaired treeline’).

3.3 Methods

3.3.1 Response data – treeline elevation

New Zealand's *Nothofagus* treelines were used to investigate the scale-dependent influences of abiotic factors on treeline elevation variation. This is a useful study system, first because *Nothofagus* treelines are typically abrupt, going from tall, closed canopy forest to short-statured subalpine shrub or grassland vegetation typically within the space of a few metres. Consequently, it is relatively straightforward to delimit the treeline boundary and determine treeline elevations across large areas using geo-referenced landcover data. Second, New Zealand *Nothofagus* treelines span seven degrees of latitude, resulting in a broad climate gradient from north to south. There is also considerable local heterogeneity in abiotic conditions across this extent due to variation in geology and topography, along with a strong east-west climate gradient with conditions ranging from maritime to continental (Leathwick and Whitehead 2001). Regions west of the main continental divide in the South Island, for example, have up to eight times the annual rainfall relative to regions east of the main divide. As such, we expected to see corresponding variation in treeline elevation over these spatial scales.

I delineated *Nothofagus* treelines (Figure 3.2a) across the entire country using the New Zealand Landcover Database 2 (LCDB2), which provides a complete spatial representation of landcover types across New Zealand at the *c.* 1:50,000 scale derived from satellite imagery (New Zealand Ministry for the Environment 2004). Using the LCDB2 dataset within a GIS (ArcGIS 9.3), *Nothofagus* treelines were identified as lines demarcating the polygon boundaries between *Nothofagus* and subalpine/alpine landcover classes. Treeline sample locations were generated in the GIS at 500 m intervals along delineated *Nothofagus* treelines (Figure 3.2b), allowing a sufficient sampling intensity at the finest scale of interest (see next section), while generally corresponding to the resolution of the environmental data available for our analyses. I only sampled treelines above 750 metres in elevation to ensure that other types of treeline boundaries, such those occurring along the edges of streams in high-elevation headwater catchment areas, were not included in our analysis. By sampling all 27,171 kilometres of *Nothofagus* treeline above 750 masl at 500 m intervals, I generated 53,912 sampling locations. The elevation (masl) at each treeline sampling point was then extracted in the GIS from a 25 m resolution digital elevation model for New Zealand (Barringer *et al.* 2002).

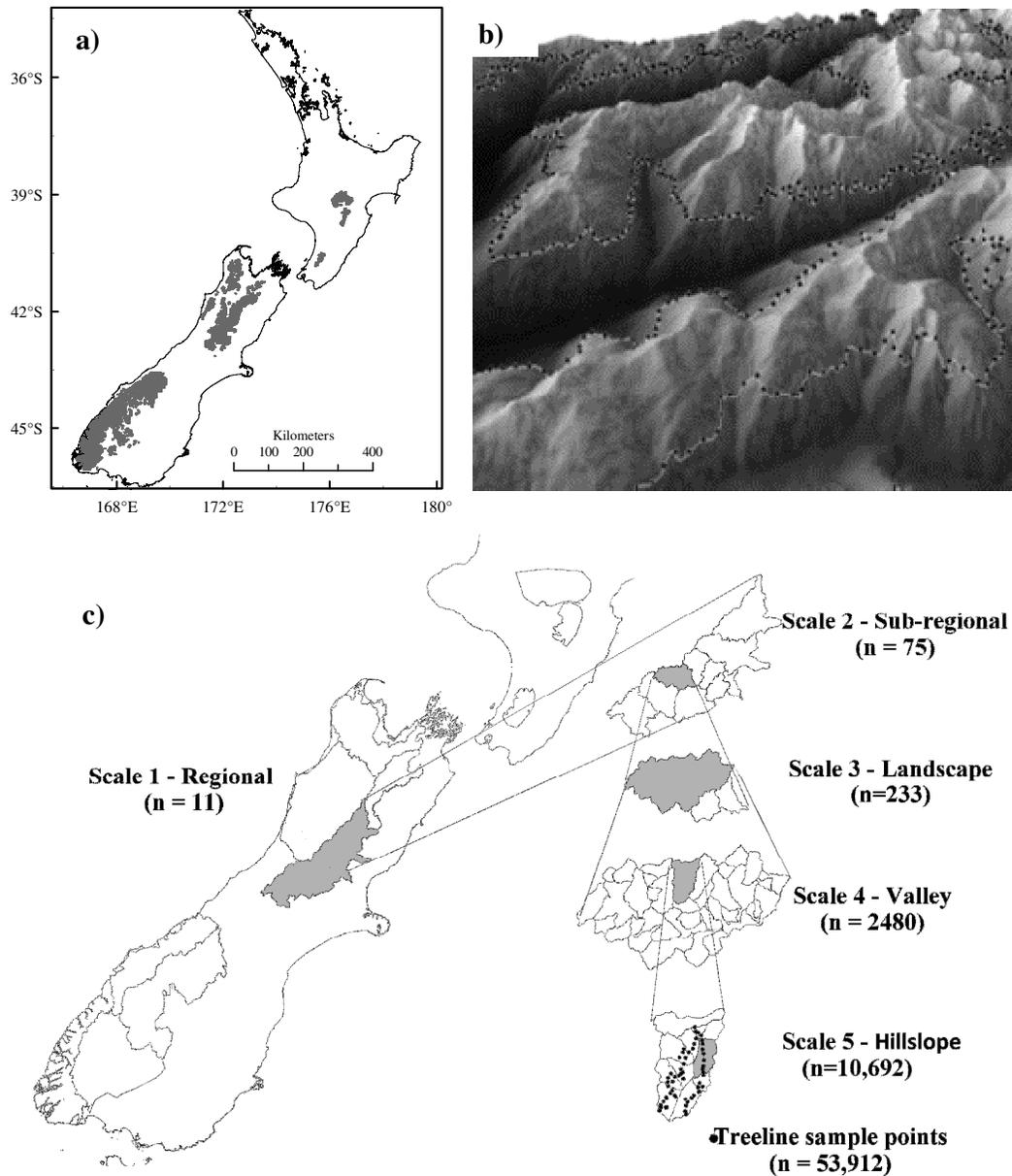


Figure 3.2 Figures showing a) the geographic distribution of *Nothofagus* treelines (grey areas) in New Zealand investigated in this study; b) a close-up example of the treeline sampling locations (black dots), spaced at 500 m intervals along delineated treelines and c) a depiction of the hierarchical sampling scheme at the five scales; a total of 53,912 sampling locations were generated across the study extent.

3.3.2 Spatial scale

I developed a hierarchical spatial framework in order to examine the relationships between *Nothofagus* treeline elevation and abiotic factors at different spatial scales (Table 3.1). To do this, I used the New Zealand River Environment Classification (REC) dataset (Snelder *et al.* 2004), which classifies river catchments by size ranging from the smallest 1st order headwater streams to the largest 6th order rivers, to characterise the spatial configuration of mountain areas across New Zealand as a series of naturally-nested spatial units (Figure 2c). The largest scale units (Scale 1) are the catchments of 6th order rivers that were combined into 11 catchment units representative of New Zealand's broad climatic zones (e.g. Garr and Fitzharris 1991). The remaining 4 scales are nested within these and define increasingly smaller units, down to Scale 5, which comprises local-scale, valley hillslopes (Table 3.1).

3.3.3 Abiotic factors

Eight abiotic factors likely to be important in influencing treeline elevation were identified: solar radiation, mountain mass, cold air ponding, atmospheric water availability, exposure to high winds, two soil quality factors (soil nutrients and soil moisture), and earthquake disturbance intensity. These were factors for which data could be extracted or derived from available spatial datasets for each of 53,912 sampling locations using standard GIS procedures and that were not confounded with elevation due to the way they were derived. While data for two of the factors (extreme wind days and vapour pressure deficit) were originally created using interpolation procedures that incorporated elevation adjustments, only weak correlations with elevation were present in these datasets within the treeline zone ($r = 0.26$ and $r = -0.26$, respectively – Appendix B.1) and were therefore deemed suitable for inclusion in the statistical analyses. I classed these factors as thermal modifiers, physiological stressors or disturbances, and attempted to predict whether each factor would exert a positive or negative influence on treeline elevation, and the spatial scales at which that influence would be most critical.

Table 3.1 Derivation and description of the five scales comprising the hierarchical, spatial analysis framework used in the study.

Scale	Number of spatial units	Derivation using nested catchment data	Description of spatial units	Mean (\pm SD) treeline length (km)
1 – Regional	11	Multiple, adjacent 6 th order catchments	Correspond to broad climatic regions across country	2470.1 (1317.9)
2 – Sub-regional	75	Individual 6 th order catchments	Large catchments within broad, scale 1 zones, separated by large mountain range systems	362.3 (334.5)
3 – Landscape	233	Individual 5 th order catchments	Multi-valley catchments within large scale 2 regions, each separated by a significant mountain range	116.6 (117.6)
4 – Valley	2480	Aggregated 3 rd , 4 th , and 5 th order catchments	Individual valleys within scale 3 units	11.0 (12.4)
5 – Hillslope	10692	Aggregated 2 nd , 3 rd , 4 th , and 5 th order catchments	Portions of scale 4 valleys (valley hillslope sections)	2.5 (2.6)

Table 3.2 A description of the abiotic drivers of treeline position examined, and their predicted influences on treeline elevation at each of the five scales (Scales 1 to 5: regional, sub-regional, landscape, valley, and hillslope).

Abiotic factor	Factor category	Ecological mechanism	Data and variables used for analysis	Predicted association with treeline elevation
Solar radiation	Thermal modifier	Heat loading, varying with latitude and aspect	<i>Solar radiation</i> (total annual sum) calculated using GIS-based algorithm	Positive, strongest at regional and hillslope scales
Mountain mass	Thermal modifier	Heat retention and decreased exposure to wind etc.	<i>Mountain mass index</i> calculated in GIS as the total area above 1200 m altitude, within a 20 km neighbourhood of treelines	Positive, strongest at sub-regional and landscape scales
Cold air ponding	Thermal modifier Physiological stressor	Lower minimum temperatures Higher frost prevalence	<i>Compound topographic index (CTI)</i> , a GIS-derived index of terrain concavity	Negative, strongest at landscape to hillslope scales
Atmospheric water availability	Physiological stressor	Increased evaporative demand and desiccation stress	<i>Vapour pressure deficit (VPD)</i> ; 100 m resolution raster surface	Negative at valley and hillslope scales
Wind exposure	Physiological stressor	Dessication stress, physical abrasion and damage	<i>Extreme wind days</i> (per year); 500 m resolution raster surface	Negative, strongest at valley and hillslope scales
Soil quality (nutrients and moisture)	Physiological stressor	Soil resource limitation	Scores from PCA of spatial soils data; <i>PC1 - soil fertility</i> , <i>PC2 - soil moisture</i>	Negative, strongest at valley and hillslope scales
Earthquake intensity	Disturbance	Catastrophic forest removal due to landslips	<i>Earthquake intensity</i> – 500m GIS grid of expected mean peak ground acceleration	Negative, strongest at regional and sub-regional scales

Thermal modifiers

Solar radiation: The amount of solar radiation reaching the earth's surface is a primary determinant of the thermal environment (Pierce *et al.* 2005) and is correlated with air temperature (Meza and Varas 2000). At a broad scale solar radiation input is largely determined by the effect of latitude on the sun's position in the sky, and at finer scales by cloudiness, differences in atmospheric transmissivity, and shading effects caused by the configuration of the local landscape. At the largest scale I predict a strong, positive, relationship between potential solar radiation and treeline elevation (Table 3.2), reflecting that the critical temperature threshold for *Nothofagus* will occur at higher elevations with higher radiation input. I also predict local scale effects because, at a given latitude in New Zealand, more north-facing slopes receive greater radiation input, and would be expected to have higher treelines. I used the 'solar radiation' tool in ArcGIS 9.3, based on the algorithm in Fu and Rich (2002), to calculate potential annual solar radiation (in watt hours/m²) for each treeline location. This algorithm accounts for the effects of latitude, aspect, and the degree of shading from the surrounding terrain, to calculate the amount of solar radiation reaching the land surface assuming no cloud cover and constant atmospheric conditions.

Mountain mass: Mountain mass (the "*Massenerhebung*" effect, e.g. Grubb 1971) is a thermal modifier resulting from larger and taller mountains providing more protection from prevailing winds and having greater heat retention than smaller more isolated mountains, leading to higher treelines (Hoch and Körner 2005). The mountain mass effect is closely associated with the concept of continentality (Holtmeier 2009), in that continental mountain ranges tend to be larger, have greater seasonal thermal amplitudes (higher summer and lower winter temperatures) and typically have higher treelines than those near the coast (Jobaggy and Jackson 2000). I therefore predicted a positive relationship between mountain mass and treeline elevation at a regional to landscape scale (Scales 1 to 3 in Table 3.1). I calculated an index of mountain mass as the land area (km²) above 1200 masl within a 20km neighbourhood (10km radius) around each treeline sample location, generally corresponding to the average elevation at which the *Nothofagus* forest-alpine transition occurs across the country.

Cold air ponding: Low solar radiation, high atmospheric pressure, and low wind conditions often cause denser, colder air to drain down mountain slopes and pond in valleys and other

concave terrain features in mountain systems (Daly *et al.* 2010). The result is a decoupling of these areas from the free atmosphere leading to lower temperatures on average (Lindkvist *et al.* 2000). This effect is a recognised feature of New Zealand mountain environments (Sturman and Tapper 2006). I therefore predict that, at the valley and local scales (Scales 4 and 5), treelines in convergent topographic zones will have lower treeline elevations due to cold air ponding. I used the compound topographic index (CTI – Moore *et al.* 1991) as a measure of topographic convergence (Bader and Ruijten 2008). CTI at a given location is calculated as $\ln(A_s/\tan \beta)$, where A_s is the contributing upslope catchment area, and β is the local slope angle in degrees. A 200 m resolution CTI grid was computed for New Zealand by first computing surfaces for A_s and $\tan \beta$ using tools available within ArcGIS 9.3 and then combining these grids using the above formula. CTI values were then extracted for each treeline location.

Physiological stressors

Atmospheric water availability: At broad scales, higher vapour pressure deficits characterise drier, warmer regions that typically also display higher average treeline elevations (Daniels and Veblen 2003). However, atmospheric water deficits can occur at locales with high levels of solar radiation, low relative humidity, and consistently high downslope winds due to strong topo-climatic effects, a situation common in New Zealand (Leathwick and Whitehead 2001). A combination of cold soil and high atmospheric water deficit greatly increases evaporative demands on trees, leading to desiccation stress and causing reductions in leaf-level gas exchange (Goldstein *et al.* 1985, Sullivan and Sveinbjörnsson 2011), which typically slows growth (Muller *et al.* 2011). This type of stress might prevent the establishment of new trees above the current treeline and, in certain locations, prevent the treeline from reaching its temperature-driven limit. I therefore expect lower treelines where atmospheric water availability is low, suggesting we should see strong effects at the valley and hillslope scales. As a measure of atmospheric water availability, we extracted values for vapour pressure deficit (VPD) at treeline locations from a 100 m-resolution gridded VPD dataset covering New Zealand (Leathwick *et al.* 2002a)

Wind exposure: High and persistent winds on exposed sites can affect trees' physiological function (Holtmeier 2009). Wind exposure can result in higher water loss from leaves via

increased transpiration, leading to leaf desiccation, particularly in late winter (Wardle 1981). Strong winds can cause physical abrasion to leaves and remove protective cuticle waxes (Hadley and Smith 1989), causing further water loss and increasing rates of leaf death (Marchand and Chabot 1978). Indirectly, treeline locations subject to high winds have less snow cover, which can result in lower spring moisture availability and less protection from intense solar radiation afforded by snow cover to seedlings (Holtmeier 2009). I therefore predict a negative relationship between the degree of high wind exposure and treeline elevation, with this effect dependent on local topography and thus manifest at valley and local scales. As a measure of relative exposure to extreme winds, the mean annual number of days with wind gusts exceeding 33 knots was extracted for the treeline locations from a long-term, 500 m-resolution gridded dataset for New Zealand (Wratt *et al.* 2006).

Soil quality: Soil conditions, including variation in soil texture, chemical properties, depth, and moisture holding capacity, can affect resource availability at treeline, exerting considerable influence on tree physiological functioning. For example, low soil moisture, particularly during summer, can cause various drought-related physiological responses in trees that ultimately lead to reduced growth and mortality (McDowell *et al.* 2011). Fertiliser addition has been shown to increase tree height growth at treeline (e.g. Sveinbjörnsson *et al.* 1992), suggesting soil nutrients can be a growth limiting factor. I expect a negative relationship between treeline elevation and soil conditions; at locations where soil quality decreases with elevation, treelines should occur at lower elevations with better soil nutrient and moisture conditions. This relationship should be most evident at landscape to local scales (Scales 3 to 5).

Data for soil chemical and physical properties were extracted in the GIS from the 1:50,000-scale New Zealand Land Resource Inventory (LRI) spatial dataset (Newsome *et al.* 2000). For each treeline location I extracted estimates of mean percent carbon (C), cation exchange capacity (CEC), potential rooting depth (m), percentage of gravel, amount of profile total available water (PAW, mm), and the amount of profile readily available water (PRAW, mm) (Newsome *et al.* 2000). I then summarised variation in these features using principle components analysis (PCA), with the first two PC axes accounting for 78% of the variability in the six soil variables. The highest scores for PC axis 1 were for variables describing aspects of soil fertility (CEC, C, gravel) while those for PC axis 2 were for variables representing potential soil moisture availability (PAW, PRAW). I subsequently

used the scores from these two axes as separate explanatory variables in modelling, with higher values for both axes 1 and 2 representing higher levels of fertility and moisture availability, respectively.

Disturbance

Earthquake intensity: New Zealand is highly tectonically active and earthquakes constitute a major source of large-scale disturbance in New Zealand's mountains, by causing landslides which have historically damaged or removed large areas of forest (Wells *et al.* 2001). I expected that, in areas subjected to higher mean earthquake intensities over time, there would be a signature of generally lower treelines and that the signal of this effect would be most apparent at the regional scale (Scale 1). Other disturbances, such as those caused by wind and snow avalanches, are also important at New Zealand treelines (Cullen *et al.* 2001), but the data were lacking to investigate their effects. As an index of the relative degree of the intensity of historical earthquake disturbance at treeline locations, I used a New Zealand-wide spatial dataset of the expected mean peak ground acceleration (PGA) within a 150 year return interval, expressed as the proportion of the acceleration due to gravity (Stirling *et al.* 2002).

3.3.4 Statistical analysis

The data for analyses comprised treeline elevation and the eight abiotic factors extracted at the 53,912 sampling points, along with five categorical variables that identified the spatial unit of each sample point at each of the five spatial scales of organisation (e.g. the specific region, sub-region, landscape, valley and hillslope each sample point was located in, Table 3.1). The analysis comprised two steps that aimed to: 1) partition the variation in treeline elevation and in each of the eight environmental variables across the five spatial scales; 2) quantify the relationships between treeline elevation and environmental variables at each spatial scale.

Variance partitioning

To partition variation in the data across the five spatial scales, I fitted nine separate hierarchical regression models with treeline elevation and each of the eight abiotic factors as

response variables and the five categorical variables identifying the spatial unit of each location as explanatory variables. These five explanatory variables were included as nested random effects as follows:

Eq. 3.1

$$Response \sim \text{Normal}(\mu + Scale5, \sigma^2)$$

$$Scale5 \sim \text{Normal}(Scale4, \sigma_5^2)$$

$$Scale4 \sim \text{Normal}(Scale3, \sigma_4^2)$$

$$Scale3 \sim \text{Normal}(Scale2, \sigma_3^2)$$

$$Scale2 \sim \text{Normal}(Scale1, \sigma_2^2)$$

$$Scale1 \sim \text{Normal}(0, \sigma_1^2)$$

where *Response* is the value of the response variable at each of the 53,912 locations, with these modelled as drawn from a normal distribution with an overall mean (μ), a parameter measuring the deviation of the response in each of the 10,692 scale 5 units from the overall mean (*Scale 5*), and unexplained variation (σ^2 , i.e. the amount of variation not accounted for by differences among scale 5 units). Deviations of scale 4 units from the overall mean for the scale 5 units within which they were nested were then modelled as drawn from a normal distribution with a different mean for each scale 4 unit (*Scale 4*), measuring the average deviation from the overall mean, and associated variance (σ_5^2) which is the amount of variation not accounted for by differences among scale 4 units that can be ascribed to variation among scale 5 units. This was repeated up to the coarsest scale where the scale 1 means were modelled as drawn from a normal distribution with mean zero (because we are modelling these as deviations from the overall mean μ) and associated variance. The variance terms associated with units at each spatial scale quantify the amount of variation in the response variable that resides at that scale independent of variation at other spatial scales. The above framework was implemented as hierarchical regression models using the function “lme” in the “nlme” package within R, version 2.12 (R Development Core Team 2010). The variation in each response variable residing at each spatial scale was then determined using a

variance components analysis (as per Crawley 2007, p. 638-640), which is calculated as the squared standard deviations of the random effects at each scale (from the lme model output summary) expressed as a proportion of the total variance.

Relationships between treeline elevation and abiotic factors at each scale

For each response variable the hierarchical regression model quantifies how much of the total variation resides at each spatial scale. One can also extract from each model the random effects coefficients at each spatial scale, which are the relative means of the response for each unit at each scale independent of variation at other spatial scales. Thus, for each response variable the random effects coefficients quantify the relative difference among locations at each of the five spatial scales. Using these coefficients, I then examined the extent to which variation in treeline elevation was explained by variation in the eight abiotic factors independently at each scale. To do this, I fitted linear regression models with the random effect coefficients for treeline elevation as the response variable and the random effect coefficients for each of the eight abiotic factors as the explanatory variables at each of the five scales (see Appendix B.2 for further details). The random effects coefficients for each abiotic factor were standardised to a mean of zero and standard deviation of one prior to fitting the regression models so that their relative effects could be compared. I first fitted models including each abiotic factor separately (univariate regressions).

To identify the combination of abiotic factors that best accounted for variation in treeline elevation at each scale I used multiple regression with the random effects coefficients for treeline elevation as the response and those for all eight abiotic factors as explanatory variables, at each spatial scale. The random effects coefficients for the compound topographic index (CTI) and earthquake intensity variables were strongly correlated with those of several other variables (Pearson's $r > 0.5$) at Scale 1 and CTI and earthquake intensity were therefore removed from modelling at that scale; strong collinearity was not present among the random effects coefficients for any of the other variables at the five scales (Appendix B.3). I constructed a set of alternative regression models based on all possible additive combinations of the eight explanatory variables at each scale, as there was no *a priori* reason to exclude particular abiotic factors at a given scale. I ranked these models using the small sample version of Akaike's Information Criterion (AIC_c) and determined their model-averaged parameter estimates (Anderson 2008). For each variable, its relative importance was quantified at each scale by summing the Akaike model probabilities for all models in the

set containing the variable (Anderson 2008). The coefficient of variation (R^2) of the top-ranked model at each of the five scales was used as an indication of the amount of variance in treeline elevation explained by the abiotic environment at each scale. The residuals of top-ranked models were checked for significant spatial autocorrelation using Moran's I correlograms (Appendix B.4). Univariate regression models were fitted with the "lm" function in R, and multiple regression analyses, information-theoretic model comparisons, and Moran's I tests were carried out using the Spatial Analysis in Macroecology (SAM) software, version 4.0 (Rangel *et al.* 2010).

3.4 Results

3.4.1 Variance partitioning

The elevation of the *Nothofagus* treeline varied widely across the country, ranging from 800 to 1740 metres above sea level (masl) (mean of 1110 masl and standard deviation of 173.8 masl). Seventy seven percent of this variation was captured by the five-scale, nested catchment framework (Figure 3.3). Most (46%) of the variation in treeline elevation resided at the largest (regional) spatial scale (Scale 1), with the four smaller scales accounting for 10%, 4%, 8% and 9% of the variance, respectively. The remaining 23% of the variation in treeline elevation was unaccounted for by our spatial framework.

The eight abiotic factors showed different patterns of variance partitioning across scales (Figure 3.3). Most (*c.* 40-60%) of the variation for vapour pressure deficit, peak ground acceleration, mountain mass index, and topographic convergence resided at the broadest two scales. Conversely, most of the variation in soil fertility, soil moisture, and extreme wind days resided at the smaller two scales (valley and hillslope). About 25% of the variation in solar radiation resided equally at both the largest and smallest scales of the framework.

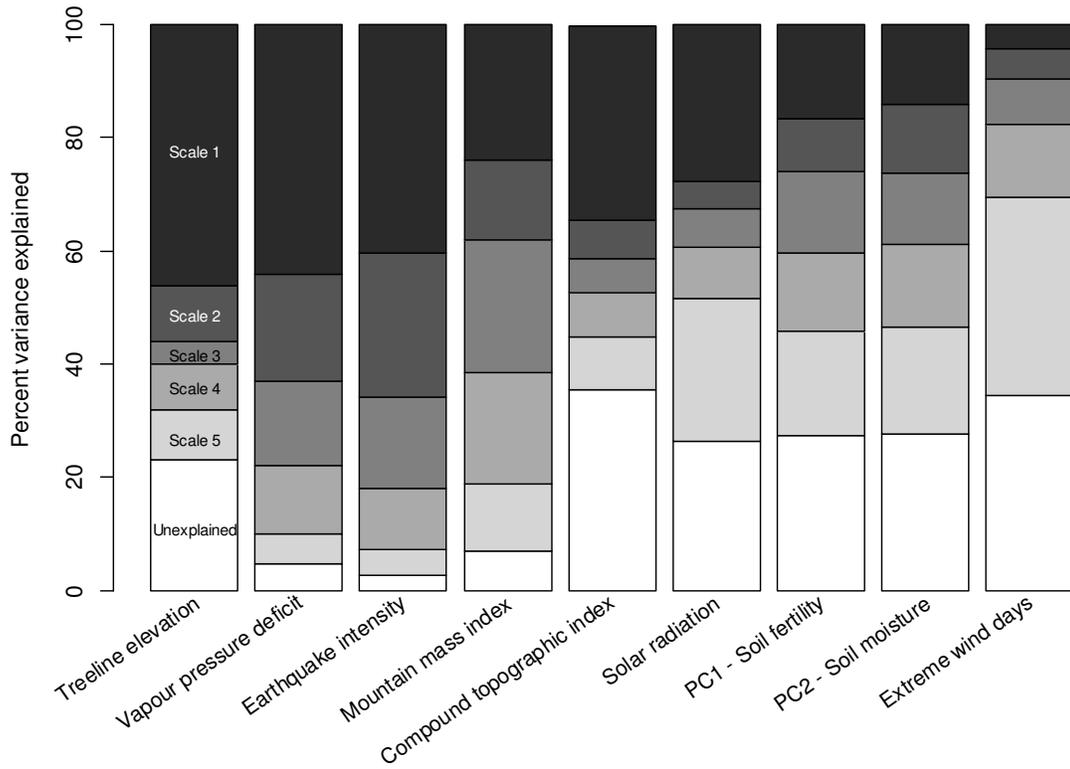


Figure 3.3 Variance partitioning of random effects for treeline elevation and eight abiotic explanatory factors across the five nested scales, from regional (Scale 1) to hillslope (Scale 5). See Table 3.2 for descriptions of abiotic factors.

3.4.2 Relationships between treeline elevation and abiotic factors

At the regional scale (scale 1), treeline elevation was significantly correlated with three of the eight abiotic factors: positively, with solar radiation, and negatively, with soil fertility and peak ground acceleration (Figure 3.4). At the four smaller scales (scales 2 to 5), the standardized regression coefficients for all abiotic factors were much smaller than for scale 1. At the sub-regional (scale 2) and landscape (scale 3) scales, mountain mass index and solar radiation showed the strongest positive associations with treeline elevation, and the compound topographic index (CTI) showed a significant negative relationship. Of the eight abiotic factors, extreme wind days was most strongly, and positively, correlated with treeline elevation at the two smallest scales, although solar radiation also displayed a significant positive association, and CTI and vapour pressure deficit significant negative associations at these scales. Solar radiation was the only factor to be significantly correlated with treeline elevation across all scales. The sizes of the confidence intervals around the parameter estimates decreased from the broadest to finest scales, reflecting a concomitant increase in the number of spatial units (sample size; see Table 3.1).

The top-ranked multivariate regression models, based on AIC_c , explained 82%, 52%, 44%, 45% and 50% of the variation in treeline elevation at each of scales 1 to 5, respectively (Table 3.3). Model-averaged parameter estimates and relative importance values for each explanatory variable indicated that the solar radiation and mountain mass index were strongly associated with treeline elevation at the three broadest scales, scales 1, 2 and 3 (Table 3.3). The cold air ponding index, CTI, had relatively strong associations with treeline elevation from scales 2 to 5. Both extreme wind days and water balance ratio displayed significant positive associations with treeline elevation at the two finest scales, scales 4 and 5. Soil fertility and moisture were not strongly associated with treeline elevation in general; soil fertility was included in top-ranked models for scales 3, 4, and 5, although its effect was relatively small, and soil moisture was only included in the top-ranked model at scale 2. PGA, as a measure of earthquake disturbance, had a relatively strong association with treeline elevation at the broadest, regional scale, although its relative importance across the model set was low. Although PGA was included in top-ranked models at the two smallest scales, effect sizes were small. Going from larger to smaller scales (i.e. scale 1 to scale 5), an increasing number of variables were selected for inclusion in top-ranked models, almost certainly because of the increase in sample size (Table 3.3). Moran's I correlograms indicated that there was no statistically significant spatial autocorrelation in the residuals of the top-ranked models at the five scales (Appendix B.4).

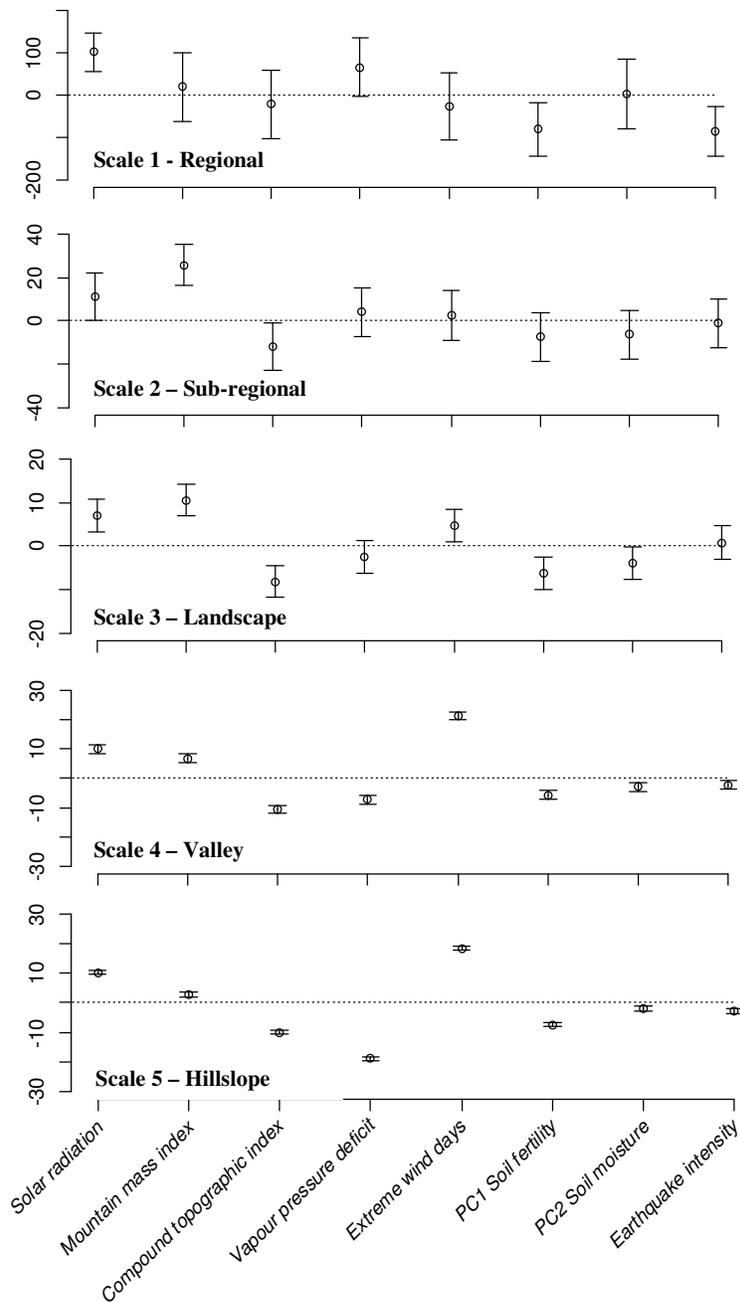


Figure 3.4 Effect sizes resulting from univariate linear regressions of random effects coefficients for treeline elevation modelled against those for the eight abiotic factors at each of the five scales. Values are standardised parameter estimates \pm 2 standard errors. Factors with error bars not overlapping with the zero line are considered significant effects ($p < 0.05$).

Table 3.3 Model selection results for multiple linear regression models explaining *Nothofagus* treeline elevation at the five study scales. A multi-model approach was taken where all additive combinations of abiotic factors were included in regression models at each scale. Presented are model-averaged parameter values ± 2 standard errors and the relative importance rankings of each factor (in parentheses), computed across all models at each scale. A relative importance of 1 signifies that a given factor was present in all possible models at that scale. Shown in bold are the factors comprising the top-ranked model, based on AIC_c , at each scale and the R^2 for these models. The factor CTI was excluded from the Scale 1 model set due to strong collinearity with other variables.

Scale	Solar radiation	Mountain mass index	Vapour pressure deficit	Compound topographic index – CTI	PC1 - Soil fertility	PC2 - Soil moisture	Extreme wind days	Earthquake intensity	R^2
1 Regional	107.18 \pm 45.66 (0.98)	47.94 \pm 20.7 (0.51)	10.73 \pm 4.02 (0.05)	----- -----	-39.51 \pm 6.62 (0.10)	28.37 \pm 5.01 (0.09)	12.37 \pm 3.96 (0.06)	----- -----	0.82
2 Sub-regional	19.66 \pm 8.98 (1)	29.89 \pm 8.45 (1)	-0.02 \pm 2.11 (0.23)	-12.37 \pm 8.02 (0.97)	-5.78 \pm 3.85 (0.41)	-8.17 \pm 5.67 (0.65)	4.39 \pm 3.00 (0.33)	0.68 \pm 2.37 (0.23)	0.52
3 Landscape	9.56 \pm 3.07 (1)	15.24 \pm 3.13 (1)	-3.91 \pm 2.91 (0.85)	-9.43 \pm 3.16 (1)	-5.88 \pm 3.15 (1)	0.61 \pm 0.92 (0.27)	4.41 \pm 3.04 (0.96)	-1.43 \pm 1.27 (0.34)	0.44
4 Valley	5.31 \pm 1.20 (1)	5.01 \pm 1.19 (1)	-6.06 \pm 1.26 (1)	-10.42 \pm 1.15 (1)	-3.66 \pm 1.16 (1)	-0.49 \pm 0.40 (0.35)	18.23 \pm 1.23 (1)	-3.53 \pm 1.23 (1)	0.45
5 Hillslope	2.34 \pm 0.59 (1)	3.16 \pm 0.53 (1)	-14.37 \pm 0.55 (1)	-9.78 \pm 0.53 (1)	-3.45 \pm 0.53 (1)	-0.07 \pm 0.14 (0.28)	14.78 \pm 0.62 (1)	-3.48 \pm 0.53 (1)	0.50

3.5 Discussion

This study describes a novel approach for quantitatively examining patterns of scale-dependence in treeline elevation, using New Zealand's *Nothofagus* treelines as a case study. Our approach provides a means to characterise the spatial structure of mountain systems, using nested river catchments, and to incorporate this structure into a hierarchical statistical analysis framework. There are two main benefits of this framework. First, it allows one to decompose the variation in treeline elevation by spatial scale and to identify the scale(s) at which most variation resides. Second, one can identify the abiotic factors most strongly correlated with treeline elevation at each of these spatial scales and thus infer how different processes that operate at different scales combine to produce variation in treeline elevation.

Variability in treeline elevation, and the abiotic factors most strongly associated with this variability, differs considerably across the five spatial scales. There is a shift from a dominant influence of thermal modifying factors at larger scales to a combination of thermal-, stress-, and disturbance-related factors at finer scales, on treeline elevation (Figure 3.4 and Table 3.3). On the whole, treeline elevation varied in response to abiotic variation as predicted by our conceptual model. Broad-scale factors modifying the thermal environment at treeline were highly correlated with treeline elevation, supporting the notion that there is a critical thermal threshold to tree growth that determines regional treeline position (e.g. Körner and Paulsen 2004). Further, with the exception of the influence of wind exposure, factors included in our analyses as physiological stressors acted at finer scales to lower treelines below the mean regional treeline position as expected. These results support the hypothesis laid out in the conceptual model that treeline elevation variation is largely due to the physiological response of trees to a spatially-heterogeneous abiotic environment across a range of scales. Results are also consistent with the hypothesis that both temperature-driven, growth limitation and stress-related, recruitment limitation processes are likely involved in the formation and maintenance of these abrupt treelines (Harsch and Bader 2011).

Variation in *Nothofagus* treeline elevation across New Zealand is strongly associated with factors that influence thermal regimes. Nearly half the variation in treeline elevation resides at the largest, regional scale (Figure 3.3), and over 80% of this variation can be explained by positive associations with solar radiation input and mountain mass, the two factors with the highest relative importance and which comprised the top-ranked model at this scale (Table 3.3). These results corroborate the findings of previous broad-scale studies showing strong associations among treeline elevation, latitude, and mass-related temperature

variation (Wieser and Tausz 2007 and references therein), and are consistent with the overall role that temperature is thought to play in determining treeline elevation at broad scales (Körner and Paulsen 2004). Soil fertility, soil moisture, and earthquake intensity also had moderately strong effect sizes at the regional scale, although low relative importance values indicate that these factors have a poor ability to explain variation in treeline elevation in comparison to solar radiation and mountain mass at this scale when considered across all possible models.

Relative to the strong influence of thermal modifiers on treeline elevation at the regional scale, the finer-scale effects are smaller, as evidenced by much less variation in treeline elevation residing at smaller scales (Figure 3.3), models that explain less of that variation at these scales (Table 3.3), and variables with smaller effect sizes (Figure 3.4 and Table 3.4). Nonetheless, effects due to cold air ponding, atmospheric water availability, soil fertility, earthquake-related disturbance, and wind exposure were relatively strong at one or more of the finer scales examined. There is a relatively strong and consistent negative association between the topographic index (CTI) and treeline elevation at the four smaller scales, consistent with our prediction that topography favouring cold air drainage and increased frost prevalence will cause lower treelines. Wardle (2008) suggested that the tendency for *Nothofagus* treelines in New Zealand to form at higher elevations on spurs and other convex landforms, and at lower elevations in gullies and in valley heads, was due to cold air ponding effects and our results provide quantitative support for this observation. Other studies have similarly found lower treelines in areas where topography acts to lower minimum temperatures locally and increase the likelihood of frost occurrence (e.g. Tranquillini 1979).

At the valley and hillslope scales (Scales 4 and 5), vapour pressure deficit was relatively strongly and negatively associated with treeline elevation, consistent with my prediction that sites with lower atmospheric water availability would be more susceptible to some degree of desiccation stress, preventing trees from recruiting beyond the current treeline. While water deficits are relatively common at coniferous treelines in the Northern hemisphere (e.g. Vostral *et al.* 2002), they are thought to be less prevalent at Southern Hemisphere treelines (Cochrane and Slatyer 1988), although dieback due to desiccation stress has been noted for *Nothofagus* in New Zealand (McCracken *et al.* 1985). Cochrane and Slatyer (1988), studying water relations at *Eucalyptus pauciflora* treelines in Australia, found little evidence that shoot dieback was caused by low water potentials alone but suggested that damage could be caused by a combined effect of frost damage and low water availability.

Certainly, this could be case in New Zealand (Wardle 2008) and may be particularly detrimental in convex topographic zones where treelines are more likely to have been pushed downhill by disturbances, and where there would be higher vapour pressure deficits and potentially higher frost potential due to the effects of cold air drainage.

At the finest three scales, there was a weak negative association between soil fertility and treeline elevation, again consistent with our predictions. This result suggests that poorer soil quality at higher elevations can limit tree establishment and growth, forcing treelines to lower elevations where soils are typically deeper, more developed, and nutrients are in greater supply (Butler *et al.* 2007). Finally, at the valley and hillslope scales, there was a weak negative effect of earthquake-related disturbance on treeline elevation. This may indicate that although earthquakes are broad-scale phenomena, their impacts on treelines manifest at local scales, typically in the form of localised landslips (Wardle 2008).

While the effect of wind exposure was relatively strong at the smallest two scales, as was expected, it was unexpectedly positively associated with treeline elevation, implying that valleys and hillslopes with greater wind exposure (i.e. more westerly-facing slopes) have elevated treelines. While wind exposure can locally depress treelines due to abrasion damage (Holtmeier 2009), there are several possible explanations for the contradictory result found in this study. Wind exposure may be acting as a proxy for other factors that can affect treeline elevation. For instance, and similar to our findings, Bader and Ruijten (2008) found higher treeline elevations on windy, westerly-facing locations relative to more sheltered, easterly-facing locations. They suggested that this was due to the latter slope aspect receiving greater early-morning solar radiation loads, thus subjecting seedlings to cold-induced radiation damage. Wind also plays a significant role in the pattern of snow distribution at treeline (Holtmeier and Broll 2010). At less windier locations, there may be a higher prevalence of late-lying snow in the spring, the effect of which is to shorten the growing season and decrease the time available for seedlings to complete their growth and harden off for winter (Walsh *et al.* 1994). Finally, wind may simply not influence *Nothofagus* treeline elevation; instead, if wind exposure generally increases with elevation, and if other abiotic factors act to lower treeline elevation, a spurious positive correlation between treeline elevation and wind exposure might be generated.

Over 20% of the variation in *Nothofagus* treeline elevation was unaccounted for by the spatial structure, much of which will reside at even finer scales than that of hillslope. Treeline position can vary over much shorter distances (10s of metres) due to the effects of abiotic-

biotic interactions and feedbacks (e.g. Alftine and Malanson 2004, Batllori *et al.* 2009, Elliott 2011), herbivory (Speed *et al.* 2010), pathogens (Tomback and Resler 2007), mycorrhizal host availability (Hasselquist *et al.* 2005), and seed dispersal (e.g. Cuevas 2000). Future treeline research may thus benefit from combining top-down correlative approaches, such as the one presented here, with bottom-up process based models and experiments across a range of scales and sites to gain further insights into the mechanisms driving treeline patterns and processes.

Correlative studies of treeline patterns, such as this, rely on the availability of high quality, high resolution, and spatially-explicit abiotic data to infer relationships. Unfortunately, data on key environmental variables (such as temperature at each treeline location) are often lacking, necessitating the use of proxy variables for certain factors, or relatively coarse-resolution or inaccurate data for others. This may explain the relatively weak and sometimes unexpected associations of several factors in this study, and why much of the variation in treeline elevation was unexplained by our models, particularly at finer scales. For example, spatially-explicit datasets for factors such as soil conditions and natural disturbances are typically unavailable or are of relatively coarse resolution. Indeed, the relatively weak effects of the soil and earthquake factors used in our analysis may well be indicative of the relatively low resolution of the datasets used to characterise their effects. Further, while spatially-explicit climate datasets are available, these typically interpolate data from climate stations. For factors such as temperature, frost occurrence, and wind speed, such interpolations are notoriously inaccurate in mountainous areas (Daly 2006) because climate stations are sparse and complex mountain topography generates considerable local variability (Ashcroft and Gollan 2011). The use of regional or synoptic level atmospheric models that can account for the complex topo-climatic processes occurring in these areas may provide a means to generate more accurate climatic datasets, and one of these models will be investigated in the next chapter.

Chapter 4

Evaluation of a mesoscale atmospheric model for generating fine-scale topo-climatic data in alpine zones

4.1 Introduction

Ecological studies rely heavily on the use of long-term, spatially-explicit, climatic datasets. Such datasets are typically derived from weather station observations that are averaged over a 30-year period and then spatially-interpolated to all locations on a regular grid, thus providing a relatively “smoothed” representation of climate variability across large areas. However, it is well-recognised that such spatially-interpolated data for variables such as temperature extremes, wind speed, relative humidity, and solar radiation, are less accurate in mountainous areas (Daly 2006). Mountainous areas are frequently underrepresented in terms of the distribution of weather stations, and interpolation uncertainty in these areas is therefore usually higher (Bolstad *et al.* 1998, Minder *et al.* 2010). Furthermore, in comparison to lowland areas, mountain climates are locally highly variable due to the influence of local mountain structure and topographic variation on surface energy balance, air flows, and boundary layer effects (Sturman and Tapper 2006). These ‘topoclimatic’ effects include phenomena such as aspect-related insolation differences, mountain-valley winds, and cold air drainage and ponding (Daly 2006, Daly *et al.* 2010). Indeed, studies using networks of portable microclimatic data loggers have clearly demonstrated the large degree to which topography affects estimates of meteorological parameters in complex terrain (e.g. Lindkvist *et al.* 2000, Lookingbill and Urban 2003, Pepin and Norris 2005, Chung *et al.* 2006, Lundquist *et al.* 2008, Yang *et al.* 2011, Ashcroft and Gollan 2012).

Accurate meteorological data that account for such topoclimatic effects may therefore be critical for modelling the influence of environmental variability on ecological patterns and processes in alpine areas. For instance, topoclimatic effects have been shown to dominate the occurrence and abundance of butterflies in Spain (Illán *et al.* 2010), to influence the performance of vegetation distribution models (Ashcroft 2006, Ashcroft *et al.* 2008), and to modify the extent to which climate change may determine the future distribution of high-altitude habitats (Ashcroft *et al.* 2009, Shoo *et al.* 2011, Dobrowski 2011). Similarly, topoclimatic conditions, such as the prevalence of temperature extremes, high winds, solar radiation variability, and low moisture conditions, can be influential on many aspects of plant physiological function and population dynamics in high-elevation zones (Korner 2003,

Holtmeier 2009). However, many ecological studies investigating topoclimatic effects have had to rely on data collected via on-site sensors, thus limiting the feasible extent over which studies could be carried out. As such, there have been few investigations of the importance of topoclimate in determining landscape-scale ecological patterns, largely due to the unavailability of spatially-explicit topoclimatic data. Therefore, it is of interest to investigate new approaches for generating topoclimatic data at treeline to support such analyses.

Mesoscale atmospheric models provide one approach for generating topoclimatic data in a practical manner across complex mountain landscapes (Fast 1995). Mesoscale models are numerical models that solve for a set of physically-based equations governing air flow, turbulence and thermodynamics (Pielke 1984). One of the benefits of such models is their portability: they can be run for any location without the need for parameterisation with existing meteorological data. One such model, The Air Pollution Model (TAPM – Hurley *et al.* 2005), has been applied successfully for a range of scenarios across Australia (Hurley *et al.* 2005, 2008), and for a much more limited set of situations in New Zealand (Zawar-Reza *et al.* 2005a, b, Gimson *et al.* 2007) and elsewhere (Chen *et al.* 2002, Mahmud 2009). The TAPM model explicitly accounts for three-dimensional topographic variability in its mechanics and is therefore capable of simulating topoclimatic effects (Gimson *et al.* 2007). However, there is still a limited amount of information regarding TAPM's reliability for simulating meteorological data in New Zealand in mountainous areas at resolutions finer than 1km (Gimson *et al.* 2007). If it could be demonstrated that TAPM can perform well at high elevations in complex terrain, it would enable the model to be used in place of, or in conjunction with, interpolated climate data for spatially-explicit ecological investigations in mountain environments.

As a contribution towards quantifying TAPM's performance in mountainous areas, I investigate the application of TAPM at two high-elevation weather station locations in New Zealand: Mt Ruapehu Chateau (39° 12.0' S, 175° 32.5' E, 1097 metres above sea level) in the North Island, and Craigieburn Forest (43° 9.0' S, 171° 43.0' E, 914 metres above sea level) in the South Island. The TAPM model is used to generate 200 m resolution meteorological data for January and July over the years 2001 to 2007 at each weather station and then compared with weather station observations for the same time period. I use both graphical summaries and goodness of fit statistics to compare simulated and observed data in order to address the following questions:

1. On average, does TAPM produce accurate estimates for a range of meteorological variables for the months of January and July?
2. Are simulated trends consistent between two geographically disparate locations for the different variables?
3. What are some potential implications for the use of TAPM-generated data in treeline research?

4.2 Methods

4.2.1 TAPM model

The Air Pollution Model, TAPM V.4 (Hurley 2008a) is a prognostic, mesoscale atmospheric model produced by CSIRO in Australia, which can be used to predict three-dimensional meteorology and air pollution concentrations at scales ranging from coarse (1000 to 1500 km) to fine (< 500 m). The model is highly spatially portable because local meteorological data are not required to parameterise and run the model. Instead, TAPM numerically solves for a range of physical equations that characterise atmospheric flow, thermodynamics, moisture conservation, turbulence, and dispersion in order to produce meteorological and pollution predictions (Hurley *et al.* 2005). The model uses a nested grid approach, whereby synoptic-scale analyses/forecasts drive the model at the boundaries of the coarsest grid, while the finer-scale grids are used to resolve more local-scale phenomena such as terrain-induced air flows (Hurley *et al.* 2005). Thus, the model can be used to produce meteorological data at relatively fine scales while accounting for local meteorological phenomena such as sea breezes, valley winds, and cold-air ponding events (Hurley *et al.* 2005), typical of New Zealand's mountain environments (Sturman and Tapper 2006). Further detail regarding the workings of the model is presented in Hurley *et al.* 2005 and (Hurley 2008a).

4.2.2 Climate station data

Meteorological observations from over 200 weather stations across New Zealand were initially examined for their potential alignment with the TAPM-simulated data, in terms of both the time period of interest and the types of meteorological variables measured. An

additional guiding criterion was that the weather stations needed to be located in the mountains, at or near treeline elevations. Only about 30 weather stations are located above 700 metres above sea level; of these stations, the operation of many was discontinued prior to the year 2000, rendering them unsuitable for comparison with the TAPM simulations. A number of other stations were recently established and also did not coincide temporally with the years over which simulations were run. Two stations, Mt. Ruapehu Chateau in the North Island and Craigieburn Forest in the South Island (hereafter called Ruapehu and Craigieburn), fulfilled the suitability criteria and were used for subsequent analyses (Figure 4.1). I downloaded meteorological observations for Ruapehu and Craigieburn for the study time period using NIWA's CliFlo online database (<http://cliflo.niwa.co.nz/index.html>). Downloaded Ruapehu data consisted of hourly data for temperature, relative humidity, wind speed, rainfall, and global solar radiation. Data at Craigieburn comprised daily summaries of minimum and maximum temperature, 9 am temperature, mean daily wind speed, total rainfall, and mean daily global solar radiation.

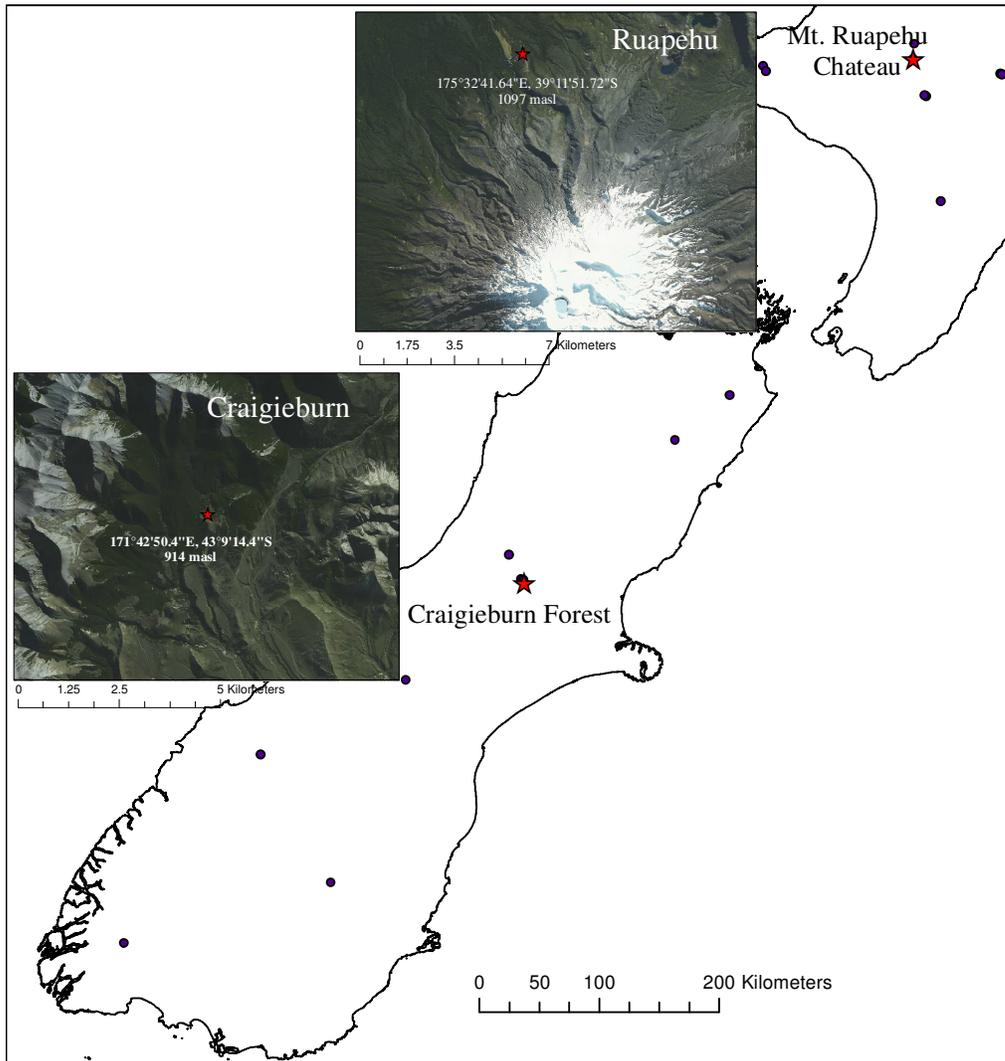


Figure 4.1 Location of the Mt. Ruapehu Chateau and Craigieburn Forest weather stations in New Zealand (stars) and all other weather stations above 700 m in elevation (black dots). Inset figures show further details at the location of each of the weather stations.

4.2.3 TAPM model parameterisation

To initialise TAPM, a range of datasets provided with the model software were used, including 6-hourly synoptic scale meteorological data at a 100km resolution and datasets describing variation in terrain, land cover, soil texture as an index of soil moisture content, leaf area index, and monthly mean sea surface temperatures (Hurley 2008b). Several user-defined input parameters are also required to configure the model (Table 4.1). Meteorological outputs from the model comprise hourly data for air and screen-level temperatures ($^{\circ}\text{C}$), screen-level relative humidity (%), wind speed (m s^{-1}) and direction ($^{\circ}$), rainfall (mm), total solar radiation (W m^{-2}), and net radiation (incoming minus outgoing radiation - W m^{-2}) over the period of time for which the model is run. For this study, TAPM was configured and run for January and July, for 2001 through to 2007. A four-nested-grid setup was used for the model runs; grid spacings in both the X and Y dimensions, from coarse to fine, were 12,800 m, 3,200 m, 800 m, and 200 m. This grid setup follows the recommendations (Hurley 2008b) of maintaining a grid spacing ratio of between two to four and of choosing an outer grid domain large enough to ensure that the boundary region is adequately distant from the central region of interest. The finest grid spacing (200 m) also fulfils the study requirement of producing meteorological data at a scale fine enough to be representative of site-level conditions (e.g. at a weather station (this chapter) or at treeline locations (Chapter 5)). For each nested grid, the model was run for 35 grid points, equating to a 7×7 km grid extent at the finest (200 m) grid scale. Two sets of model runs were carried out for the two months and seven years, with each of the sets being centred on one of two weather station locations, Ruapehu or Craigieburn Forest, for which meteorological observations could be extracted and compared to the TAPM output.

Table 4.1 Input parameters used to initialise the TAPM model at the Ruapehu and Craigieburn weather station locations.

Grid set up	Grid domain 1	Grid domain 2	Grid domain 3	Grid domain 4
Grid points	35 x 35	35 x 35	35 x 35	35 x 35
Grid spacing	12 800 m	3200 m	800 m	200 m
Vertical levels	25	25	25	25
Grid centre coordinates	Mt. Ruapehu	39° 12.0' S	Craigieburn	43° 9.0' S
	Chateau	175° 32.5' E	Forest	171° 43.0' E

Advanced/Experimental options

Synoptic pressure gradient, temperature and moisture filtering	1.0
Synoptic pressure gradient scaling factor	Varied between 0.25 and 1.0 to obtain model stability
Boundary conditions	Vary with 3-D space and time; from synoptic analysis
Surface vegetation	Included (default data)
Non-hydrostatic pressure	Not included
Rain processes	Included
Snow processes	Not included
Prognostic eddy dissipation rate	Included
Soil moisture	Default settings
Soil temperature	Default settings
Sea surface temperature	Default settings

4.2.4 TAPM model evaluation

Time series of meteorological data simulated by TAPM were compared with those observed at the Ruapehu and Craigieburn stations to determine if TAPM was able to accurately simulate observed trends for the different meteorological variables. For the hourly Ruapehu data, observations could be directly compared with hourly-level data from TAPM simulations. For the Craigieburn site, TAPM data were summarised at the daily level to enable comparisons. This study was not aimed at determining the nature, strength, or significance of temporal trends in the data (ie time-series analyses); rather, the main aim was simply to quantify the goodness of fit, on an hourly or daily basis, of the model-simulated data in comparison to observed meteorological measurements. I made these comparisons using a combination of time-series profile plots, graphical summaries of simulated and observed data, and goodness of fit (GOF) statistics for simulated versus observed trends. I used three GOF statistics to assess the performance of TAPM with respect to simulating meteorological data: mean bias (BIAS), normalised root mean square error (NRMSE) and index of agreement (IOA). These are among a number of frequently-used statistics for comparing simulated and observed values for streamflow time-series data in hydrological studies (Legates and McCabe 1999, Gordon *et al.* 2004, Krause *et al.* 2005, Zambrano-Bigiarini 2011) and for climatic time-series data in meteorological modelling studies (Zawar-Reza *et al.* 2005c, Gimson *et al.* 2007, Mahmud 2009).

The mean bias (BIAS) was used as a measure of whether TAPM under or overestimated a given meteorological variable, on average, over a given time period. BIAS is calculated as the mean of the differences between hourly simulated (*sim*) and observed (*obs*) values across a given time period:

$$\text{Eq. 4.1} \quad \text{BIAS} = \frac{\sum(\text{sim} - \text{obs})}{n}$$

Negative BIAS values therefore indicate the average amount of underestimation compared to observed values, and positive BIAS values the average amount of overestimation, expressed in the original units of measurement of the variable of interest.

Second, the normalised root mean square error (NRMSE) was used as a measure of the degree of model simulation accuracy (RMSE), expressed as the percentage of the maximum observed variability in the data (Zambrano-Bigiarini 2011).

$$\text{Eq. 4.2} \quad \text{NRMSE} = 100 \times \left[\frac{\text{RMSE}}{\max(\text{obs}) - \min(\text{obs})} \right]$$

where the RMSE is the root mean square error and is calculated as:

$$\text{Eq. 4.3} \quad \text{RMSE} = \sqrt{\frac{\sum(\text{sim} - \text{obs})^2}{n}}$$

Third, the index of agreement (IOA) was used as a measure of the ability of the TAPM model to capture the variability and the mean of observed data, and indicates whether model trends conform well to observed trends (Willmott 1981). This metric is computed as the ratio between the mean square error and the “potential error”, with the latter term calculated as the sum of the squared absolute values of the distances from the predicted values to the mean observed value and distances from the observed values to the mean observed value (Willmott *et al.* 1985):

$$\text{Eq. 4.4} \quad \text{IOA} = 1 - \frac{\sum(\text{sim} - \text{obs})^2}{\sum(|\text{sim} - \overline{\text{obs}}| + |\text{obs} - \overline{\text{obs}}|)^2}$$

IOA is similar in structure to the coefficient of determination (R^2) of the linear correlation between observed and simulated values, and similarly produces values ranging from 0 and 1, with higher values indicating a stronger fit. However, in comparison to R^2 , IOA is considered a more realistic measure of fit in that it is more sensitive to differences in the observed and model-simulated means and variances (Willmott 1981).

4.3 Results

4.3.1 Mt. Ruapehu

Hourly time series plots for the Ruapehu station (Figures 4.2 and 4.3 and Appendix D) indicated that TAPM varied in its ability to reproduce observed trends in the five meteorological variables for January and July across the 2001-2007 time period. Hourly

variations for temperature and solar radiation appeared relatively well simulated by the model, although low minimum temperatures and maximum solar radiation values were often not well estimated. By comparison, simulated trends for wind speed and relative humidity were more variable in their hourly alignment with observed trends across each month and year, with simulations corresponding closely with observed trends for some periods of the month and diverging for others. The amount of hourly rainfall was generally not well-predicted by TAPM, with simulated values being much higher than observed values; TAPM could, however, predict reasonably well the number of days per month for which there was a rainfall event, particularly in July, although there was still an overestimation bias (Table 4.2).

Statistical measures of simulation accuracy for the five meteorological variables at the Ruapehu station decreased in the order of temperature > solar radiation > wind speed > relative humidity > rainfall for both January and July. There was good statistical agreement between hourly simulated and observed values for temperature (Figures 4.4A and 4.5A), wind speed (Figures 4.4C and 4.5C), and solar radiation (Figure 4.4E and 4.5E) across the seven years and for January and July. Simulation accuracy for these three variables was high, with relatively low BIAS values, and IOA values consistently higher than 0.8 for January (Table 4.3) and 0.7 for July (Table 4.4); NRMSE values were below 100% for January simulations (Table 4.3), indicating that model prediction error was within the range of observed data variability; for July, NRMSE ranged from about 72% to a high of 200%, indicating relatively higher model error for this month (Table 4.4). Simulated values for hourly relative humidity were moderately-well aligned with observations across the two months and seven years (Figures 4.6B and 4.7B). Mean BIAS for relative humidity was -10%, on average, for both months indicating a slight underestimation by TAPM; overall simulation accuracy was moderately good, with IOA values ranging from 0.56 to 0.69 for January (Table 4.3) and 0.56 to 0.71 for July (Table 4.4) and NRMSE values ranging between approximately 110% and 160% for both the January and July simulations (Tables 4.3 and 4.4). Hourly rainfall was highly overestimated, on average, by TAPM for both January (1.25 mm hr^{-1}) and July (1.77 mm hr^{-1}) and simulation accuracy was low for both months across all years (Figures 4.4D and 4.5D); IOA values were low (0.19-0.48) and model error was three to five times the level of observed variation (Table 4.3 and 4.4).

Table 4.2 The number of observed days with rainfall at the Mt. Ruapehu Chateau and Craigieburn Forest weather stations compared with those simulated by the TAPM model at those locations for the months of January and July over the years 2001 to 2007.

	Year	Ruapehu raindays			Craigieburn raindays		
		Observed	Simulated	(Sim - Obs)	Observed	Simulated	(Sim - Obs)
January	2001	18	26	8	13	21	8
	2002	19	24	5	22	24	2
	2003	16	21	5	18	20	2
	2004	14	18	4	17	22	5
	2005	11	20	9	13	23	10
	2006	18	26	8	15	22	7
	2007	19	21	2	17	23	6
	Mean	16.4	22.3	5.9	16.4	22.1	5.7
July	2001	17	19	2	23	17	-6
	2002	21	27	6	21	22	1
	2003	21	22	1	19	23	4
	2004	18	22	4	27	26	-1
	2005	24	26	2	23	24	1
	2006	19	24	5	23	25	2
	2007	25	28	3	20	28	8
	Mean	20.7	24.0	3.3	22.3	23.6	1.3

Table 4.3 Goodness of fit statistics for TAPM-simulated hourly meteorological data relative to hourly observations at the Mt. Ruapehu Chateau weather station for the month of January.

Variable	Year	Goodness of fit metric		
		BIAS	NRMSE (%)	IOA
A. Temperature (°C)	2001	-0.04	51.50	0.92
	2002	-0.53	55.50	0.90
	2003	-0.10	47.20	0.93
	2004	-1.02	57.10	0.90
	2005	-0.87	52.70	0.91
	2006	-0.59	47.90	0.93
	2007	-0.37	62.70	0.86
B. Relative humidity (%)	2001	-12.09	130.10	0.68
	2002	-11.63	159.30	0.56
	2003	-10.14	137.10	0.61
	2004	-11.52	116.40	0.67
	2005	-9.81	122.80	0.66
	2006	-6.21	118.80	0.69
	2007	-15.88	173.50	0.56
C. Wind speed (m s ⁻¹)	2001	-0.17	66.80	0.89
	2002	0.17	99.10	0.58
	2003	0.33	67.30	0.78
	2004	0.16	106.80	0.71
	2005	0.03	95.20	0.65
	2006	-0.13	97.70	0.88
	2007	0.49	83.40	0.59
D. Rainfall (mm)	2001	0.79	243.40	0.31
	2002	1.63	524.30	0.19
	2003	1.07	399.50	0.33
	2004	0.65	345.40	0.30
	2005	1.57	451.60	0.35
	2006	2.01	545.40	0.24
	2007	1.05	429.10	0.29
E. Solar radiation (Watts m ⁻²)	2001	86.13	74.20	0.89
	2002	58.75	83.40	0.85
	2003	42.34	67.50	0.90
	2004	38.20	64.40	0.90
	2005	nd	nd	nd
	2006	nd	nd	nd
	2007	44.59	86.10	0.83

Table 4.4 Goodness of fit statistics for TAPM-simulated hourly meteorological data relative to hourly observations at the Mt. Ruapehu Chateau weather station for the month of July.

Variable	Year	Goodness of fit metric		
		BIAS	NRMSE (%)	IOA
A. Temperature (°C)	2001	0.83	72.70	0.78
	2002	-0.14	64.50	0.85
	2003	0.62	67.20	0.83
	2004	-0.08	63.80	0.84
	2005	0.01	64.70	0.83
	2006	0.39	69.20	0.80
	2007	-0.62	63.40	0.87
B. Relative humidity (%)	2001	-9.21	154.40	0.56
	2002	-12.50	148.10	0.60
	2003	-9.59	130.40	0.68
	2004	-15.92	151.60	0.64
	2005	-7.99	153.80	0.67
	2006	-8.57	142.00	0.64
	2007	-5.24	111.50	0.71
C. Wind speed (m s ⁻¹)	2001	2.17	199.90	0.53
	2002	1.14	86.10	0.84
	2003	1.00	123.50	0.72
	2004	1.34	149.00	0.66
	2005	0.36	111.90	0.73
	2006	1.26	132.60	0.69
	2007	0.74	72.50	0.88
D. Rainfall (mm)	2001	0.60	302.50	0.48
	2002	1.84	433.80	0.36
	2003	1.40	458.40	0.36
	2004	2.21	681.90	0.25
	2005	2.15	513.10	0.33
	2006	1.65	360.10	0.37
	2007	2.51	506.30	0.34
E. Solar radiation (Watts m ⁻²)	2001	38.97	89.7	0.85
	2002	14.84	84.9	0.84
	2003	24.81	81.4	0.86
	2004	nd	nd	nd
	2005	nd	nd	nd
	2006	nd	nd	nd
	2007	14.47	79.8	0.87

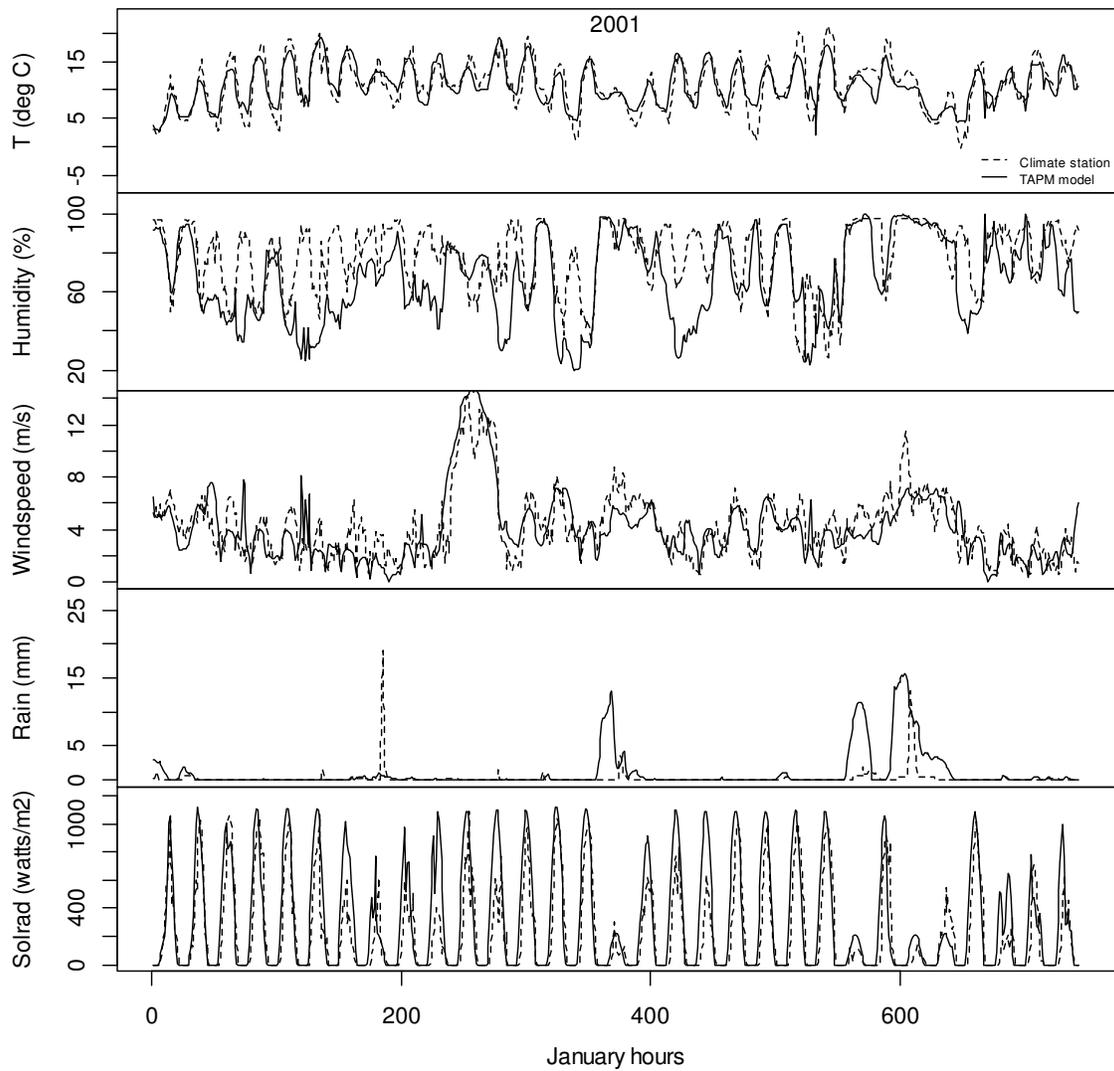


Figure 4.2 An example of hourly time series plots for TAPM-simulated versus observed meteorological variables at the Mt. Ruapehu Chateau weather station for January 2001. Plots for the full Jan 2001-2007 time period are presented in Appendix D.

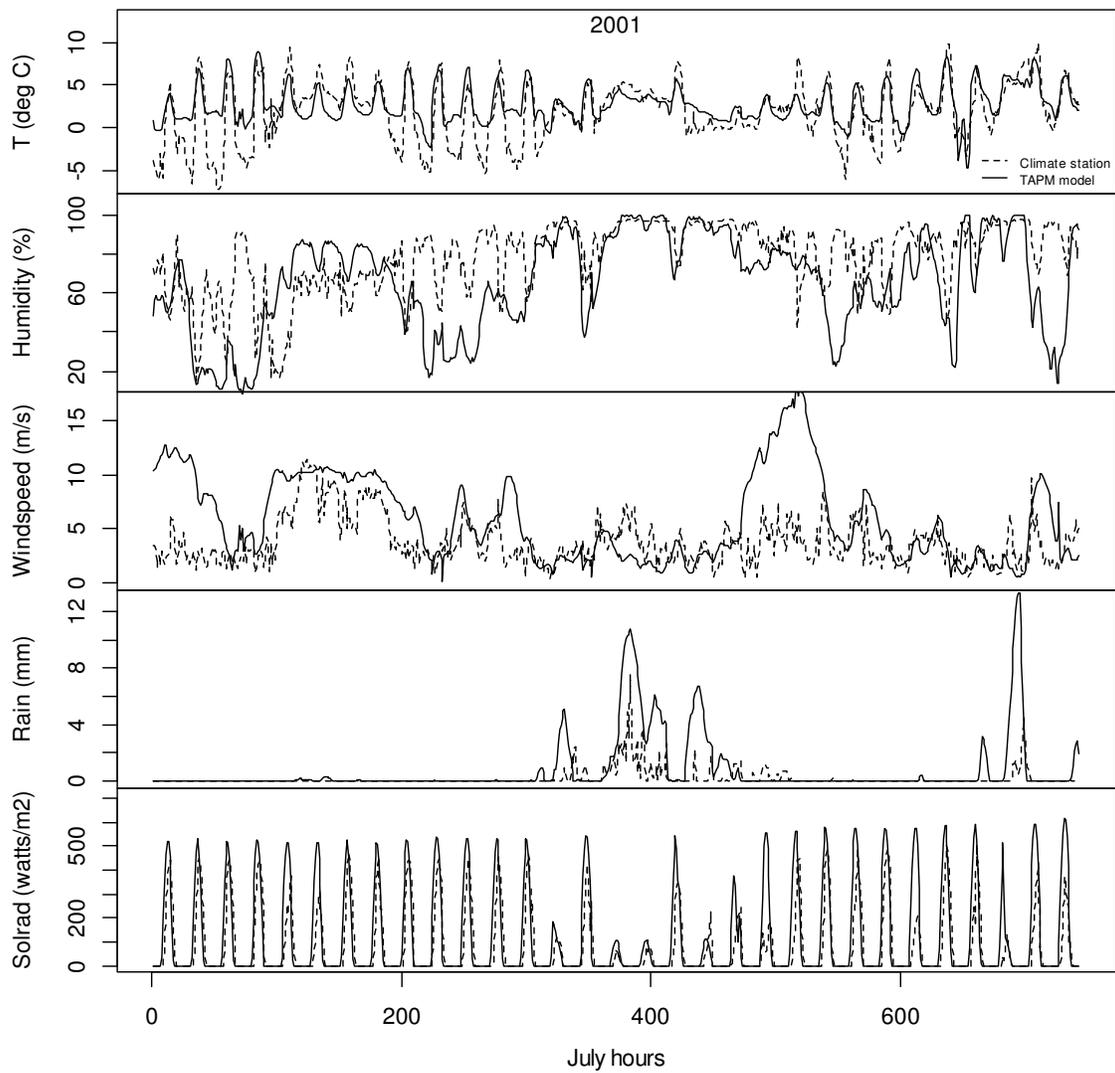


Figure 4.3 An example of hourly time series plots for TAPM simulated versus observed meteorological variables at the Ruapehu weather station for July 2001. Plots for the full July 2001-2007 time period are presented in Appendix D.

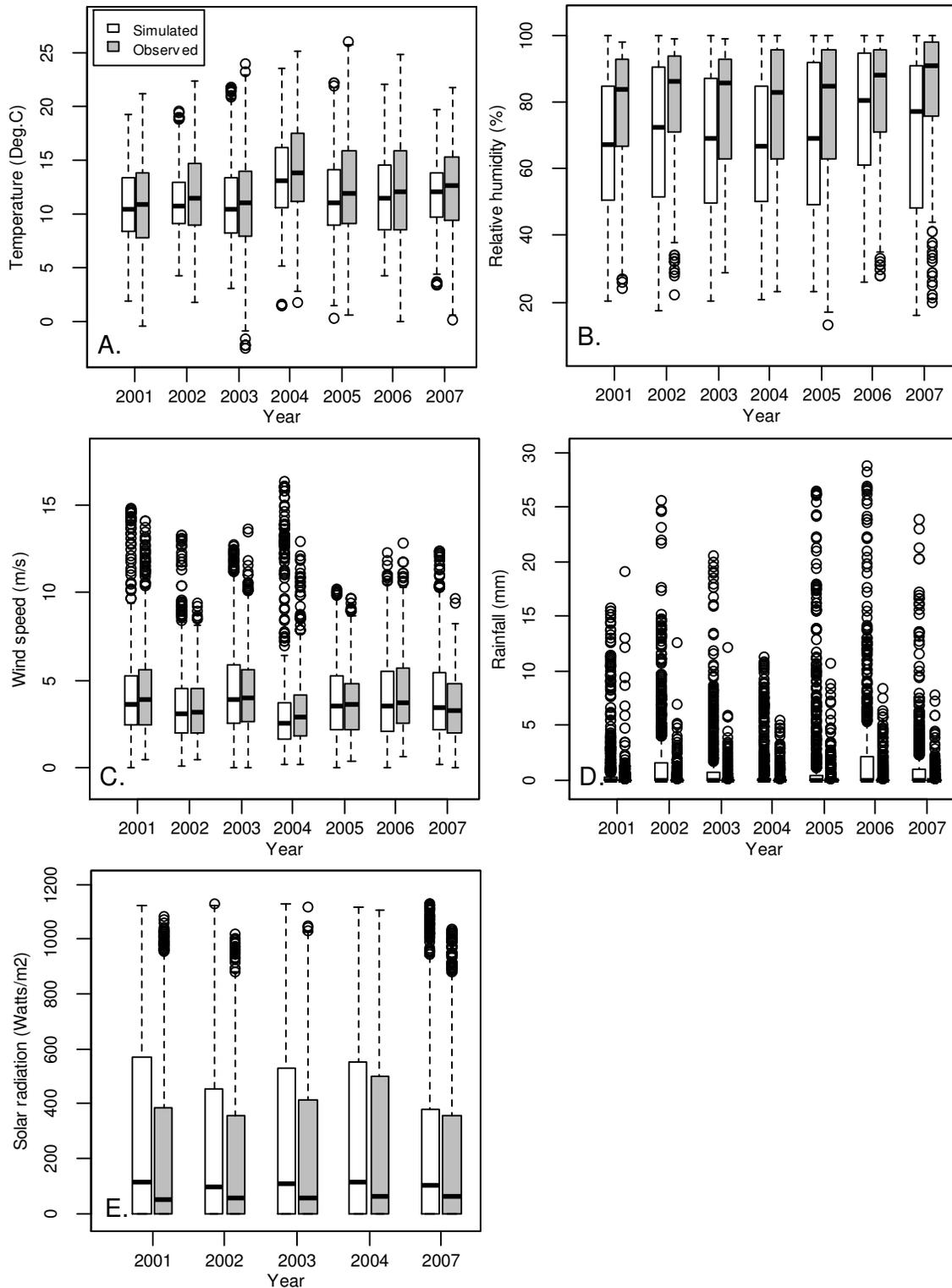


Figure 4.4 Summary of TAPM-simulated and observed January hourly meteorological data at the Mt. Ruapehu weather station.

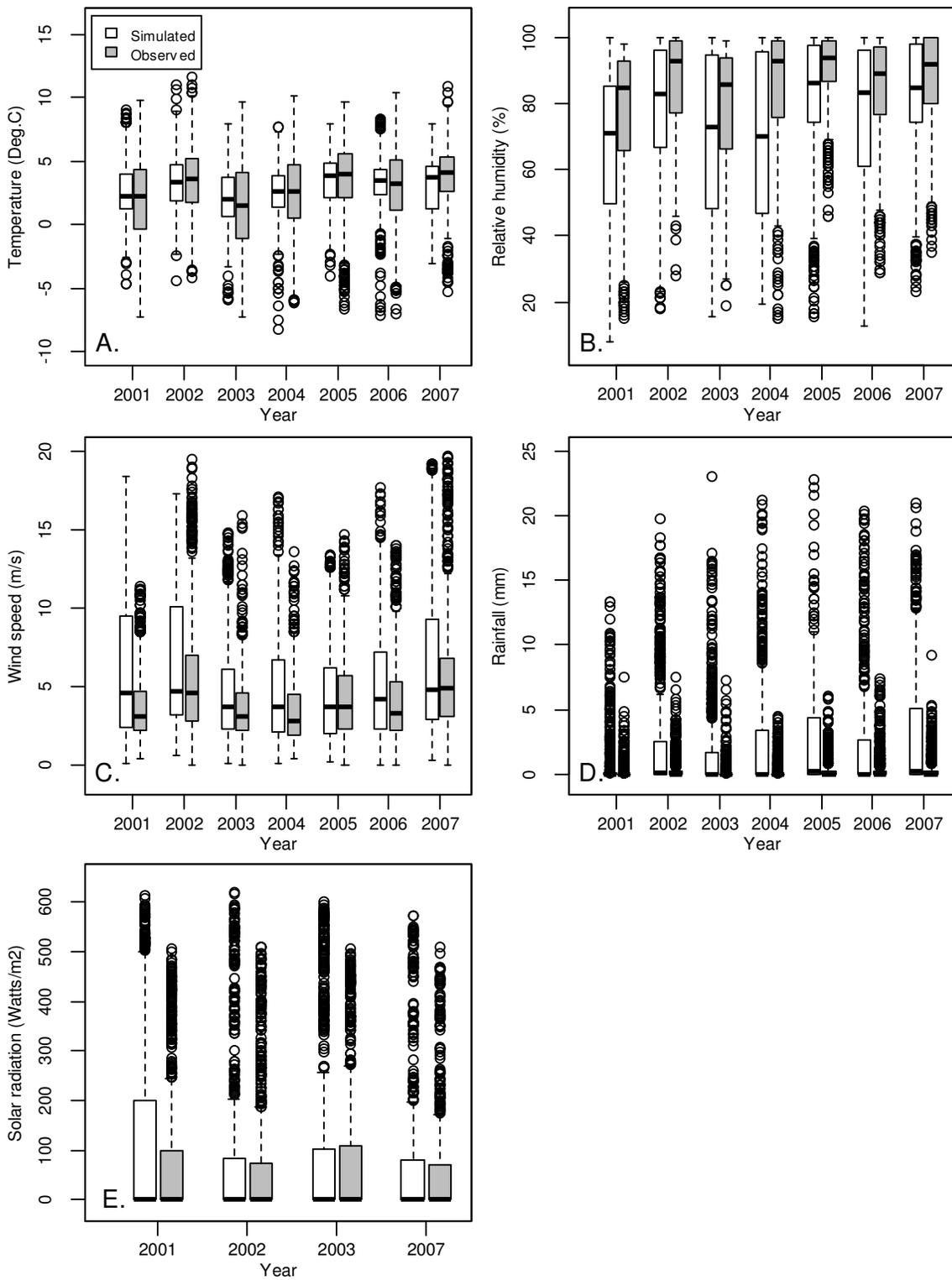


Figure 4.5 Summary of TAPM-simulated and observed July hourly meteorological data at the Mt. Ruapehu weather station.

4.3.2 Craigieburn Forest

At the Craigieburn Forest weather station, plots of daily meteorological time series (Figures 4.6 and 4.7) indicated that TAPM was relatively successful in reproducing observed trends in daily minimum and 9am temperatures and wind speed across the seven years, although the level of agreement was generally higher for the month of January than for July. While TAPM reproduced overall daily trends in maximum daily temperatures at Craigieburn, there was a consistent underestimation of this variable for both months. Conversely, mean daily solar radiation was consistently overestimated for many days in both months, across all years. Similar to the hourly-based results at the Ruapehu station, daily rainfall totals were overestimated at Craigieburn, but to a lesser degree, and the number of daily rainfall events were similarly generally well-simulated (Table 4.2).

Statistically, there was a range of variability in the accuracy of TAPM simulations among the six meteorological variables evaluated, as well as between the two months and across the seven years, in some cases. There was reasonably good agreement between the distributions of daily simulated and observed values for January minimum temperatures (Figure 4.8B), January 9am temperatures (Figure 4.8C), and both January (Figure 4.8D) and July (Figure 4.9D) maximum daily windspeeds for most years. For both months, estimates for these variables were relatively unbiased, IOA values were mostly in the range of 0.75 to 0.95, and NRMSE values were mostly lower than 100%, indicating good model accuracy and a reasonably low degree of simulation error (Tables 4.5 and 4.6). While temporal trends in simulated daily maximum temperatures were relatively well-aligned with observed trends (Figures 4.4 and 4.5), the high underestimation bias for both January (-6.2°C) and July (-3.7°C) across all years (Tables 5 and 6, and Figures 4.8A, and 4.9A) produced a relatively poor overall fit to the data, with IOA values in the range of 0.5 and 0.7 and NRMSE values in the range of 120 and 200% for both months (Tables 4.5 and 4.6). Daily rainfall amounts at Craigieburn for both months were somewhat better-simulated than hourly rainfall at Ruapehu (Figures 4.8E and 4.9E). Nonetheless, TAPM-simulated daily rainfall was strongly overestimated, had relatively high simulation error and low accuracy for both months and for most years (Tables 4.5 and 4.6). On the whole, average daily solar radiation for both months was not well-simulated (Figure 4.8F and 4.9F); there was considerable positive bias in simulated solar radiation, leading to relatively high model error and weak model fits for January (Table 4.5) and for July (Table 4.6), although solar radiation was relatively better-simulated for July 2001 and 2002.

Table 4.5 Goodness of fit statistics for TAPM-simulated daily meteorological data relative to daily observations at the Craigieburn Forest weather station for the month of January.

Variable	Year	Goodness of fit metric		
		BIAS	NRMSE (%)	IOA
Daily maximum temperature (°C)	2001	-6.95	186.8	0.55
	2002	-4.85	112.6	0.7
	2003	-5.75	127.1	0.7
	2004	-5.62	118.2	0.71
	2005	-6.43	136	0.65
	2006	-8.3	162.9	0.57
	2007	-5.53	134.9	0.67
Daily minimum temperature (°C)	2001	-0.44	81	0.83
	2002	-0.89	98.5	0.75
	2003	-0.14	70.3	0.86
	2004	0.15	82.6	0.85
	2005	-0.37	75	0.86
	2006	-0.36	78.5	0.85
	2007	-1.22	115.3	0.74
Temperature at 9am (°C)	2001	0.4	96.6	0.75
	2002	0.15	121.8	0.66
	2003	-0.11	88.1	0.83
	2004	0.54	75.7	0.86
	2005	-0.37	109	0.72
	2006	-0.79	91.6	0.79
	2007	0.35	78.4	0.84
Daily maximum wind speed (m s ⁻¹)	2001	0.43	50	0.94
	2002	0.71	60.5	0.87
	2003	1.33	80.3	0.88
	2004	0.87	53.9	0.9
	2005	2.29	71.6	0.87
	2006	0.5	73	0.77
	2007	2.29	78.9	0.82
Daily total rainfall (mm)	2001	5.24	316.6	0.17
	2002	6.65	235.7	0.49
	2003	2.88	143.4	0.6
	2004	2.8	134.2	0.47
	2005	3.21	153.8	0.61
	2006	12.96	403.9	0.14
	2007	5.55	205.9	0.67
Daily average solar radiation (Watts m ⁻²)	2001	88.21	212.6	0.47
	2002	146.93	211.3	0.53
	2003	122.6	156.9	0.58
	2004	141.74	183.7	0.53
	2005	130.04	202.8	0.5
	2006	148.75	227.3	0.42
	2007	145.26	217.7	0.5

Table 4.6 Goodness of fit statistics for TAPM-simulated daily meteorological data relative to daily observations at the Craigeburn Forest weather station for the month of July.

Variable	Year	Goodness of fit metric		
		BIAS	NRMSE (%)	IOA
Daily maximum temperature (°C)	2001	-2.44	122.9	0.71
	2002	-3.76	143.2	0.64
	2003	-4.11	117.2	0.71
	2004	-3.35	172.7	0.5
	2005	-4.48	197.9	0.48
	2006	-3.88	138.3	0.63
	2007	-3.86	126.9	0.66
Daily minimum temperature (°C)	2001	-1.12	179.5	0.59
	2002	2.22	138.7	0.61
	2003	2.5	123.5	0.67
	2004	0.19	129.4	0.68
	2005	-0.33	97	0.73
	2006	1.87	119	0.52
	2007	0.01	61	0.9
Temperature at 9am (°C)	2001	2.04	123.8	0.51
	2002	-0.93	135.6	0.35
	2003	1.65	98.8	0.69
	2004	1.22	101.8	0.54
	2005	0.08	93.5	0.59
	2006	1.42	112.6	0.51
	2007	0.58	68.4	0.81
Daily maximum wind speed (m s ⁻¹)	2001	2.81	121.4	0.77
	2002	3.11	102.7	0.82
	2003	3.02	72.4	0.83
	2004	1.69	65.7	0.85
	2005	1.54	66	0.87
	2006	2.94	78.2	0.84
	2007	1.77	55.7	0.91
Daily total rainfall (mm)	2001	1.49	279.6	0.31
	2002	13.35	661.9	0.13
	2003	12.36	388.5	0.24
	2004	4.6	187.6	0.51
	2005	1.95	137.2	0.66
	2006	26.06	480.5	0.22
	2007	5.89	509.8	0.36
Daily average solar radiation (Watts)	2001	34.28	171.9	0.65
	2002	24.45	171.3	0.69
	2003	38.05	183.8	0.58
	2004	42.88	257.7	0.43
	2005	57.68	305.7	0.37
	2006	38.71	217.7	0.57
	2007	52.59	275.2	0.44

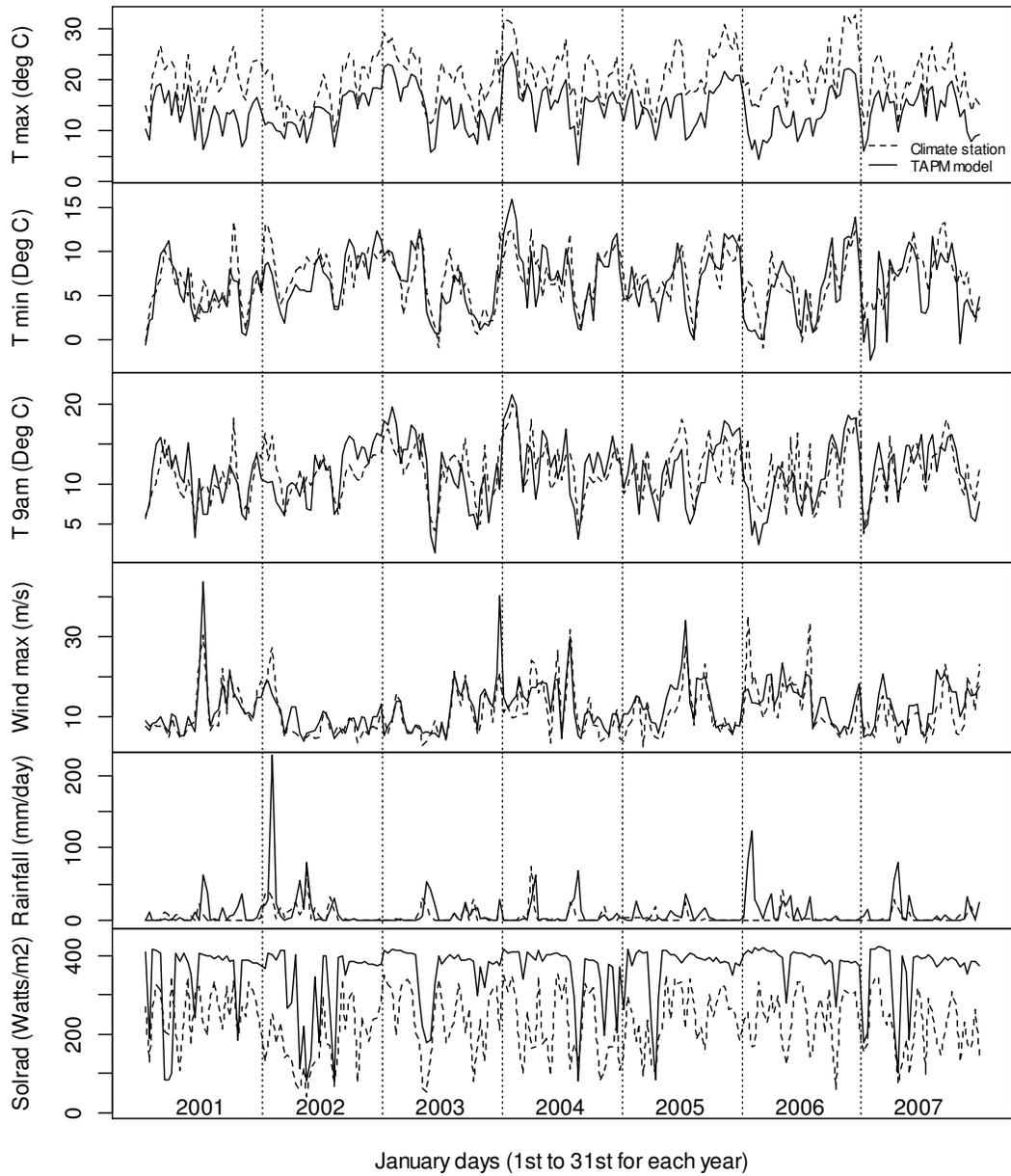


Figure 4.6 Daily time series plots for TAPM simulated versus observed meteorological variables at the Craigieburn weather station for January, for the years 2001 to 2007.

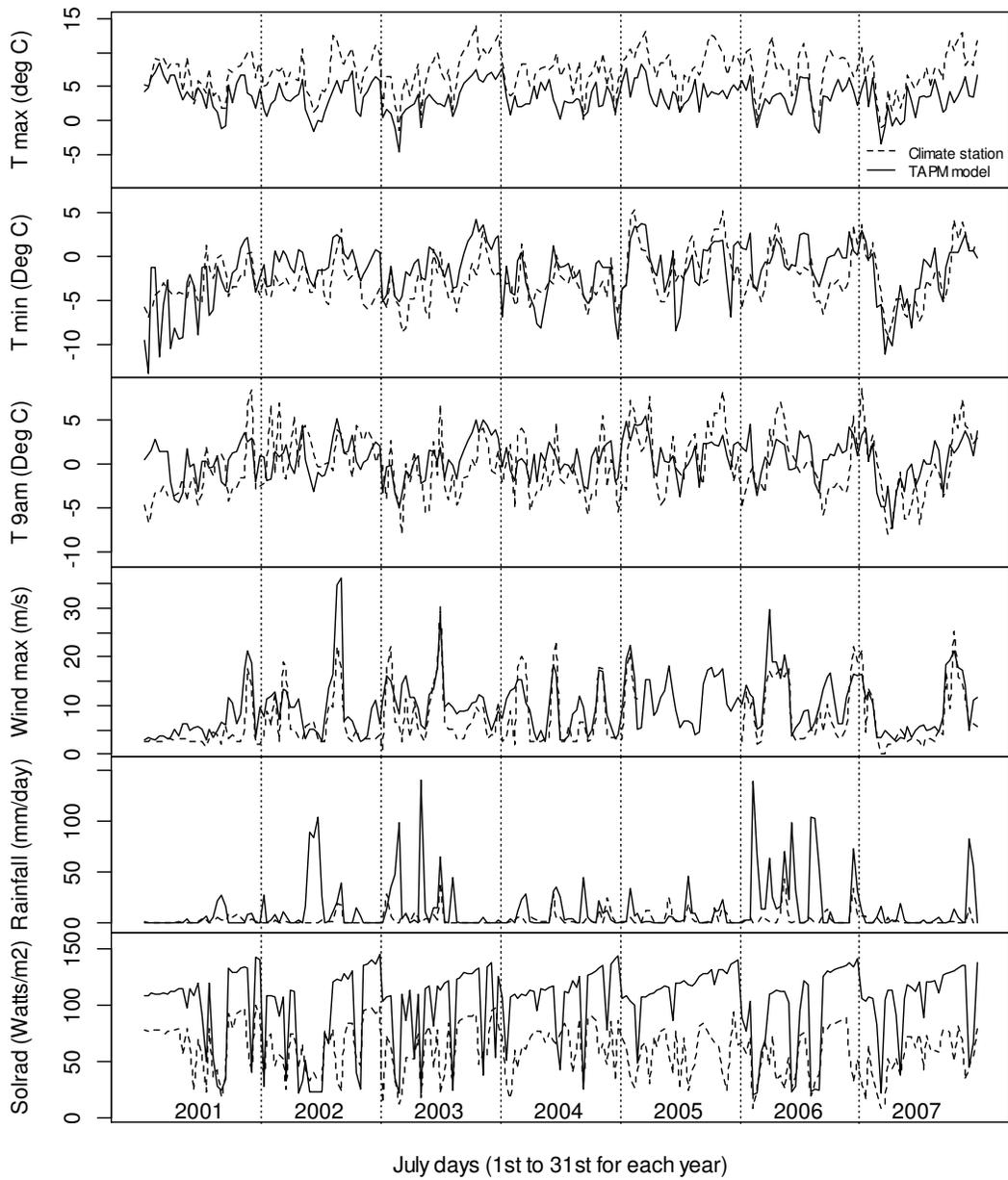


Figure 4.7 Daily time series plots for TAPM simulated versus observed meteorological variables at the Craigieburn weather station for July, for the years 2001 to 2007.

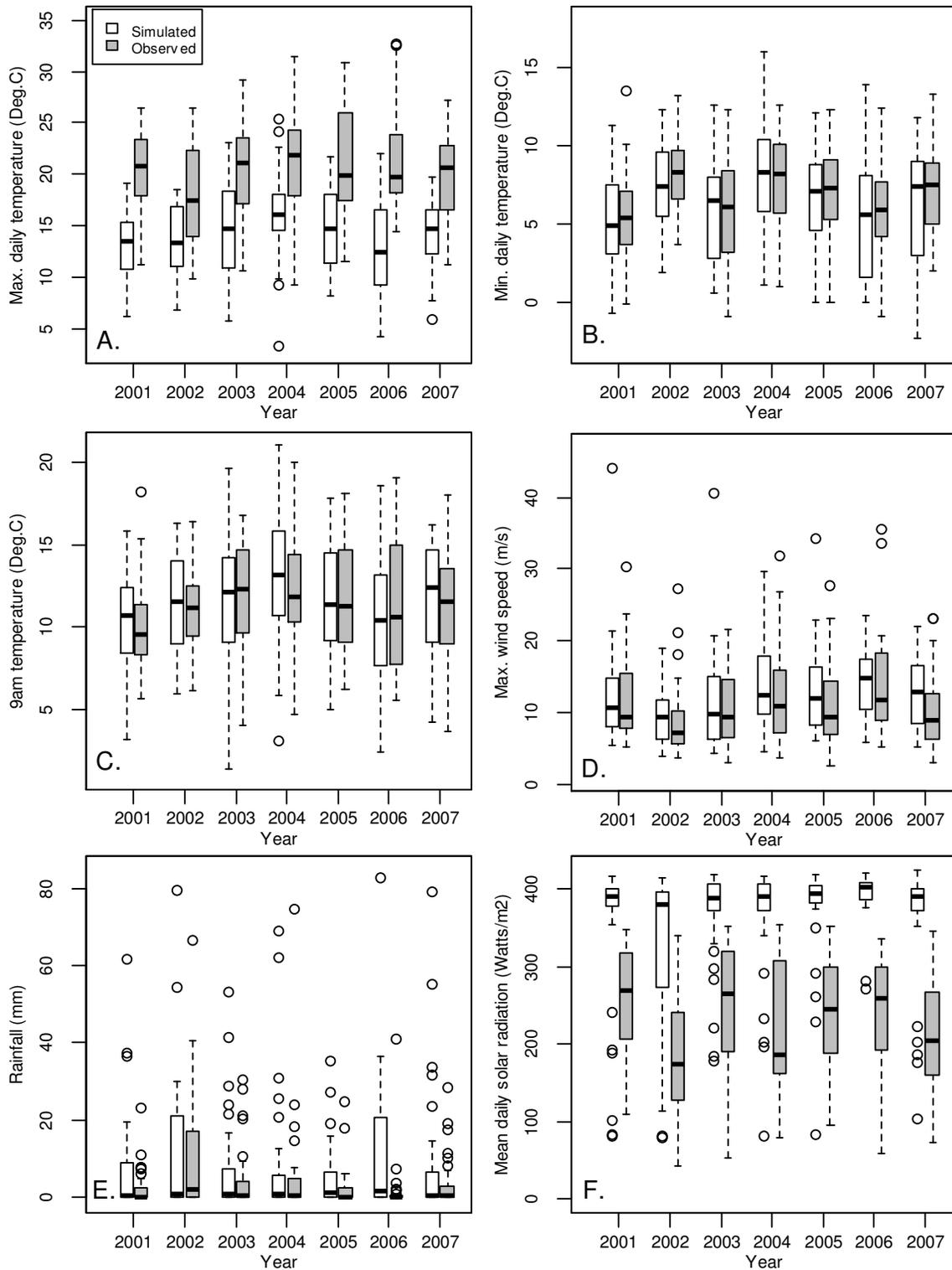


Figure 4.8 Summary of TAPM-simulated and observed January daily meteorological data at the Craigeburn Forest weather station.

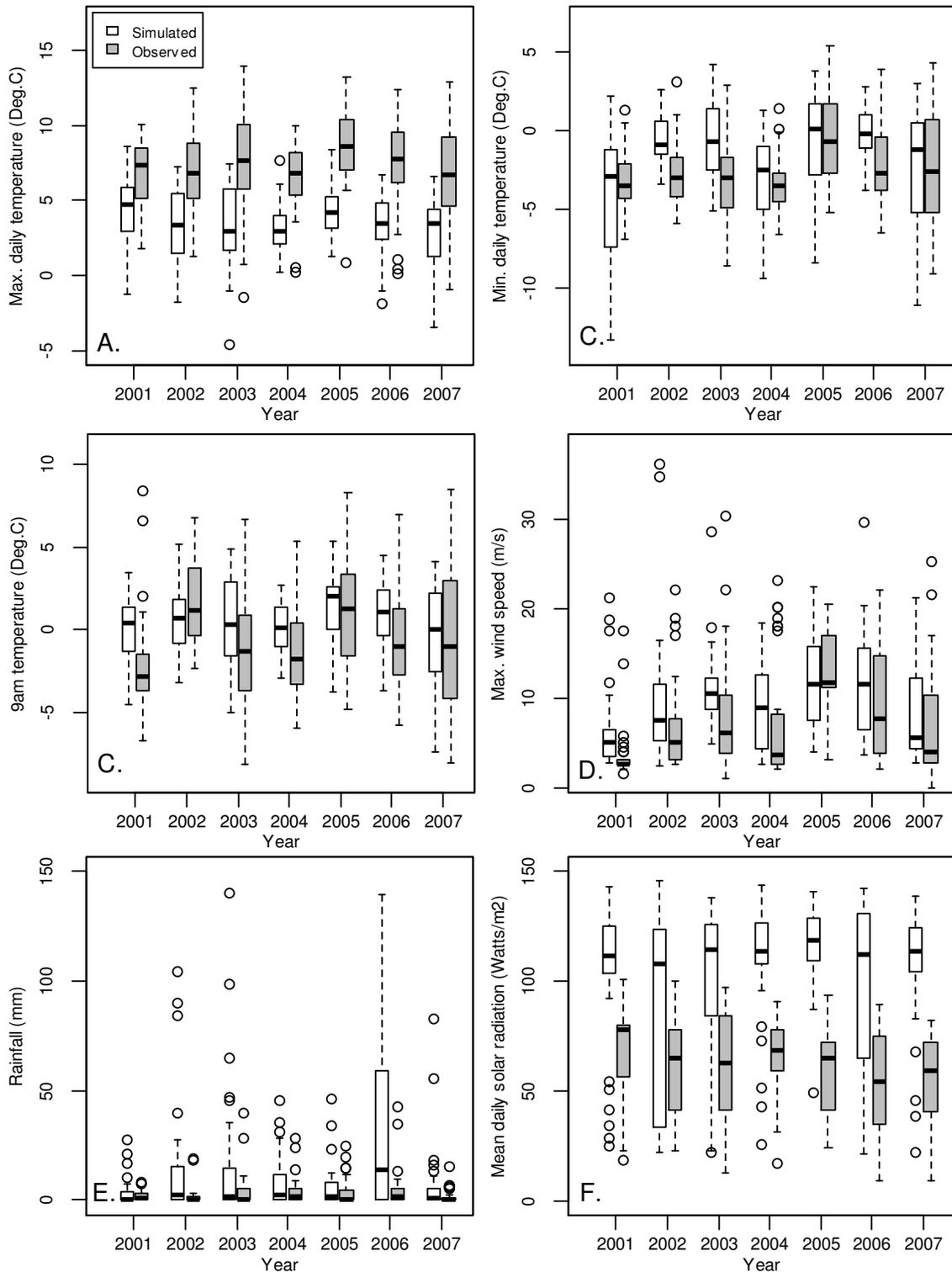


Figure 4.9 Summary of TAPM-simulated and observed July daily meteorological data at the Craigeburn Forest weather station.

4.4 Discussion

This study offers one of the first evaluations of the TAPM model at high-elevation locations in complex alpine environments. TAPM simulations carried out for both January and July, across a seven year period, at a site in each of the North and South Islands of New Zealand provided a comprehensive assessment of how the model performs in seasonal extreme conditions and in the face of potential yearly variability. Further, this study is the first to test TAPM at a scale fine enough (200 m) to determine if the model can adequately account for local topographic variation in order to produce accurate meteorological estimates. Although Gimson *et al.* (2007) suggested that a 1km resolution was the finest practical resolution at which TAPM can be applied, results from the present study suggest that the model in fact performs well at the 200 m resolution and can generate realistic estimates for a number of meteorological variables in a relatively consistent manner. This indicates that there is potential for TAPM to be used to generate data at scales applicable to local-scale ecological investigations.

Simulation results for both temperature and windspeed from this present study are consistent with those from many previous evaluations of TAPM (e.g. Luhar and Hurley 2004, Zawar-Reza *et al.* 2005c, Gimson *et al.* 2007, Hurley *et al.* 2008, Mahmud 2009, Tang *et al.* 2009) in that simulated data for these variables were relatively unbiased and reasonably accurate on the whole for both months, over the seven years. Temperature and wind speed have received the greatest treatment in the literature in terms of validating the various meteorological outputs produced by TAPM. This is because the accuracies of temperature and windspeed provide an indication of the performance of the core model processes and reflect local thermal circulation, which governs pollutant dispersal (Tang *et al.* 2009). At Ruapehu, simulated hourly temperatures were relatively unbiased, as were daily temperature minimums and 9am temperatures at Craigieburn. However, the model frequently overestimated hourly temperature minimum extremes at the former station and consistently underestimated daily maximums at the latter station. Previous assessments have similarly shown that TAPM has difficulty in accurately modelling low temperatures in particular (Zawar-Reza *et al.* 2005a, Gimson *et al.* 2007, Tang *et al.* 2009), likely due to nighttime temperature inversions and zero solar radiation and low windspeed conditions.

While TAPM was unable to resolve all of the fine scale temporal variation in wind speed that was apparent in the observed time series, particularly at an hourly scale, overall trends were nonetheless preserved, resulting in a reasonable level of simulation accuracy.

There was a slight mean overestimation of wind speed (1.14 m s^{-1}) for the month of July at Ruapehu, although this bias amounted to only about 28% of the observed variation. At Craigieburn, daily wind speed maximums were also well-captured by the model for both months over the seven years. In general, it is common for mesoscale models to overestimate windspeed during calm nights (Gimson *et al.* 2007), where low or intermittent turbulence conditions cannot be properly accounted for by the inherent model physics (Luhar and Hurley 2004).

In comparison to evaluations of temperature and windspeed, there is a paucity of published validation studies of other meteorological outputs from TAPM, such as solar radiation, relative humidity, and rainfall. Results from simulations at Ruapehu suggest that hourly solar radiation can be reasonably well-simulated by TAPM, although there is tendency towards consistent overestimation at times of peak daily solar radiation of about 25 to 50 W m^{-2} , on average, for these hours. These hourly positive biases become more pronounced when solar radiation is averaged at a daily time scale because the greatest overestimations coincide with the hours of the day when solar radiation values are at their highest levels. For hourly relative humidity, TAPM produced accurate estimates for some days of the month in both January and July, while for other days there was a considerable degree of underestimation due to the model not being able to adequately simulate the diurnal pattern. The consequence of this is an overall underestimation bias of about 10% for both January and July, resulting in only moderately-good simulation accuracies, on average, for relative humidity. In one of the only studies that has evaluated TAPM simulation accuracy for solar radiation (net radiation) and relative humidity, Luhar and Hurley (2004) found similar results to the present study: a mean positive simulation bias for solar radiation and a mean negative bias for relative humidity, for a year-long simulation of meteorological data at a site near Perth, Australia.

No published evaluations of TAPM-simulated rainfall quantities could be found. However, results from the present study suggest that TAPM-simulated rainfall amounts are strongly positively biased at both sites, although simulations appear to be more accurate for daily quantities at Craigieburn. Nonetheless, the number of simulated and observed rainfall days per month corresponds quite well, on average, across years at both sites, suggesting that the model can at least predict the occurrence of rainfall on a coarse level in a relatively consistent manner.

The evaluation of TAPM's applicability in mountain environments could be further extended beyond what was carried out in this study. Comparisons of TAPM outputs against

further weather stations or spatially-distributed observations (collected with temperature loggers, for instance) that cover a range of topoclimatic conditions in mountain areas are warranted. For instance, it would be useful to evaluate in more detail the model's performance in different parts of a valley system or across several valleys. Further, an evaluation of the model's sensitivity to the resolution and accuracy of input datasets (eg. landcover, DEM) and input settings (eg. soil moisture) in these mountainous regions would also indicate whether improvements in the accuracies of meteorological outputs due to changes in model parameterisation might be gained.

Overall, TAPM results were relatively consistent between sites and among the seven years for the different variables examined. This suggests that much of the simulation error displayed in the results is systematic and inherent to the model architecture rather than due to external, location-related variability. The fact that many of the results concur with those found by others at numerous locations globally, also lends confidence to the model's widespread applicability. While it is clear that the absolute accuracies of simulations may vary among the meteorological variables, inaccuracies appear relatively consistent in time and for the two sites examined, and simulated data should thus be useful in characterising relative spatial differences in topoclimate among high-elevation sites, assuming that similar trends hold at other locations.

Chapter 5

Do topoclimatic-related stressors limit local-scale treeline elevations?

5.1 INTRODUCTION

It is well-accepted that the tree limit, the uppermost elevation at which erect trees can subsist, is a global bioclimatic phenomenon ultimately determined by temperature (Körner and Paulsen 2004). However, it is also clear that treelines can often deviate from this potential climatic treeline, relegated to lower elevations by the influence of a host of factors that operate at regional to local scales (Holtmeier and Broll 2005, Malanson *et al.* 2011, Chapter 3 in this thesis). These factors include: differences in regional climate regime (heat and moisture) that affect tree growth and generally mediate finer-scale influences on treeline (Daniels and Veblen 2003); disturbances that have historically pushed treelines to lower positions (e.g. Daniels and Veblen 2003, Leonelli *et al.* 2009), spatial variation in the distribution of moisture and nutrients related to geomorphology (Butler *et al.* 2007), and local-scale topoclimatic variability (Holtmeier and Broll 2005). Treeline seedlings are particularly vulnerable to the detrimental influences of local-scale topoclimatic factors on photosynthetic function and carbon acquisition (Cairns and Malanson 1998, Germino *et al.* 2002, Johnson *et al.* 2004). For example, while a given location may have adequate conditions for tree growth as characterised by average growing season warmth, this effect may be locally superseded by stressors, such as extreme levels of light and wind, which impair seedlings' physiological functioning and ultimately limit their recruitment to higher elevations (Smith *et al.* 2009). Thus, there is a growing recognition that both regional-scale and local-scale factors can act as primary drivers of treeline variation. However, while it is relatively easy to obtain GIS-based data for investigating regional-scale climatic influences on treelines across a range of sites, accurate and spatially-explicit topoclimatic data at local scales are typically not available. Thus, in order to understand how treelines may respond regionally to climatic change, datasets and methods will be required for characterising and modelling both regional-scale and finer-scale climatic effects across large areas (Holtmeier and Broll 2007).

However, modelling local-scale, topoclimatic influences on treelines is challenging. One common method employed to account for topographic effects in ecological studies is the

use of indices derived from digital elevation models (DEMs). These indices are used to model aspects of local terrain shape and configuration that may reflect variation in conditions related to disturbances, geomorphology, soil and water distribution, and climate across the landscape (Moore *et al.* 1991). A number of treeline studies have used DEM-derived indices to highlight the important role that topography plays in influencing treeline variability (Brown 1994, Allen and Walsh 1996, Walsh *et al.* 2003, Dullinger *et al.* 2004, Bader and Ruijten 2008b). For example, Brown (1994) used three DEM-derived topographic characteristics to explain the presence of four treeline transition vegetation types. Similarly, Bader and Ruijten (2008b) found that a DEM-derived topographic index was a significant factor in explaining the presence/absence of forest within the treeline zone; the index described convex landscape zones where cold air drainage occurred and caused inverted treelines. In New Zealand, there is anecdotal evidence that *Nothofagus* treeline elevation varies locally due to landform-mediated topoclimatic effects, reaching higher elevations on steeper, convex landforms than on gentler concave forms (Wardle 1985c, 2008), although the pervasiveness of this pattern across the country has not yet been evaluated.

Nonetheless, there are limits to the extent to which local-scale topoclimate effects, in particular, can be sufficiently represented by DEM-derived indices. Daily variation in local wind speeds, for instance, are the result of a range of meteorological processes inducing effects such as valley and downslope winds, cold air ponding, and differential irradiation, which are highly variable in space and time (Daly *et al.* 2010). Therefore, new approaches that can capture these “topoclimatic” processes and generate meteorological data that can be used for treeline investigations are warranted. One such approach would be to use prognostic, numerical climate models that are capable of generating accurate estimates of meteorological parameters in complex terrain and that can be applied to different sites without the need for local data. A number of readily-available meso-scale atmospheric models are suited to this task. For example, The Air Pollution Model (TAPM) produced by CSIRO Australia (Hurley 2008a) is a mesoscale model that has been applied at sites worldwide (e.g. Hurley *et al.* 2008) and has been shown to be able to account for topographically-mediated meteorological processes such as cold air drainage and ponding in complex terrain (Hurley *et al.* 2005, Mocioaca *et al.* 2009). Thus, it would be of considerable interest to apply such a model across a range of treeline sites in order to investigate the potential influences of topographically-mediated climate on treeline position.

Daily and monthly variation in wind speed, temperature extremes, solar radiation, and relative humidity, and interactions among these variables, together define possible

topoclimatic conditions at the local treeline. These meteorological variables rarely affect treelines in isolation, but rather work synergistically to produce conditions that affect trees' physiological performance. For instance, although high winds can potentially cause direct physical damage to trees at high altitudes, this type of damage alone is typically not a critical factor in explaining treeline formation (Körner 1998). More damaging, however, is when the action of wind combines with other topoclimatic variables to produce conditions stressful to plant function. Such an example might be when high winds combine with high temperatures and low relative humidities during hot summer months to produce conditions where desiccation stress is more likely to occur (Köhler *et al.* 2006, Moyes *et al.* 2013). Similarly, while low nighttime temperatures on their own will likely have little impact on seedlings at treeline, when combined with low windspeeds and high amounts of outgoing radiation, frost-inducing conditions are generated that can affect leaves and buds, especially early in the growing season (Jordan and Smith 1994). There are also potential positive effects: for example, locations that generally have higher warmth and higher inputs of sunlight, in the absence of other stressors, might be expected to have conditions more suitable for tree establishment and growth (Cairns and Malanson 1998). Hence, research that is able to explore the relevance of these combined effects across different locations will be able to provide new insights into the importance of topoclimate in determining local treeline variability.

This study offers a country-wide analysis of the influence of topoclimate on local, within-site variation in treeline elevation at abrupt *Nothofagus* treelines across New Zealand. Abrupt treelines are particularly ideal for investigations of topoclimatic effects; the characteristic abrupt form of these treeline boundaries is thought to arise largely from the action of processes such as photoinhibition, desiccation, and frost damage that affect seedling recruitment and survival, rather than from temperature-driven growth limitation (Harsch and Bader 2011, Martínez *et al.* 2011). Indeed, a 15-year monitoring study of treeline advance at *Nothofagus* treeline sites throughout New Zealand showed that treelines have not moved uphill despite warmer temperatures, and that the lack of sheltered microsites limits seedling recruitment above the treeline (Harsch *et al.* 2012). To characterise topoclimatic conditions at treeline in this study, a mesoscale atmospheric model (TAPM) is used to generate local scale (200m) January and July meteorological data for over 2100 treeline locations at 28 study sites across New Zealand. Using these data, I aim to address the following questions:

1. What is the influence of topoclimatic factors on local-scale treeline elevation variation, after accounting for landform and regional-scale effects?

2. Do factors driving within-site treeline variability differ between the summer and winter months?

5.2 METHODS

5.2.1 Defining *Nothofagus* treelines, study sites, and treeline sampling locations

Treelines were identified in GIS using New Zealand Landcover Database 2 data as the polygon boundaries between the “Indigenous Forest” landcover class and four adjacent subalpine landcover classes (see Chapters 2 and 3 for further description). Once identified, these treeline boundaries were extracted as line features in the GIS and points were generated along these treelines at an average spacing of approximately 1km in order to capture local scale variability. These points formed the basic unit for extracting the elevation, meteorological and landform data at treeline that were used for subsequent analyses. Next, I chose 30 treeline site locations across the country at which atmospheric modelling with the TAPM model would be carried out; due to time constraints, TAPM could not be practically applied across all *Nothofagus* treelines, thus necessitating the identification of a subset of sites for which the model could be run within a reasonable timeframe. Overall, the 30 sites were located such that the full range of spatial and climatic variability in *Nothofagus* treelines was being represented, while being adequately spatially separated so that each site was within a distinct mountain range or valley area. The number of study sites was ultimately reduced from 30 to 28 as problems were encountered with running the TAPM model at two of the locations (Figure 5.1). The mean distance from each site location to the next closest site was 32.4km.

5.2.2 Generating meteorological data at treeline sites

The Air Pollution Model (TAPM) V.4, developed by CSIRO in Australia, was used to generate meteorological data at the 28 study sites for the purpose of characterising topoclimatic conditions. TAPM is a prognostic, numerical atmospheric model that predicts three-dimensional meteorology at scales ranging from relatively coarse (1000 to 1500 km) to fine (< 500 m) (see Hurley 2005 and 2008a for further details regarding the model). The ability of the TAPM model to produce accurate meteorological data has been assessed across a large range of locations and conditions globally (e.g. Hurley *et al.* 2008, Mahmud 2009,

Tang *et al.* 2009), including New Zealand (e.g. Zawar-Reza *et al.* 2005b, Gimson *et al.* 2007, Zawar-Reza and Sturman 2008). Further, in support of this present study, TAPM performance was assessed at both a North and South Island weather station location near treeline for the months of January and July over a seven year period (see Chapter 4 in this thesis). Generally, this assessment showed that TAPM could relatively accurately predict temperature and windspeed at these sites, while solar radiation was moderately overpredicted and relative humidity underpredicted. However, what was clear was that prediction accuracies were relatively consistent between sites and among years for the different variables examined. This suggested that while high absolute accuracies may not be achieved for some parameters, inaccuracies are relatively consistent, and simulated data should thus be useful in characterising relative spatial differences in topoclimate among sites.

For this study, I ran TAPM for both January and July 2002 at the 28 sites; the year 2002 was chosen in order to temporally align meteorological data with the landcover data from which treelines were extracted. The TAPM model was run at a 200m resolution within a 7 x 7km extent centred on each site location, resulting in the generation of meteorological estimates for 1225 grid cells at each site for each of the two months. Meteorological outputs consisted of hourly estimates of screen-level temperature ($^{\circ}\text{C}$) and relative humidity (%), wind speed (m s^{-1}), global solar radiation (W m^{-2}), and outgoing long-wave radiation (W m^{-2}). To obtain TAPM-generated data at each treeline sample point, I generated grids within ArcGIS at each site that spatially coincided with the grid layout used by TAPM (Figure 5.1). Each cell in the TAPM grid was given a unique identifier based on its location in the grid, starting at the lower left corner (1,1) and moving left to right along rows to the top right corner (35,35). The GIS grid was set up to exactly replicate this system, thereby creating a way to link the TAPM meteorological data with the treeline sample points that were located within coinciding grid cell in the GIS. To verify that all treeline sample points at each site were located at treeline, I visually assessed sample points against a georeferenced, 15m resolution, SPOT 5 satellite imagery (see Figure 5.1, inset). Points that were not within 50m of the treeline seen on the imagery, or could not be verified as being at treeline due to the presence of shadow or cloud in the imagery, were removed from the dataset. This process resulted in a total of 2189 points located at treeline across the 28 sites for which meteorological data were extracted and used for subsequent analyses. Treeline elevation was also extracted in the GIS for each point from a 25-m resolution digital elevation model for New Zealand (Barringer *et al.* 2002).

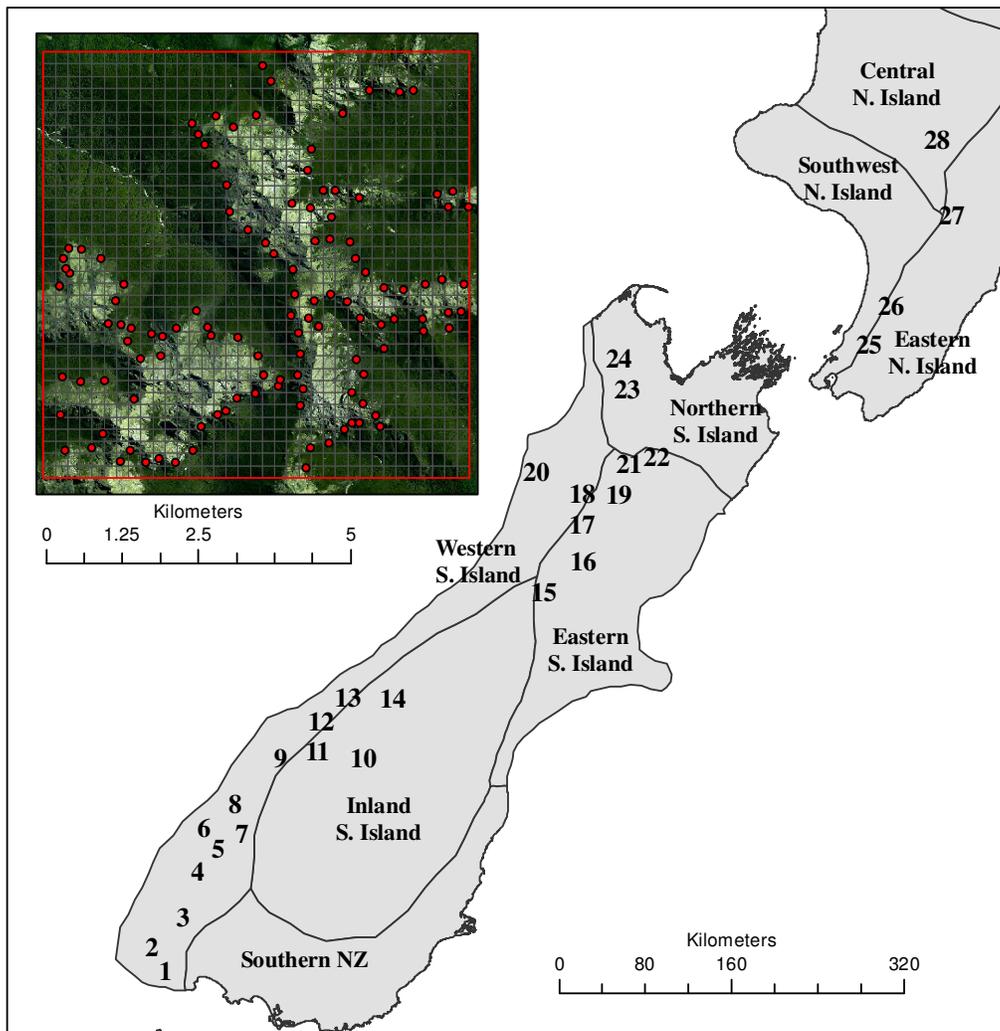


Figure 5.1 Location of the 28 study sites relative to broad climatic regions. The inset (top left) illustrates how treeline locations at a given site were overlaid with a 200m resolution, 7x7km grid in order to link treeline elevations with corresponding TAPM-generated meteorological outputs. In the background of the inset is the SPOT 5 satellite which was used as a basis to verify that treeline points were accurately located at treeline.

5.2.3 Response variable – treeline elevation deviation from site-level maximum

At each site (7 x 7 km area), it was assumed that the treeline observation occurring at the highest elevation provided a reasonable index of the potential, climatically-driven treeline in that locale. Thus, in the absence of disturbances and topoclimatic stressors, all treelines in the vicinity should theoretically reach this maximum observed local elevation due to the dominant effect of mean growing season temperature. Based on this assumption, the difference in treeline elevations at each sample location from their site-level maximum was calculated and used as the response variable in statistical modelling (“elevation deviation from maximum”). This response variable also provided a standardised measure of treeline variability across the 28 sites in that it removed possible confounding effects due to the negative trend between treeline elevation and latitude that occurs across New Zealand.

5.2.4 Within-site topoclimatic influences on treelines

Hourly meteorological data produced by the TAPM model were used to derive topoclimatic variables for early summer (January) and mid-winter (July) that have the potential to impact on tree physiological function at treeline. Three of the variables, insolation, frost index, and photoinhibition index, were computed for both months while two others, summer desiccation index and winter desiccation index, were specific to January and July, respectively:

Insolation – I calculated this variable as the total daytime solar radiation at a location, summed for both January and July. Differences in solar radiation loadings among treeline locations typically reflect either differences in topographic orientation relative to the sun (i.e. aspect differences) or differences in the amount of cloud cover over time. Insolation is a key topoclimatic variable at treeline, and can exert both positive and negative effects. In general, locations with higher solar radiation, that are not also subjected to cold nighttime/early morning temperatures (see photoinhibition index below), are likely to have more favourable conditions for growth due to increased warmth.

Photoinhibition potential – There is considerable evidence from treeline research that increased daytime and nighttime sky exposure is generally detrimental to seedling establishment above existing treelines, typically attributed to cold-induced photoinhibition effects (Wardle 1985a, Ball *et al.* 1991, Germino and Smith 1999, Germino *et al.* 2002, Bader *et al.* 2007, Giménez-Benavides *et al.* 2007).

I calculated the relative potential for photoinhibition at all locations as a simple multiplicative index using TAPM data:

$$\text{Eq. 5.1 Photoinhibition index} = \frac{\sum_{\text{daytime}} [(T_{\text{site,max}} - T_{\text{hourly}}) \times \text{SolRad}_{\text{hourly}}]}{N_{\text{daytime}}}$$

In this formulation, hourly temperature values (T_{hourly}) are rescaled relative to the overall observed site-level maximum temperature such that lower temperatures result in higher photoinhibition index values. $\text{SolRad}_{\text{hourly}}$ are hourly solar radiation values. The product of rescaled hourly temperatures and $\text{SolRad}_{\text{hourly}}$ are then summed across all daytime hours and divided by the number of monthly daytime hours (N_{daytime}) for both January and July.

Desiccation potential –Desiccation stress can occur at treeline in both summer and winter (Tranquillini 1979, Harsch and Bader 2011). During hot summer months, desiccation conditions can result from the combination of relatively high daytime wind speeds and temperatures and low relative humidities. These conditions can increase transpiration rates and dry out thin soils, leading to drought stress (Cui and Smith 1991, Kullman 2005). In winter months, cold temperatures periodically induce frozen soils and plant tissues, while high wind conditions and low relative humidities increase transpiration rates, thus increasing the potential for desiccation damage of treeline seedlings and trees (Baig and Tranquillini 1980, Wardle 1981b, Sowell *et al.* 1996). High wind speeds can also exacerbate these effects by causing direct abrasion damage to the cuticles of exposed leaves, thereby increasing the potential for water loss (Hadley and Smith 1983).

I calculated a summer desiccation index using January meteorological data as:

$$\text{Eq. 5.2 Summer desiccation index} = \frac{\sum_{\text{daytime}} [T_{\text{hourly}} \times \text{WS}_{\text{hourly}} \times (100 - \text{RelHum}_{\text{hourly}})]}{N_{\text{daytime}}}$$

T and WS are hourly temperature and wind speeds, respectively and *RelHum* is hourly relative humidity scaled relative to a maximum humidity of 100% such that lower humidity values contribute towards a higher desiccation index.

A winter desiccation index was similarly calculated using July meteorological data, but averaged across the whole day (i.e. 24 hours) and with low temperatures (inducing possible frost drought conditions) contributing to high index values:

$$\text{Eq. 5.3 Winter desiccation index} = \frac{\sum_{\text{daytime}} [(T_{\text{site,max}} - T_{\text{hourly}}) \times \text{WS}_{\text{hourly}} \times (100 - \text{RelHum}_{\text{hourly}})]}{N_{\text{daytime}}}$$

Frost potential – Cold nighttime temperatures combined with low wind speeds and high levels of outgoing, long-wave radiation can lead to frost conditions (Lindkvist *et al.* 2000). Frost damage to mature trees at treeline is rarely significant and is not considered a major treeline-forming factor (Körner 1998, Cieraad *et al.* 2012). However, early summer frosts can cause significant damage to new leaves of seedlings (King and Ball 1998) and is considered a potential limiting factor for the establishment of trees above existing treelines in certain regions of the world (Germino and Smith 2000, Piper *et al.* 2005) including *Nothofagus* treelines in New Zealand (Wardle 1985c, Greer and Buxton 1989).

TAPM-derived hourly data were used to calculate a relative index of the potential for frost occurrence for treeline locations at each of the 29 sites:

$$\text{Eq. 5.4 Frost index} = \frac{\sum_{\text{nighttime}} [(T_{\text{site_max}} - T_{\text{hourly}}) \times (WS_{\text{site_max}} - WS_{\text{hourly}}) \times (-NetRad_{\text{hourly}})]}{N_{\text{nighttime}}}$$

$T_{\text{site_max}}$ and $WS_{\text{site_max}}$ are the maximum, site-level temperature and wind speed values, and are used to rescale hourly temperatures (T_{hourly}) and wind speeds (WS_{hourly}) to a reverse scale at each site. In this way, temperatures and wind speeds that are low relative to the site-level maximum for these variables contribute towards a higher frost index value, while those that approach the site-level maximum contribute towards a lower frost index. $NetRad_{\text{hourly}}$ is the hourly net radiation, computed by TAPM as the difference between incoming solar radiation and outgoing radiation emitted from the land surface; $NetRad_{\text{hourly}}$ values during nighttime hours are negative as there is no incoming solar radiation. Hourly frost index values calculated in this manner are then summed across all nighttime hours in each of January and July, and divided by the number of monthly nighttime hours for those months ($N_{\text{nighttime}}$).

5.2.5 Within-site landform influences on treelines

Two additional variables, slope gradient and surface curvature, were derived from DEM data to investigate the impact of landform on treeline elevation deviation. I chose these variables to test Wardle's (1985a) assertions that *Nothofagus* treelines are higher on steep slopes and convex curvatures. Both variables are key landform parameters at treeline, influencing possible disturbance and local climatic processes, as well as affecting soil property distributions. Percentage slope gradient was derived from DEM data at each location using the "Slope" function within ArcGIS 10.1. The slope gradient is calculated as the rate of maximum change in elevation among a 3x3 neighbourhood of DEM cells surrounding a focal

cell location. The degree of convexity or concavity of the landsurface was derived from DEM data at each treeline location using the “curvature” function within ArcGIS 10.1. This function determines surface curvature for each cell of the DEM by fitting a fourth order polynomial to the elevation surface within a 3x3 moving window centred around a given cell location. The resulting value from this calculation is either positive, signifying a convex shape, or negative signifying a concave shape (Zeverbergen and Thorne 1987).

5.2.6 Among-site, regional-scale influences on treelines

Within-site treeline variation, and local abiotic influences, might also be mediated by regional climatic and disturbance influences. Treelines may vary, for example, according to the relative location of sites along a latitudinal gradient, with respect to the coast (i.e. coastal versus inland), and with respect to main zones of catastrophic disturbance (e.g. Sveinbjörnsson 2000, Chapter 3 in this thesis). As such, mean values for growing season temperature, mountain mass, precipitation, and earthquake intensity were extracted for each 7x7 km site area to represent these potential among-site differences across New Zealand. Growing season temperature and precipitation data for the sites were extracted from 500 m resolution gridded climate layers for New Zealand (Wratt *et al.* 2006). A mountain mass index, which represents the effect of mountain size on the regional thermal regime, was derived in the GIS by determining the amount of area above 1200m within each of the study site zones. Earthquake data were extracted from a 500 m resolution spatial dataset of the expected mean peak ground acceleration (PGA) within a 150 year return interval, expressed as the proportion of the acceleration due to gravity (Stirling *et al.* 2002).

5.2.7 Data analysis

To model possible local- and regional-scale influences on treeline elevation deviation from maximum, eleven alternative mixed-effects regression models were created, with all models including a random “site” effect to account for the spatial clustering of treeline observations within sites:

Model M0 - a random intercept-only model, including no fixed effects, and is used as a null-type model against which to evaluate the relative strength of the other models.

Model M1 – a ‘global model’, including fixed effects for the two local-scale landform factors (slope gradient and curvature), the four local-scale topoclimatic factors (insolation, desiccation index, photoinhibition index, frost index) and the four regional-scale factors (mean growing season temperature, precipitation, mountain mass index, and earthquake intensity).

Model M2 – a ‘local-scale factor model’, including fixed effects for the combined landform and topoclimatic factors, but not the regional-scale factors.

Model M3 – an ‘regional-scale factor model’, including fixed effects for only the four regional-scale factors.

Model M4 – a ‘topoclimate factor model’, including fixed effects for only the four topoclimatic factors.

Model M5 – a ‘landform factor model’, including fixed effects for only the two landform factors.

It was of interest to determine whether the types or strengths of topoclimatic effects on treeline elevation deviation differed between summer and winter months and, therefore, separate model sets were created using January and July topoclimate data. Data for the four topoclimatic factors varied for the two months, while those for the two landform and four regional-scale factors remained constant regardless of month. These latter two sets of factors were included in both the January and July model sets to maintain symmetry in the model specifications between the two months and to determine if topoclimatic effects emerged for both months after accounting for landform and regional-scale effects. All fixed effects were standardised to a mean of zero and standard deviation of one prior to modelling. For the global models, there were only relatively weak correlations ($r < 0.5$) among variables and therefore multicollinearity was not considered an issue. Mixed-effects modelling was carried out using the function “lme” within the “nlme” package (Pinheiro *et al.* 2009) in R version 1.14 (R Core Team 2012). The 11 alternative models were assessed using a model comparison framework based on Akaike’s Information Criterion for small sample sizes (AIC_c) and Akaike model weights ($AIC_c Wt$) (Anderson 2008); the model in a given model set with the lowest AIC_c and highest $AIC_c Wt$ value ranking was considered to have the most support. Model comparisons were carried out with the R package “AICcmodavg” (Mazerolle 2011).

5.3 RESULTS

5.3.1 Variation in treeline elevation deviation from maximum

There was a large amount of variation in the deviation of treeline elevations from the maximum site-level treeline elevation within and among sites (Figure 5.2). Treeline elevations ranged from near the site-level maximum (i.e. 0m elevation deviation) to 500m lower in elevation at some sites. For the majority of treeline locations, elevations were predominately in the range of 100 to 250m lower than the maximum potential treeline. The greatest degree of deviation and overall spread in treeline elevations was evident for a number of sites along the spine of the lower Southern Alps in the South Island (sites 6, 8, 9, 11, 12, 13) (Figure 5.1).

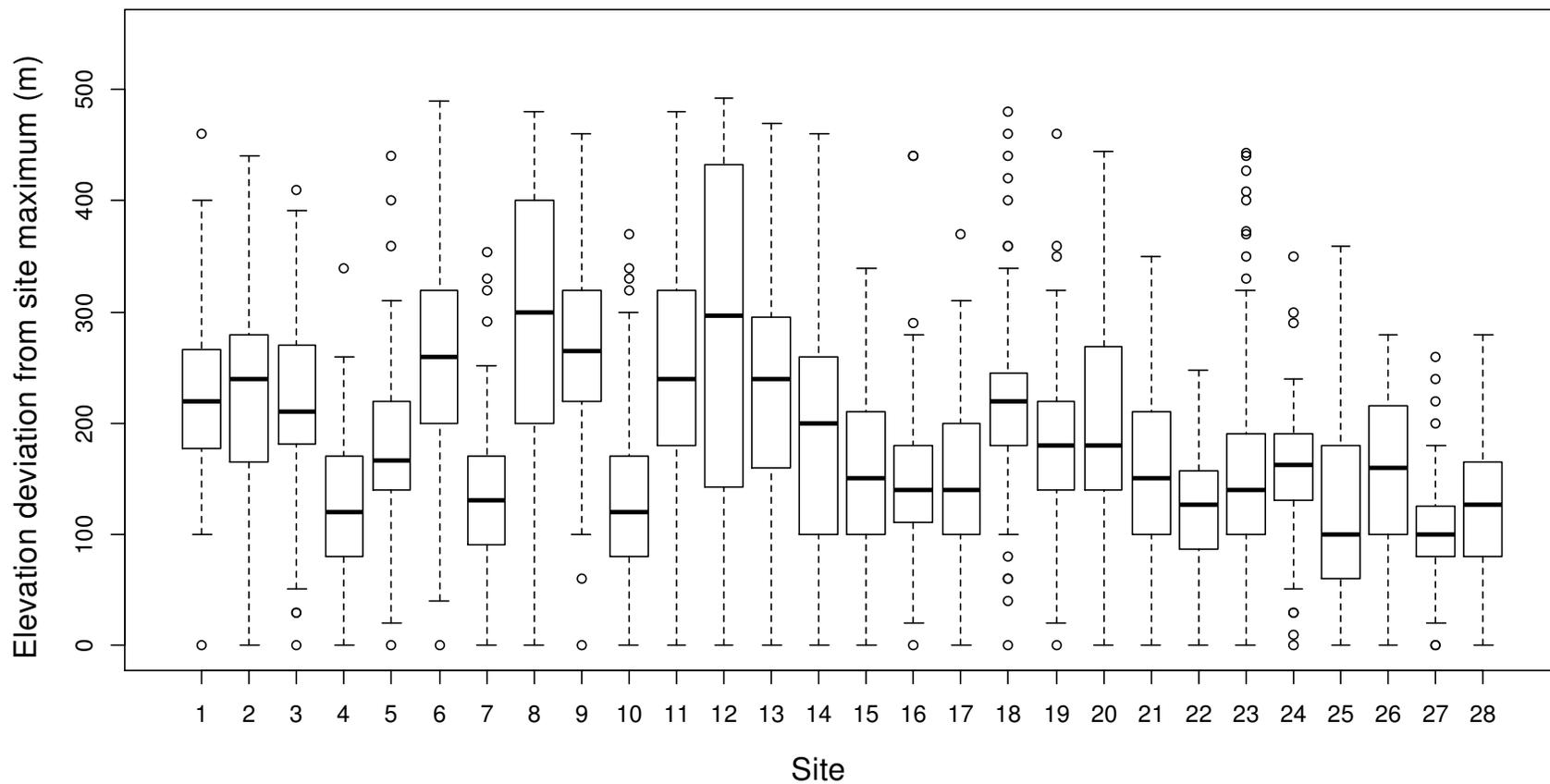


Figure 5.2 Distribution of treeline elevation deviations (m) from the maximum site-level treeline elevation at each of the 28 sites examined in the study. The deviation values therefore reflect the degree to which treeline elevations are lower than the site maximum (elevation deviation =0).

5.3.2 Variation in topoclimatic and landform variables

Sampled treelines occupied a wide range of topographic situations across the country (Figure 5.3). Slope gradients were moderately variable at the 28 sites, although slopes at the southernmost sites were relatively more variable and steep than the rest of the country. Curvature values varied consistently between -2 (concave) to 2 (convex) at all sites. There was a large range of topoclimatic variation occurring both within and among the 28 sites (Figures 5.4 to 5.7). Total solar radiation (insolation) was about four to five times higher, on average, during January in comparison to July (Figure 5.4). Generally, within-site insolation was also more variable in January than July, although similar among-site patterns were observed. Mean photoinhibition index was about two to three times higher in January than July (Figure 5.5). There was considerable among-site variation in the photoinhibition index although trends were quite similar for both months; within-site variability was also high for many sites (Figure 5.5). The mean January desiccation index was relatively low and not highly variable for many sites across the country, with the exception of several sites in the lower Southern Alps (Figure 5.6). Mean July desiccation index was generally more variable than July both among and within sites and was relatively high for sites along the main spine of the Southern Alps in the South Island (Figure 5.6). Of the three derived topoclimatic indices, mean frost index displayed the most among-site variation, particularly in January; within-site variation was relatively low, with the exception of a handful of sites in the South Island (Figure 5.7).

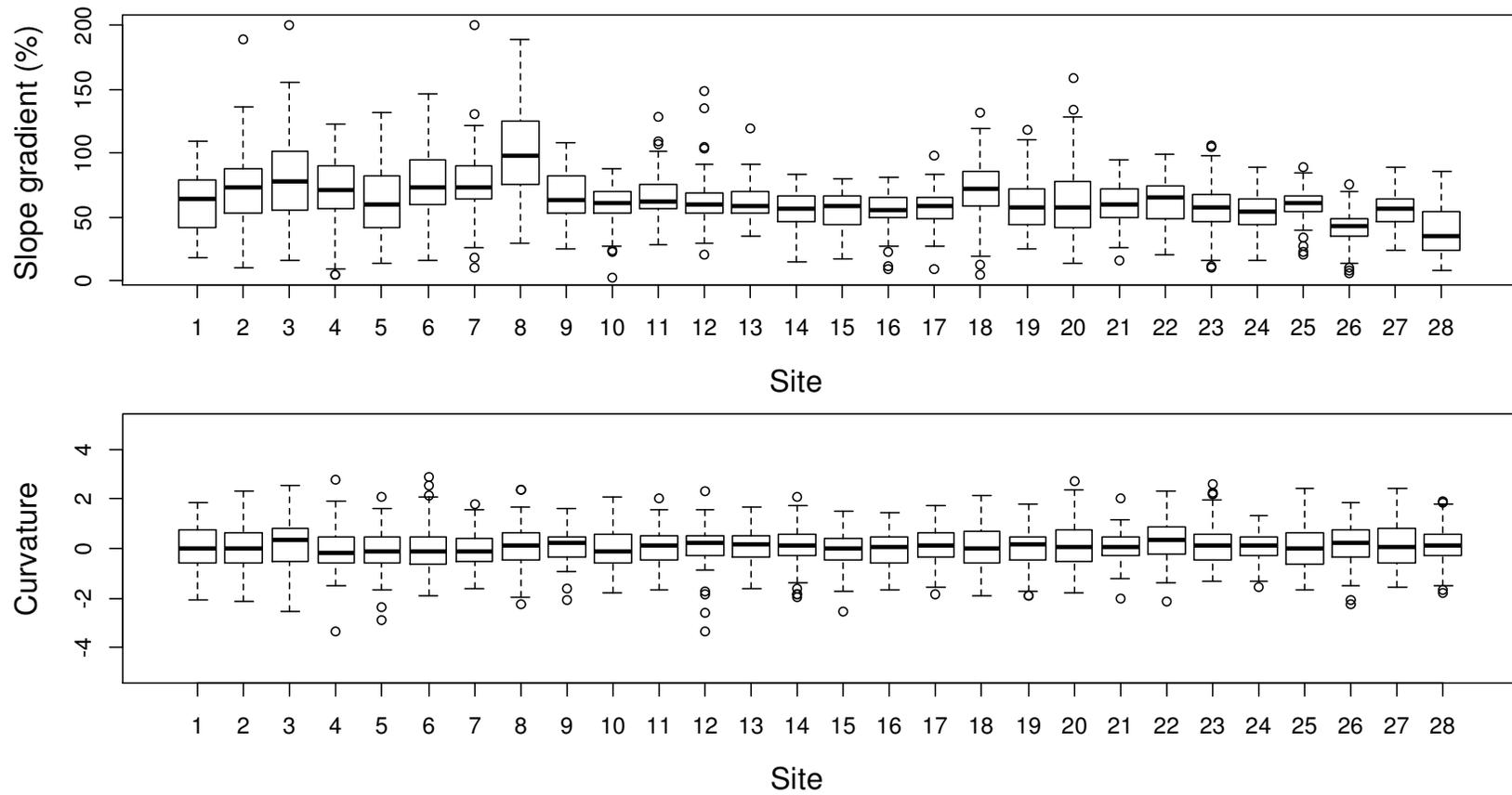


Figure 5.3 Distribution of the two landform variables, a) slope gradient; and b) curvature, at treelines for the 28 treeline sites.

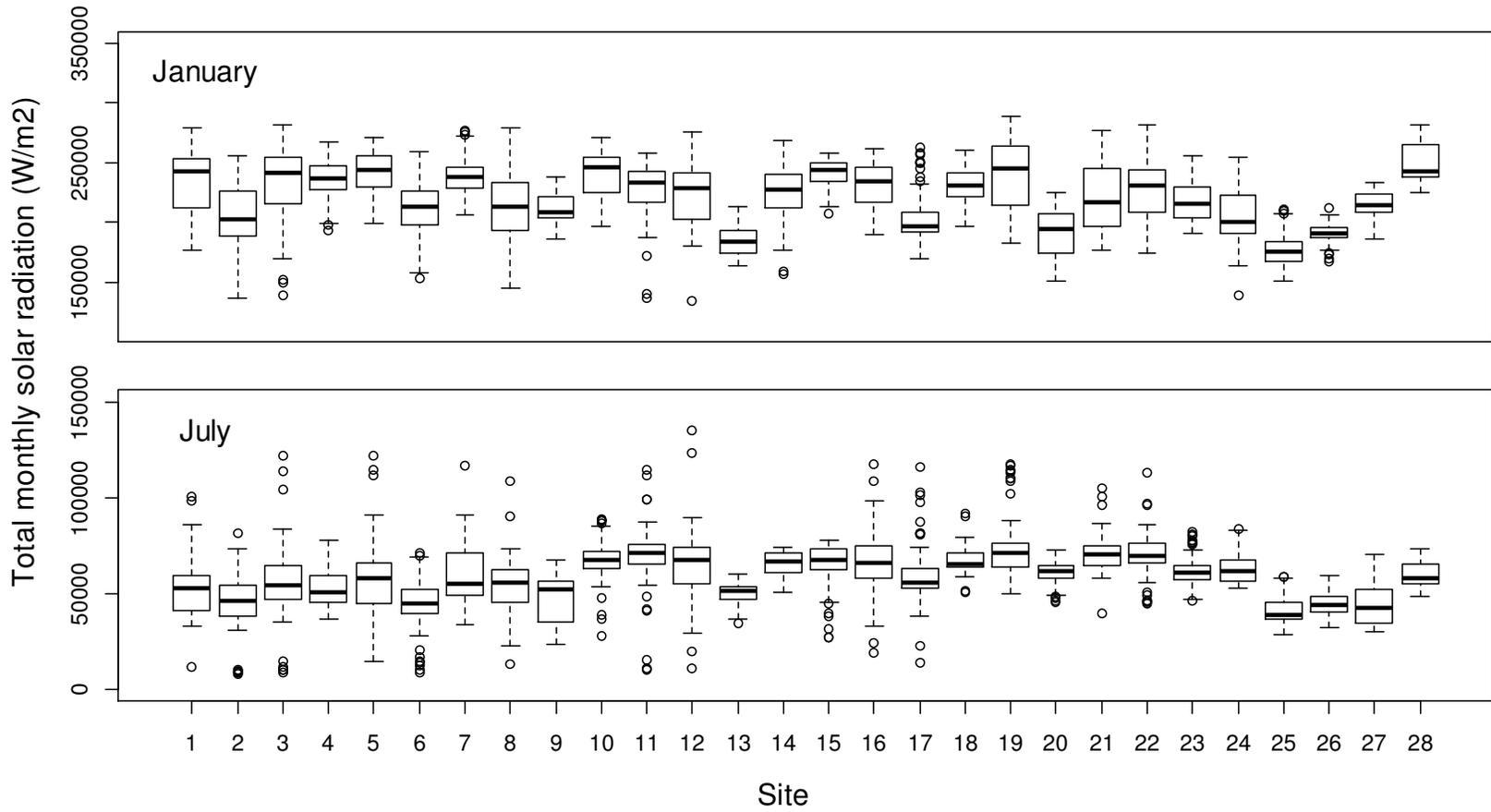


Figure 5.4 Distributions of January and July cumulative hourly solar radiation at treeline locations for the 28 treeline study sites.

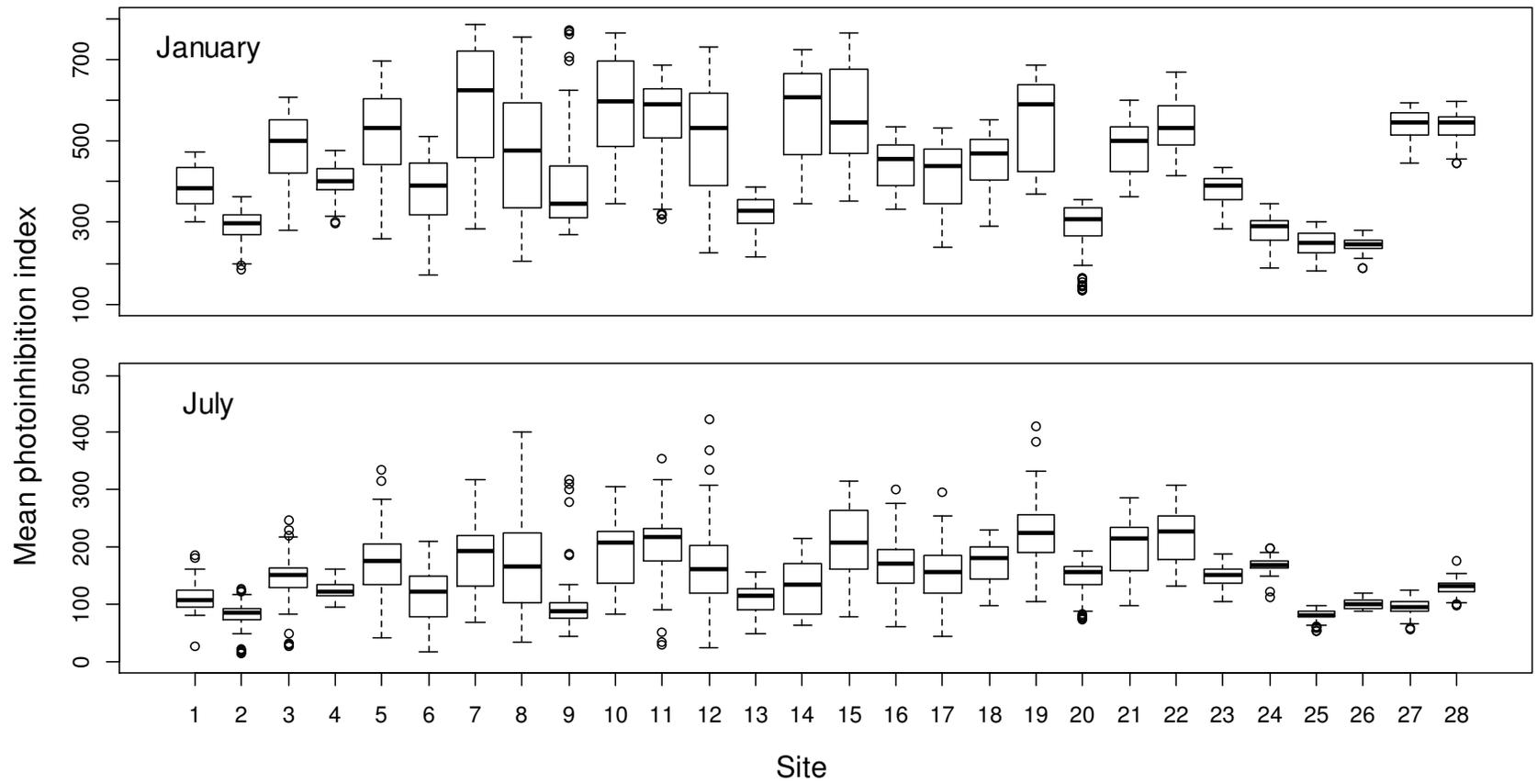


Figure 5.5 Distributions of mean January and July photoinhibition index at treeline locations for the 28 treeline study sites. Higher index values indicate a higher relative potential for photoinhibition conditions.

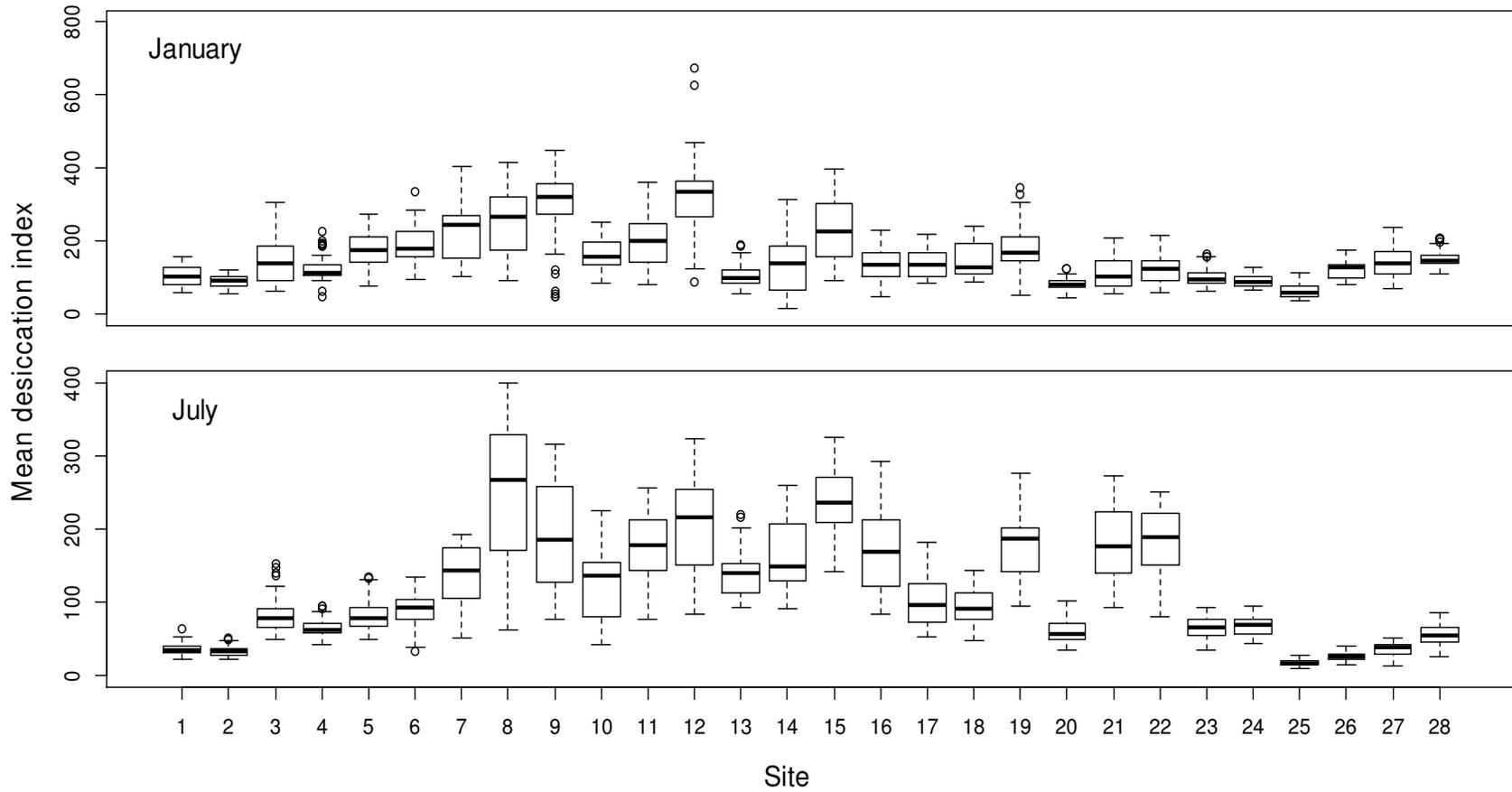


Figure 5.6 Distributions of mean January and July desiccation index at treeline locations for the 28 treeline study sites. Higher index values indicate a higher relative potential for desiccation conditions.

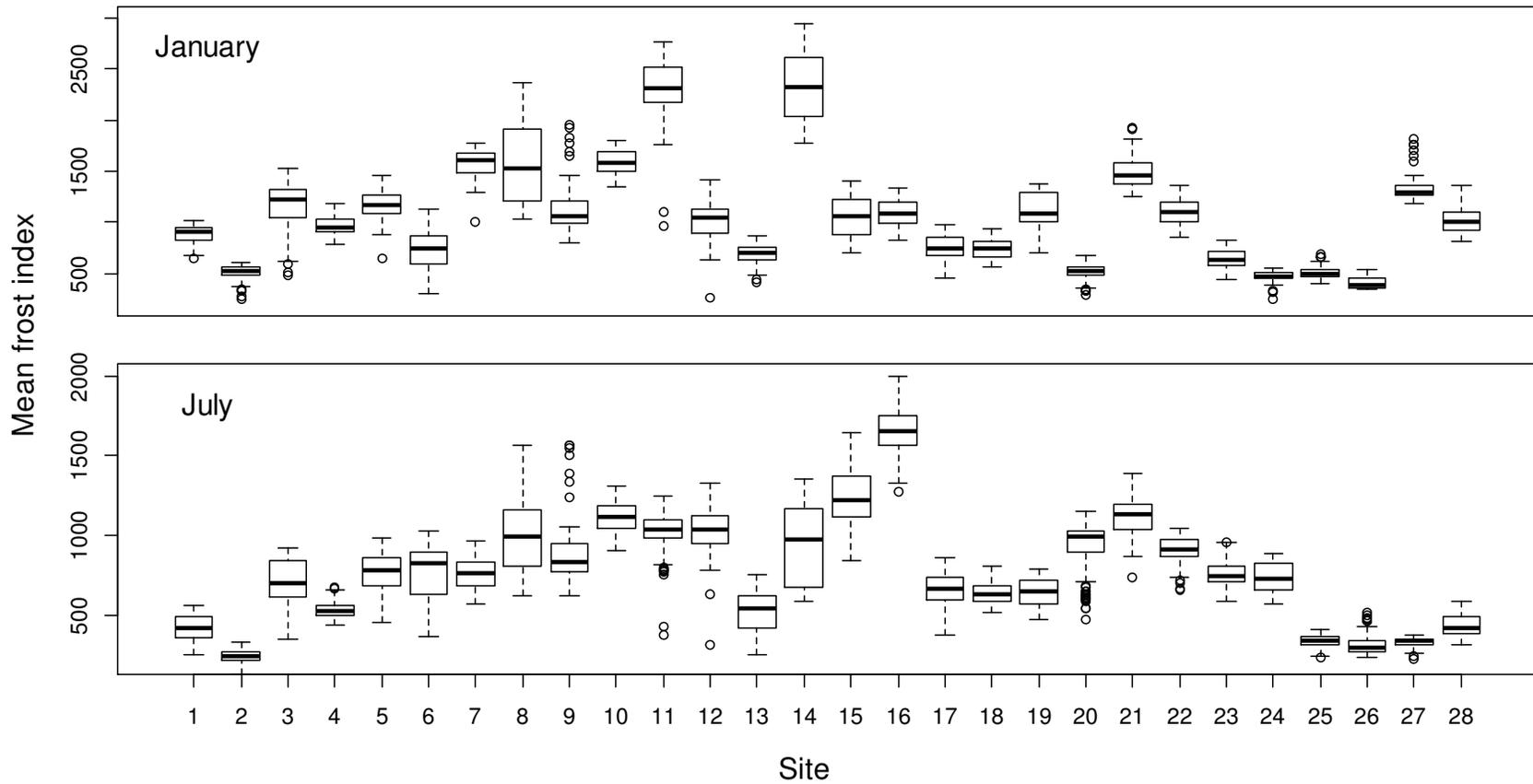


Figure 5.7 Distributions of mean January and July frost index at treeline locations for the 28 treeline study sites. Higher index values indicate a higher relative potential for frost formation.

5.3.3 Modelling results

Model selection results (Table 5.1) indicated that the global model, comprising all seven landform and topoclimatic variables, was by far the most informative model for both the January and July datasets. In comparing within-site effects (landform and topography) and among-site effects, the former model was ranked considerably higher in terms of AIC_c compared to the latter.

Effect size plots for the global models (Figure 5.8) show consistent, and significantly negative, relationships between the two landform variables and treeline elevation deviation, for both the January and July analyses. This means that treelines that show smaller deviations from the site-level maximum treeline elevation (i.e. higher treelines), are associated with more convex, steeper landforms. There were differences in the January and July topoclimatic effects on treeline elevation deviation. Results indicated that higher summer insolation values were associated with smaller deviations in treeline elevations from site-level maximum, while winter insolation did not have a significant association with treeline elevation deviation. For January, the desiccation and photoinhibition indices were significantly, positively related to treeline elevation deviation, while only the former was significant for July. This suggests that more depressed treelines, showing larger deviations from the site-level maximum, are associated with higher potential for desiccation and photoinhibition in the summer and desiccation in the winter. Three of the site-level factors were also influential in explaining treeline elevation deviation. Sites with higher mean growing season temperatures and mountain mass indices and lower total annual precipitation levels had treelines that deviated less, on average, from the local, site-level maximum.

Plots of global model predictions relative to observed values for both months (Figure 5.9) indicate that the global models were able to best-explain treeline elevation deviations in the range of 100 to 300 m, but overpredicted treeline deviations less than 100m and strongly underpredicted treeline deviations greater than 300m.

Table 5.1 Results from a multi-model comparison of eleven, candidate, mixed-effects models explaining site-level treeline variability at 28 study sites across New Zealand. The response variable is the deviation in treeline elevations from the maximum site-level treeline elevation for 2148 treeline observations. The variable “site” is included as a random effect in each model. For each month, modelling results are presented ranked by AIC_c . K is the number of model parameters, ΔAIC_c is the relative change in AIC_c for a given model from the top-ranked model, and $AIC_c Wt$ is the relative weight of evidence that a given model is the best of the set of models.

	Model	Model explanatory variables	K	AIC_c	ΔAIC_c	$AIC_c Wt$
June	M1	Global model - all variables	10	25429.6	0.0	1
	M2	Within-site model (landform+topoclimate)	9	25448.4	18.8	0
	M5	Landform model	5	25464.9	35.2	0
	M4	Topoclimate model	7	25718.9	289.2	0
	M3	Among-site, regional-scale model	7	25726.4	296.7	0
	M0	Intercept-only model	3	25742.1	312.4	0
July	M10	Global model - all variables	10	25447.0	0.0	1
	M2	Within-site model (landform+topoclimate)	9	25467.3	20.3	0
	M5	Landform model	5	25489.6	42.6	0
	M4	Topoclimate model	7	25745.2	298.2	0
	M3	Among-site, regional-scale model	7	25752.1	305.1	0
	M0	Intercept-only model	3	25767.9	320.9	0

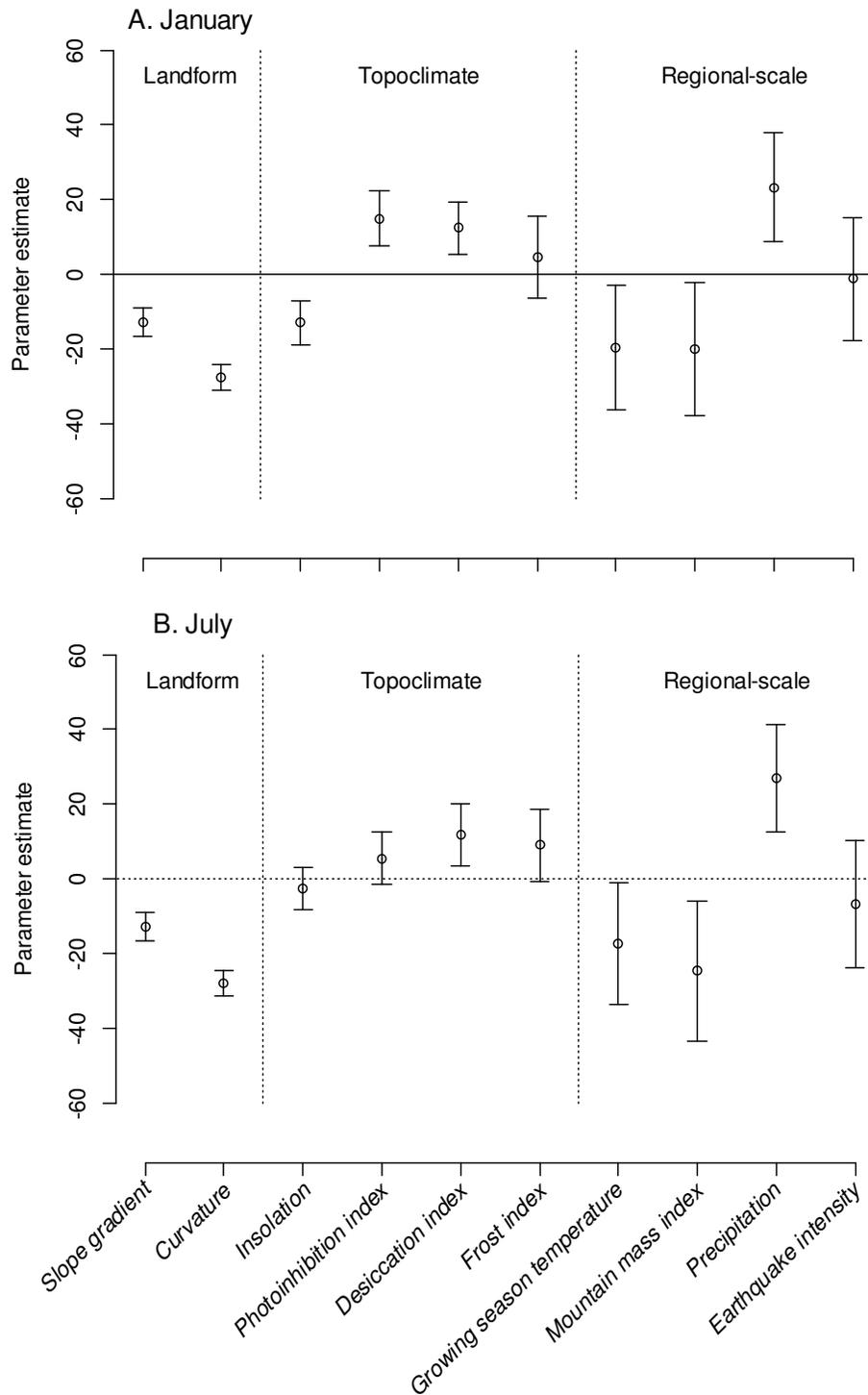


Figure 5.8 Effect sizes resulting from mixed-effects linear regressions of within-site treeline elevation deviations against four regional-scale factors, two landform factors, and four topoclimatic factors derived using both January and July meteorological data (i.e. “global models”, Table 1). Values are standardised parameter estimates ± 2 standard errors.

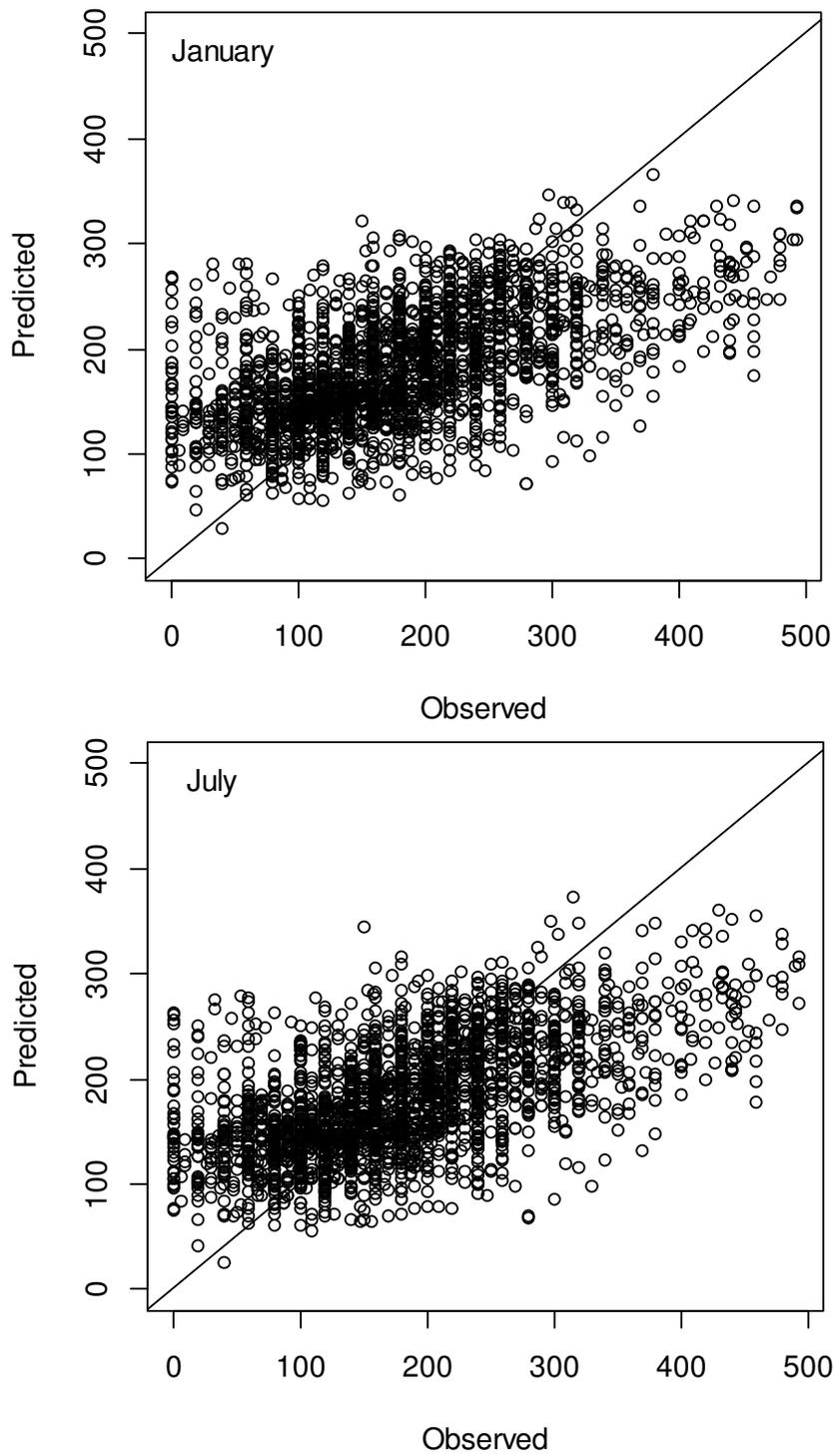


Figure 5.9 Plots of predicted values from the global models for January and July against observed values. Units represent the deviation of treeline elevations from site-level maxima (m).

5.4 DISCUSSION

Presented in this study is an analysis of the combined effects of within-site landform and topoclimate factors, and among-site regional-scale factors, on fine-scale *Nothofagus* treeline elevation variability across New Zealand. The study made novel use of a mesoscale atmospheric model to generate local-scale (200m) meteorological data at diverse treeline locations across the country. From these model-generated meteorological data, topoclimatic variables were derived that reflected possible beneficial and detrimental influences on tree physiological functioning at the local treeline. Three main results emerged from the research. First, there was a surprising degree of within-site variability in treeline elevations. Second, topoclimatic conditions at treelines across the country also varied considerably both within and among sites. Third, landform, topoclimatic and regional-scale effects together influence treeline variability at the 28 sites in a way that is consistent with their cited effects in the literature.

Most of the treeline locations investigated are positioned between 100 and 300m below the local, site-level maximum, suggesting that *Nothofagus* treelines at many locations across New Zealand are likely occurring well below their potential, temperature-based limit. To date, there has been only a limited amount of information available regarding the degree of elevational variability across the full extent of these treelines, much of it based on observations made by Peter Wardle at sites within the South Island's Craigieburn Range during the 1980's (Wardle 1985a, b, c). Wardle observed that *Nothofagus* treelines in this region are locally-depressed in valley heads and gullies and in other situations where fire had cause past removal of forest. However, his estimates placed these treelines 100m lower, at most, than what he considered to be climatic treeline. Clearly, based on results from the present study, *Nothofagus* treelines in New Zealand are more altitudinally variable than previously described. Certain areas of the country in particular, such as along the spine of the lower Southern Alps, display highly depressed treelines. On the whole, these results highlight the benefits of carrying out spatial analyses of treeline features over large spatial extents in order to provide an accurate characterisation of treeline variability.

Plots of TAPM data indicated that there was substantial topoclimatic variation among and within study sites and between winter and summer months. The three derived stress indices, in particular, were highly variable, even between proximal sites at similar latitudes. This suggests that complex topographically-mediated meteorological processes, that are characteristic of alpine areas, are likely occurring at different sites. For instance, it is well

known that the size of mountain ranges and their orientation relative to prevailing winds, valley widths and slope angles all affect valley-scale thermodynamic processes that regulate wind speeds, temperature extremes, and atmospheric moisture levels at different locations (Sturman and Tapper 2006). It thus appears that TAPM is capable of capturing local-scale climatic variation that is likely due to these processes within the treeline zone. Further work verifying the types of topoclimatic scenarios that occur in different treeline areas and what landscape characteristics are driving these differences would shed further light on particular aspects of topoclimatic effects at treelines.

There was a significant effect of both January and July topoclimatic processes on treeline elevation, after accounting for landform and regional-scale factors. Locations receiving higher summer (January) solar radiation inputs, and that were also ostensibly not subject to potential photoinhibition effects due to cold temperatures, were generally higher, although this effect was not evident in winter (July). This positive effect of solar radiation is noted by studies showing higher treelines on aspects with higher insolation levels (Danby and Hik 2007, Elliott and Kipfmueller 2010, Chapter 3 in this thesis), although this was not the case in other studies (Körner and Paulsen 2004, Treml and Banaš 2008). Higher summer insolation will generally lead to more favourable growing conditions and, thus, produce treelines that are closer to their climatically-driven maximum elevation. Conversely, treelines were lower at locations with increased potential for summer and winter desiccation stress and summer photoinhibition stress. Further, there was a marginal (although non-significant) effect due to winter frost potential. The nighttime movement of cold air from upper to lower elevations will increase the potential for frost and early morning photoinhibition, while strong daytime upslope wind movement will likely enhance desiccation conditions in both summer and winter. There will therefore likely be a combined effect of these stressors in certain locations at elevations lower than the maximum potential treeline. Compound-type effects can act across seasons; for instance, early summer frosts may disrupt the dehardening of leaf tissues thereby exacerbating desiccation damage during the following winter (Cochrane and Slatyer 1988). These types of stresses will act to maintain treelines locally at lower elevations, limiting their advance, despite possible warmer mean temperatures relative to higher elevations. These results are in line with field-based evidence of the detrimental effects of photoinhibition, desiccation, and frost on *Nothofagus* seedlings (Sakai and Wardle 1973, Wardle 1985a, c, Greer *et al.* 1989, Ball *et al.* 1991, Harsch 2010). Results are also consistent with the general hypothesis that abrupt treeline boundaries form at elevations

where strong effects of physiological stressors on seedling establishment override the more gradual effect of decreasing temperature with increasing elevation (Harsch and Bader 2011).

Results also indicate that *Nothofagus* treelines are, indeed, higher and closer to their potential maximum growth limits on steep, convex landform positions as per Wardle's (1985c) observations. This effect is contrary to what is observed at many northern-hemisphere treelines, where more exposed convex sites have been shown to be typically unfavourable for tree establishment (Holtmeier 2009). In the complex topography of New Zealand's mountains, ridge-to-valley gully features occur regularly along valley sides and likely act to channel slope-scale air movement, thus enhancing the detrimental effects mentioned above. Concave landform situations are also indicative of zones of previous, recurring avalanche and landslide disturbances. Thus, *Nothofagus* seedlings are probably able to reach higher elevations on convex, steeper slopes due to the more stable atmospheric and geomorphic conditions in these locations.

In addition to within-site influences, there was a clear influence of regional-scale factors on local-scale treeline deviations. Treelines at sites with higher mean growing season temperature and mountain mass index values and lower total precipitation values were more likely to be closer to their maximum potential. Variation in these factors essentially describe differences in thermal regime across the 28 study sites; the effect of thermal regime on treeline position in this study is consistent with previous research that has shown that warmer, drier treelines, particularly in larger, more interior mountain ranges, have higher treelines (e.g. Caccianiga et al. 2008). Nonetheless, the regional-scale model (Model M3) was poorly ranked relative to the landform and topoclimate models based on model comparisons. This suggests that although regional-scale influences are important and were part of the best-ranked global models, variation in treeline elevation was more strongly associated with within-site influences. Indeed, it is likely that regional-scale climates act to modulate or constrain local scale processes and their effects on treelines (Daniels and Veblen 2003, Elliott and Kipfmueller 2011, Chapter 3 in this thesis).

The effect of regional-scale disturbance, as represented using the earthquake intensity data, was not related to treeline variation in this study. However, the effects of disturbances, including those from fire (Ledgard and Davis 2004), heavy winds (Martin and Ogden 2006) and snowfalls (Wardle and Allen 1984), and tectonic activity (Allen *et al.* 1999, Haase 1999, Vittoz *et al.* 2001) are widespread and significant throughout *Nothofagus* mountain forests and are apparent throughout many treeline zones (Wardle 2008, Chapter 2 in this thesis). It is

highly likely that a proportion of variation in treeline elevations measured at the 28 sites in this study is indicative of this. Indeed, the poor ability of the January and July global models to explain treeline elevation deviations greater than 300m (Figure 5.9) may suggest that disturbance is a dominant treeline forming factor in these situations. *Nothofagus* species are generally slow to recolonise areas after removal, even in lower-elevation forests, due to strong competition with other species (Wiser *et al.* 1997). Thus, disturbance may be a confounding factor at many treeline sites in New Zealand and, without better datasets characterising the spatial distribution of local-scale disturbances across the country, it may be difficult to disentangle their effects from those due to climate.

Hourly meteorological data generated by the TAPM model enabled the investigation of variability in a number of factors influencing treelines that are notoriously hard to accurately quantify, particularly at local spatial scales in mountain environments. Spatially-explicit data for variables such as minimum or maximum daily temperatures, long-wave radiation, and relative humidity are key variables relevant to characterising physiological stress at treeline but, in previous studies, are typically limited to collection by on-site data loggers. Thus, this study has demonstrated that models such as TAPM have enormous potential for enabling local-scale investigations of topoclimatic effects at treeline. Clearly, two of the biggest advantages are the generation of spatially-explicit data useful for characterising stress-related effects and the ability to produce these data at any location. However, it is important to recognise that meteorological data for one year may not be representative of average topoclimatic conditions occurring at a given location, and it would therefore be useful to average model data over longer periods and for other critical parts of the year such as late spring and early autumn. Further, finer scale microhabitat and microclimate effects are likely also very important in allowing *Nothofagus* seedlings to establish above current positions (Harsch *et al.* 2012). Positive feedback processes, where established trees facilitate the recruitment of nearby seedlings, are also characteristic of abrupt treelines and affect the ability of these treelines to advance (Wiegand *et al.* 2006). Ultimately, results from this study could be used to characterise sites with different topoclimatic situations where investigations of local scale microclimate and biotic interactions could be investigated.

Chapter 6

General Discussion

The aim of this research was to investigate the treeline patterns and abiotic conditions characterising abrupt *Nothofagus* treelines across their full range in New Zealand. Specifically, the research questions were: (1) how do *Nothofagus* treelines vary spatially across New Zealand, in relation to abiotic conditions?; (2) how does spatial scale mediate the influence of abiotic factors on treeline elevation variation?; and (3) by quantifying associations between treeline pattern and abiotic variability, what insights can be gained regarding the possible processes structuring treelines across scales? To answer these questions, this study employed a range of spatial and statistical analysis techniques, enabling the investigation *Nothofagus* treelines in a spatially-extensive manner, across seven degrees of latitude.

Below, I will discuss the main contributions to treeline research offered by this work, the main limitations of the study, and some implications for future treeline research.

6.1 Treeline patterns and processes: insights gained

The ‘global approach’ (Malanson *et al.* 2011) to treeline research, championed by Christian Körner over the past two decades, searches for an underlying mechanistic explanation for why the occurrence of the life-form ‘tree’ becomes limited past certain elevations. This approach treats the high degree of local-scale variability observed at treelines around the world as “regional or local peculiarity”, resulting from ‘modulative influences’ that should be treated separately from ‘fundamental drivers’ (Körner 1998, 2012). There would be few arguments about the fact that, as a result of Körner’s approach, it is now clear that some aspect of temperature (or heat deficiency) provides a common basis for the limitation of upright tree growth worldwide (Körner and Paulsen 2004). However, it has also been voiced by many treeline researchers that an understanding of how and why treelines vary, either at or below their temperature-based limits, is equally fundamental, particularly because the factors driving local variation may determine how treelines will differentially respond to climate change spatially (Holtmeier and Broll 2005, 2007, 2012, Holtmeier 2009).

Despite this recognition, spatially-extensive analyses of treeline variability have been generally lacking in the treeline literature. Results from the investigations presented in this thesis of *Nothofagus* treelines in New Zealand have highlighted the incredible amount of treeline variability that exists across this study system. While abrupt treelines are relatively structurally simple relative to gradual treelines, the former display complex variability in their altitudinal positions, shapes, spatial configurations, and relationships with adjacent vegetation. Treeline elevations, for instance, vary considerably in space across New Zealand and, at local scales, are more likely-than-not to occur 100 to 300 m below their potential maximum elevation locally. This level of variability is much greater than what has been previously described for New Zealand treelines based on site-specific observations (Wardle 1985b, c, 2008). What this underlines is the need for the application of spatial methods that are able to characterise the complexity of treelines across large areas. There are definite limitations to the generality of conclusions that can be drawn about treeline patterns based only on information collected at disparate sites. It is now more possible than ever to apply spatial technologies to enable comprehensive characterisations of treelines in most areas of the world. The application of these technologies to treeline investigations in a consistent manner may provide a means to better define geographic variability in treelines with respect to differences in abiotic context and scale (Malanson *et al.* 2011).

Indeed, the examination of *Nothofagus* treelines relative to underlying abiotic conditions at different scales in this study enabled a comprehensive picture of treeline variability across New Zealand to be assembled. The consideration in Chapter 2 of multiple metrics of *Nothofagus* treeline variability in a multivariate pattern analysis offered a novel approach to characterising abrupt treeline variation at a landscape scale. This analysis might be considered a somewhat ‘composite’ look at these treelines, in that treeline metrics and abiotic factors were assembled, averaged, and analysed within a relatively coarse lattice of 15x15km grid cells across the country. However, the focus here was on determining if there would be emergent patterns of treeline variation, and associated signals of abiotic association, despite the large degree of environmental ‘noise’ characterising such diverse mountain environments. This analysis revealed distinct types of *Nothofagus* treelines across New Zealand that are also spatially clustered and defined by complex, overlapping abiotic effects of climate, disturbance, substrate and topography. While the expectation was that climate would largely drive landscape level patterns, disturbance emerged as a highly important factor, being highly correlated with variation in a number of the treeline pattern metrics. One of the main benefits of this extensive, landscape-scale approach is the ability to identify how

general treeline patterns and abiotic associations change in space at a nation-wide scale, which add a different perspective what is possible using site-specific data.

The idea that phenomena and processes are spatially structured is pervasive in ecology (Levin 1992). In Chapter 3 I laid out conceptual, spatial and statistical frameworks for examining how variation in *Nothofagus* treeline position was due to different abiotic influences at different spatial scales. These frameworks were structured around ideas from hierarchy theory (Allen and Starr 1982, O'Neill *et al.* 1989), predicated on the concept that the fine-scale processes driving treeline pattern are ultimately nested within and constrained by environmental conditions at larger scales. Thus, treeline elevation, which is ultimately controlled by tree-level physiological processes, will vary according to how a host of larger-scale environmental factors influence these processes from the top down at different scales (Harsch and Bader 2011). In essence, at a given location abiotic factors can act to 'push' treelines uphill (e.g. by improving thermal conditions) or 'pull' treelines downhill (e.g. by causing stress), and these factors are scale-dependent. While these ideas have been invoked in treeline research previously, both in theory development (Holtmeier and Broll 2005, Harsch and Bader 2011) and in practise (Daniels and Veblen 2003, Danby and Hik 2007b, Harsch *et al.* 2009, Elliott and Kipfmüller 2010, 2011, Elliott 2011), this study was the first to apply them across such an extensive treeline dataset, using hierarchical statistical methods that enabled abiotic effects to be teased apart at a range of spatial scales. This work confirmed theoretical expectations that thermal factors, which influence growth processes, drive much of the variation in treeline position, largely at a broad scale. Conversely, stress-related factors operate mainly at finer scales and modify the larger-scale thermal effect. Overall, the conceptual framework, the spatial framework based on nested river catchments, and the hierarchical statistical modelling methods described in Chapter 3 provide a sufficiently generic approach that could be applied to other treeline systems.

Local-scale stressors critically impact the ability of seedlings to recruit above treeline by affecting the uptake and use of carbon (Cairns and Malanson 1998, Bansal and Germino 2008). Yet, these stressors are extremely difficult to characterise spatially, and investigations of their effects have been largely limited to site-scale observations and experiments. The issue is that high topographic complexity in treeline zones induces considerable localised climatic variation that is not well-represented in the GIS-based climatic datasets that form the basis for many treeline investigations. Meteorological variables such as wind speeds, temperature extremes, and incoming and outgoing radiation are particularly difficult to capture, but these variables are key players in determining the levels of stress to which trees

are subjected at treeline. The research presented in Chapters 4 and 5 was aimed at exploring whether a mesoscale atmospheric model, TAPM, could be practically employed to generate hourly meteorological data in a spatially-explicit manner within treeline zones. In Chapter 4, testing of TAPM's performance was carried out against data from two weather stations located near treeline and for which relevant data were available. Results indicated that TAPM could relatively accurately predict temperature and wind speed, although there was more uncertainty and bias associated with predictions of solar radiation and relative humidity. However, given the complexity of the processes being modelled, results were very promising. Limiting this assessment to two weather stations could be considered a major limitation to obtaining an adequate validation of TAPM in alpine areas. However, the types of prediction errors and biases emerging from the analysis were reasonable and consistent with the many previous assessments of TAPM globally. Most importantly, prediction errors were relatively consistent across seven years' worth of data for both January and July and for the two locations. This is encouraging because it indicates that errors are due to the internal workings of the model and not driven by location-specific factors. Nonetheless, the model requires further assessment at a range of situations to better-differentiate model-inherent and externally-caused uncertainties.

In Chapter 5, TAPM was applied to 28 treeline sites across New Zealand in order to generate hourly data at a 200 m resolution that could be used to characterise topoclimate effects. To my knowledge, this is the first time such a process-based, atmospheric model has been applied to investigate treelines. One of the main novel uses of the model output was the generation of indices to represent the potential for frost, desiccation, and photoinhibition at over 1200 treeline locations across the country. These effects have typically been quantified in previous treeline studies using field or laboratory measurements (e.g. Sakai and Wardle 1973) or indirectly inferred through site-scale experimental manipulations and observations (e.g. see Smith *et al.* 2009). Excitingly, there was a signal for the effect of winter and summer desiccation stress and summer photoinhibition stress on site-level treeline elevation variation, after accounting for landform and regional-scale effects. This supports the idea that abrupt treelines are likely maintained, typically at relatively low elevations, at least in part by stress-related effects that limit recruitment beyond the tall forest (Bader *et al.* 2007, Harsch *et al.* 2012). Based on the analysis in Chapter 5, it was also evident that past disturbances have likely depressed these treelines in many areas, making them lower in elevation than what would be expected from physiological effects alone. It was also shown that landform effects, specifically due to slope gradient and curvature, have clear correlations with *Nothofagus*

treeline elevation, confirming the previous hypothesis that *Nothofagus* is more likely to reach its highest elevations on steep, convex landforms that are less likely to be affected by disturbance and meteorological variability (Wardle 1985c). Regional-scale factors characterising differences in thermal regimes from site-to-site also exerted significant influences on average site-level treeline variation, although these effects were less influential than the within-site effects.

6.2 Final words and future research

The approaches taken in this thesis have been mainly observational and correlative, begging the question: what can such analyses add to understanding treelines relative to site-specific and experimental approaches that are explicitly aimed at uncovering processes? I suggest, first of all, that this thesis has shown that by examining the nature of associations between abiotic factors and treeline variability at different scales it is certainly possible to gain insight into likely causative processes. It is clear that broad-scale treeline studies covering large spatial domains are key to characterising the full range of variability that exists and revealing the factors that likely most important for constraining treeline variation. This is particularly the case for variables that cannot be manipulated such as geology, catastrophic disturbances, topography, and soil characteristics. Second, an understanding of the abiotic context across treelines will be critical to determining the future response of treelines to climate change in different locations, especially in areas where topoclimatic or landform factors are more influential than temperature in governing treeline processes (Leonelli *et al.* 2009, 2011). Lastly, broad-scale studies can provide crucial information regarding how to direct future work at a site scale, by indicating the areas that are most contrasting or that fulfil particular conditions, and by suggesting potential new hypotheses that can be addressed via experiments. Certainly, for New Zealand's *Nothofagus* treelines, results from this thesis could be used in this way. For instance, it would be useful to investigate local-scale treeline recruitment patterns and trade-offs between facilitation and competition effects at treelines occurring near their temperature-based maximum as compared to those that are highly depressed (e.g. as indicated in Chapter 5).

On the whole, this research has made significant contributions towards the development of new analytical approaches to characterising treeline patterns and examining treeline-environment relationships, and towards advancing our understanding of treeline processes in general. It would be useful to apply the approaches developed in this thesis to

other abrupt treelines to determine if similar patterns and abiotic factors influence treelines at national scales elsewhere in the world.

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Appendix A

Chapter 2 Appendices

A.1 Moran's I correlograms for investigating the spatial autocorrelation structure of the HSIN and VSIN treeline pattern metrics.

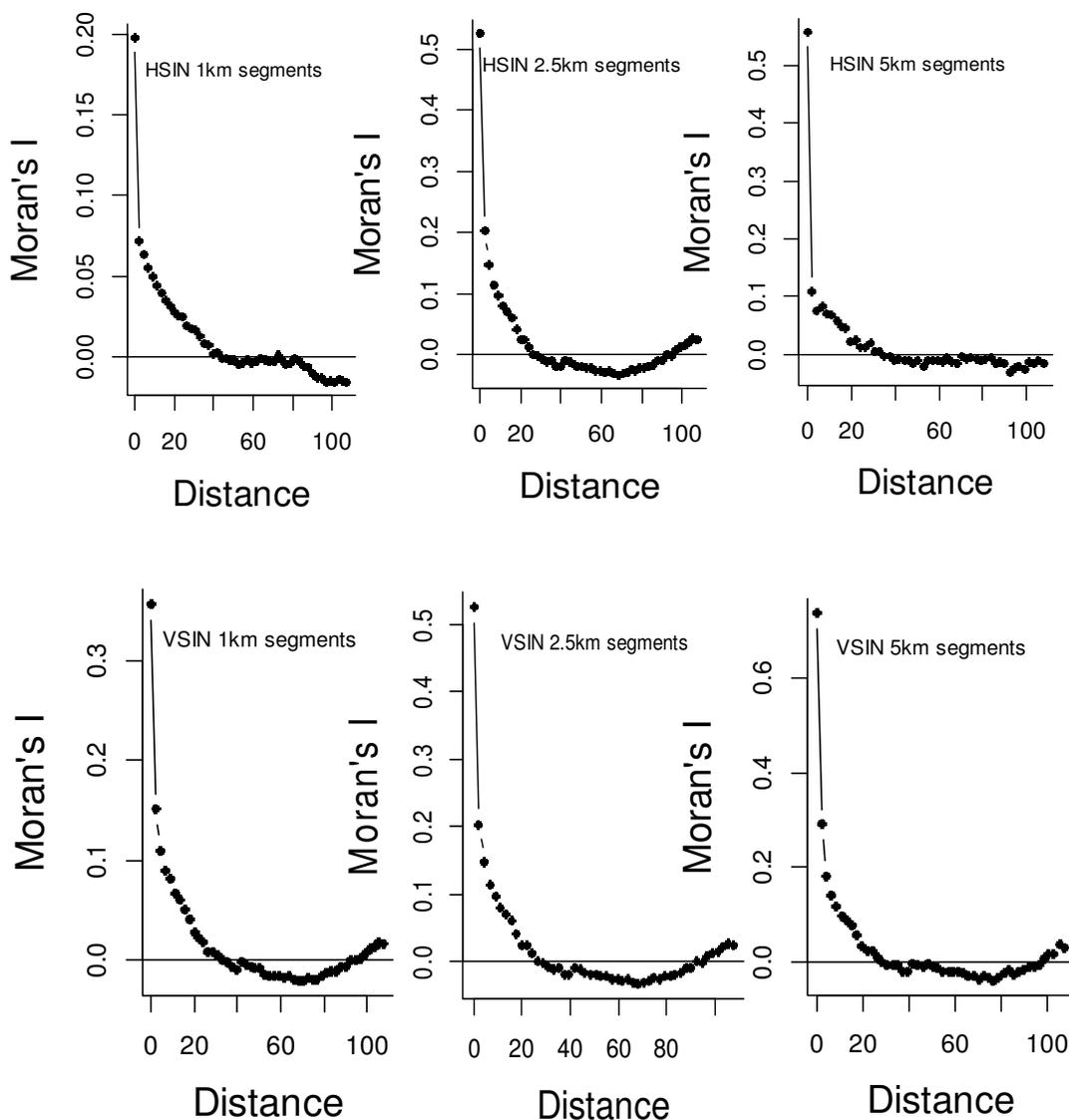


Figure A.1 Moran's correlograms to assess the degree of spatial autocorrelation in the HSIN and VSIN treeline metrics computed at 1, 2.5 and 5km segment lengths.

A.2 Maps showing the distribution of climatic, substrate, topographic and disturbance factors within the 230 landscape zones.

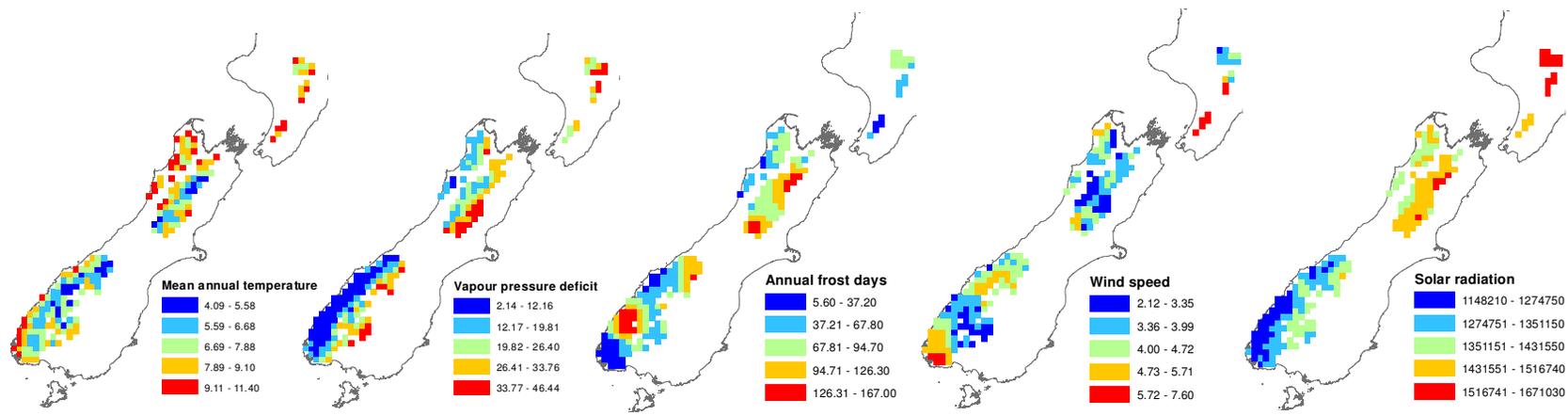


Figure A.2 Maps showing the spatial distribution of climatic factors used in the study, across the 230 treeline landscape zones.

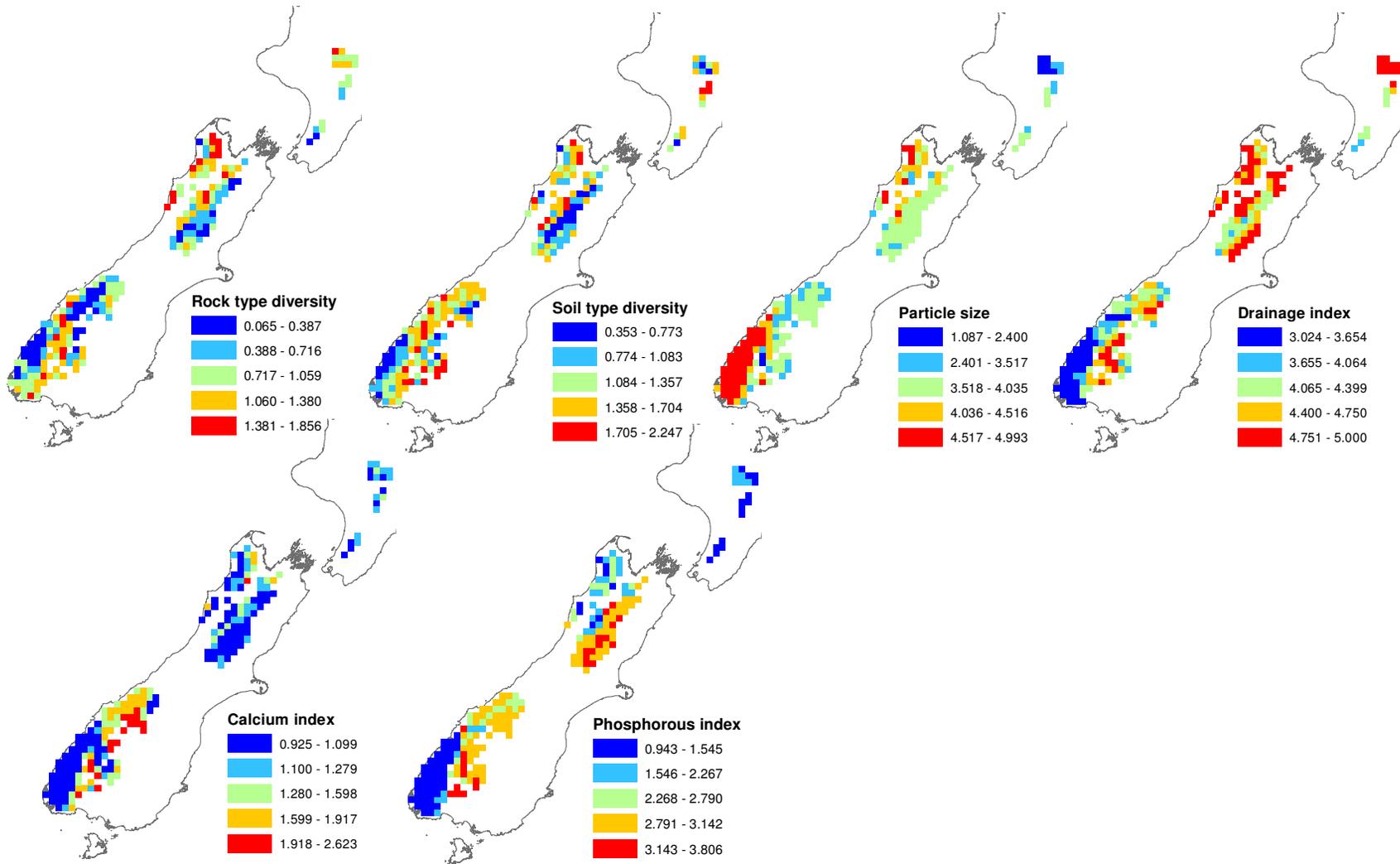


Figure A.3 Maps showing the spatial distribution of substrate factors used in the study, across the 230 treeline landscape zones.

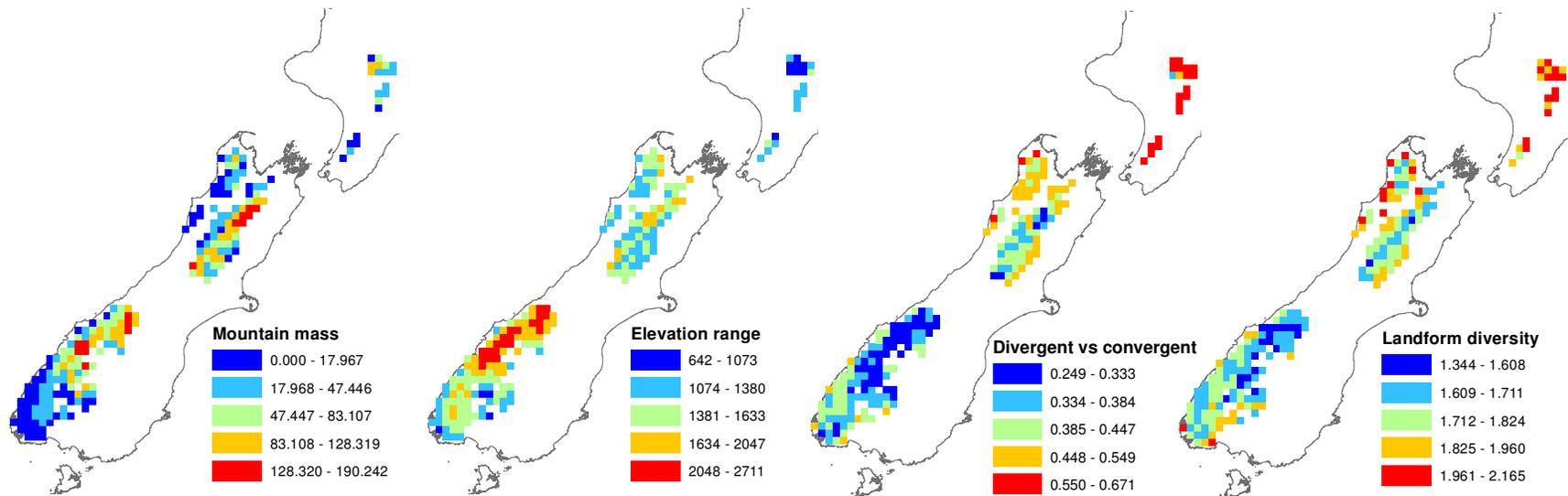


Figure A.4 Maps showing the spatial distribution of topographic factors used in the study, across the 230 treeline landscape zones.

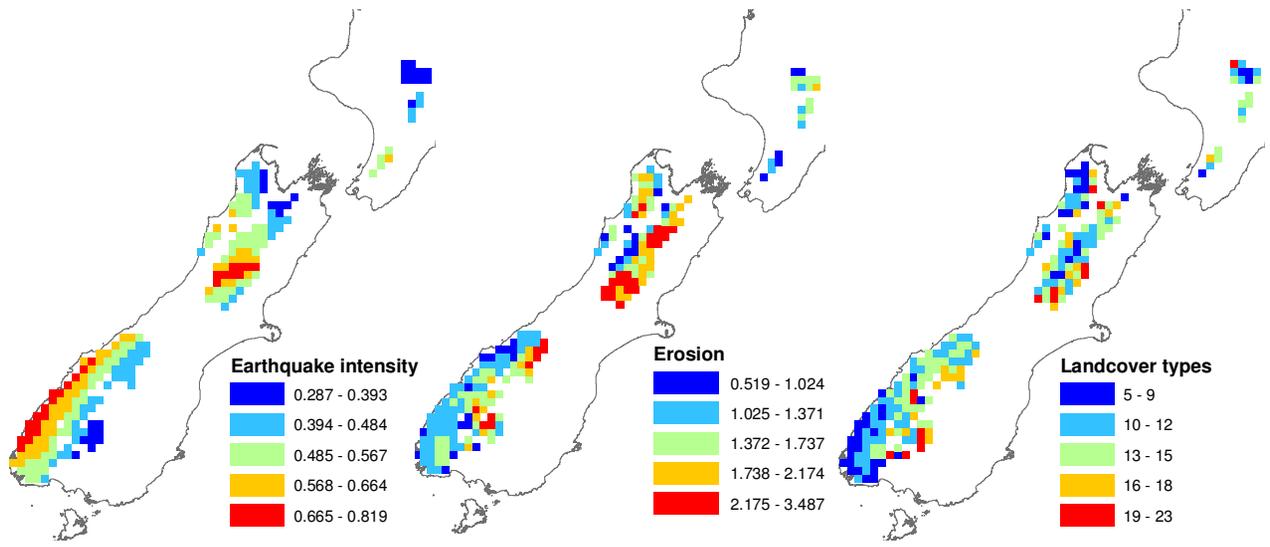


Figure A.5 Maps showing the spatial distribution of disturbance factors used in the study, across the 230 treeline landscape zones.

A.3 AIC rankings of GIS models explaining variation in treeline pattern metrics that include different autocorrelation structures.

Note: the best ranked models are shown in bold

Response	Autocorrelation structure	Model			
		Climate	Substrate	Topography	Disturbance
Elevation	No autocorrelation structure	2951.6	2912.7	2911.6	2981.6
	corSpher	2679.3	2676.6	2685.8	2703.3
	corLin	2741.2	2676.5	2799.6	2774.1
	corGaus	2701.7	2699.9	2706.6	2723.5
	corExp	2676.7	2675.6	2683.2	2702.2
	corRatio	2686.5	2683.0	2694.4	2710.9
Horizontal sinuosity	No autocorrelation structure	145.5477	176.9953	178.56351	140.3892
	corSpher	17.74632	32.1874	19.71279	13.25664
	corLin	36.05923	61.37972	57.88392	36.16178
	corGaus	16.7734	34.64686	26.00287	15.0068
	corExp	13.37214	31.47899	18.50835	11.53836
	corRatio	11.55297	29.97331	19.20979	10.09071
Vertical sinuosity	No autocorrelation structure	-937.524	-895.6801	-965.5543	-925.4092
	corSpher	-1045.87	-1020.676	-1071.9891	-1058.0132
	corLin	-1031.61	-988.5261	-1045.4716	-1026.717
	corGaus	-1038.67	-1013.12	-1064.9431	-1050.9435
	corExp	-1041.31	-1019.734	-1069.3348	-1055.7159
	corRatio	-1041.99	-1018.852	-1068.1846	-1055.3797
Adjacent vegetation index	No autocorrelation structure	-13.9793	-28.30805	-18.83451	-35.43338
	corSpher	-147.424	-145.8954	-143.60756	-155.69381
	corLin	-120.625	-109.3417	-117.2637	-79.31224
	corGaus	-139.077	-135.825	-136.68877	-145.50591
	corExp	-146.097	-143.8745	-144.21357	-153.44451
	corRatio	-143.486	-140.7933	-141.31018	-150.40732
Contiguity index	No autocorrelation structure	-274.742	-286.2885	-277.8924	-310.733
	corSpher	-363.35	-337.9558	-358.0666	-369.6633
	corLin	-310.671	-315.8566	-310.5827	-339.9591
	corGaus	-356.277	-335.4475	-350.3946	-364.4967
	corExp	-363.463	-340.1036	-358.6193	-372.1563
	corRatio	-358.784	-338.8092	-353.8424	-370.762
Orientation index	No autocorrelation structure	1201.023	1200.476	1199.501	1196.086
	corSpher	1162.875	1168.69	1166.342	1155.816
	corLin	1185.852	1184.61	1185.646	1180.729
	corGaus	1163.327	1161.019	1166.814	1155.95
	corExp	1165.109	1163.108	1168.479	1157.841
	corRatio	1164.556	1162.609	1168.282	1157.503
Compactness index	No autocorrelation structure	25.71875	44.4368	45.66706	30.88846
	corSpher	-50.0879	-11.95615	-33.55959	-33.10973
	corLin	-57.7849	-30.49198	-40.61015	-54.58436
	corGaus	-62.9471	-37.44694	-47.60737	-57.1261
	corExp	-63.6178	-30.68727	-48.38666	-52.36626
	corRatio	-67.236	-37.37246	-51.97853	-59.80786

Appendix B

Chapter 3 Appendices

B.1 Assessment of correlations between three GIS-based, gridded climatic variables and elevation in the *Nothofagus* treeline zone across New Zealand.

As the response variable used in the Chapter 3 regression analyses was treeline elevation, it was necessary to avoid using available climatic data that were possibly highly correlated with elevation due to the way they were derived. I initially considered three spatial climatic datasets for use in analyses: mean growing season temperature, extreme wind days, and vapour pressure deficit. The spline interpolation procedures used to generate these datasets from long-term weather station records included elevation-related adjustments (Leathwick *et al.* 2002a) to account for changing climatic processes with increasing elevation. For example, temperatures decrease with increasing elevation due to the lapse rate effect. The inclusion of elevation as a covariate in the interpolation procedures therefore aims to locally adjust the broad spatial estimates derived from the weather station data alone.

I assessed the degree to which these three datasets were correlated with elevation in the general zone of transition from forest to alpine vegetation, between 500m and 1500m above sea level. I did this by randomly generating 1000 points in the GIS within this transition zone in areas where *Nothofagus* treelines occur across New Zealand. At these points, elevation was extracted from a 25m resolution digital elevation model, and values for the three climatic variables. The temperature and extreme wind days datasets were at a 500m resolution and were obtained from the New Zealand National Institute for Water and Atmosphere (Wratt *et al.* 2006) and the VPD dataset was at a 100m resolution and was available as part of the Land Environments of New Zealand database (Leathwick *et al.* 2002b).

Mean growing season temperature was strongly correlated with elevation within the *Nothofagus* treeline forest-alpine transition zone (Figure A1 a), while extreme wind days and vapour pressure deficit were only weakly correlated with elevation (Figures A1 b and c).

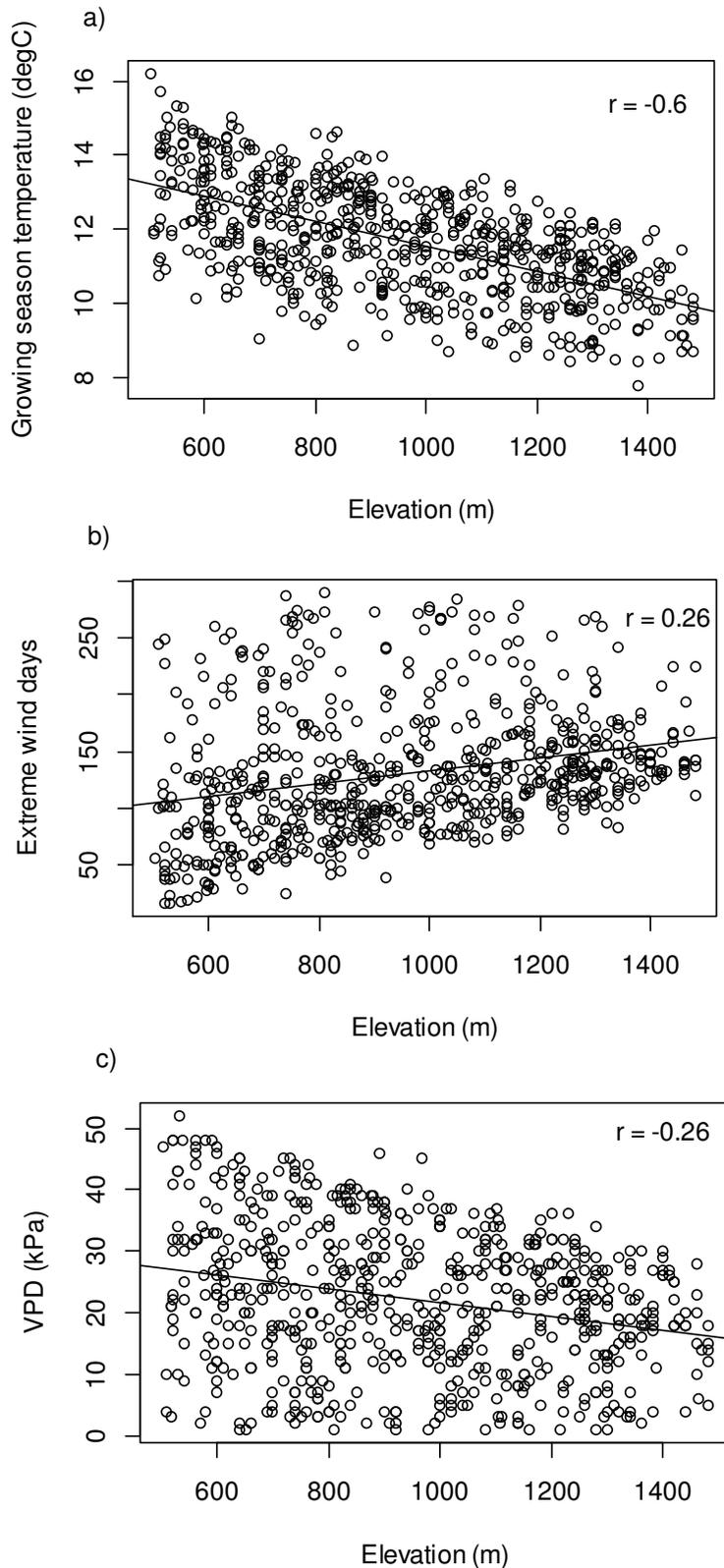


Figure B.1 Scatterplots showing trends between three climatic variables and elevation extracted at 1000 random points within the *Nothofagus* treeline forest-to-alpine transition zone (500 – 1500m elevation) across New Zealand.

B.2 A description of the hierarchical data structure and regression analyses using random effects coefficients carried out in Chapter 3.

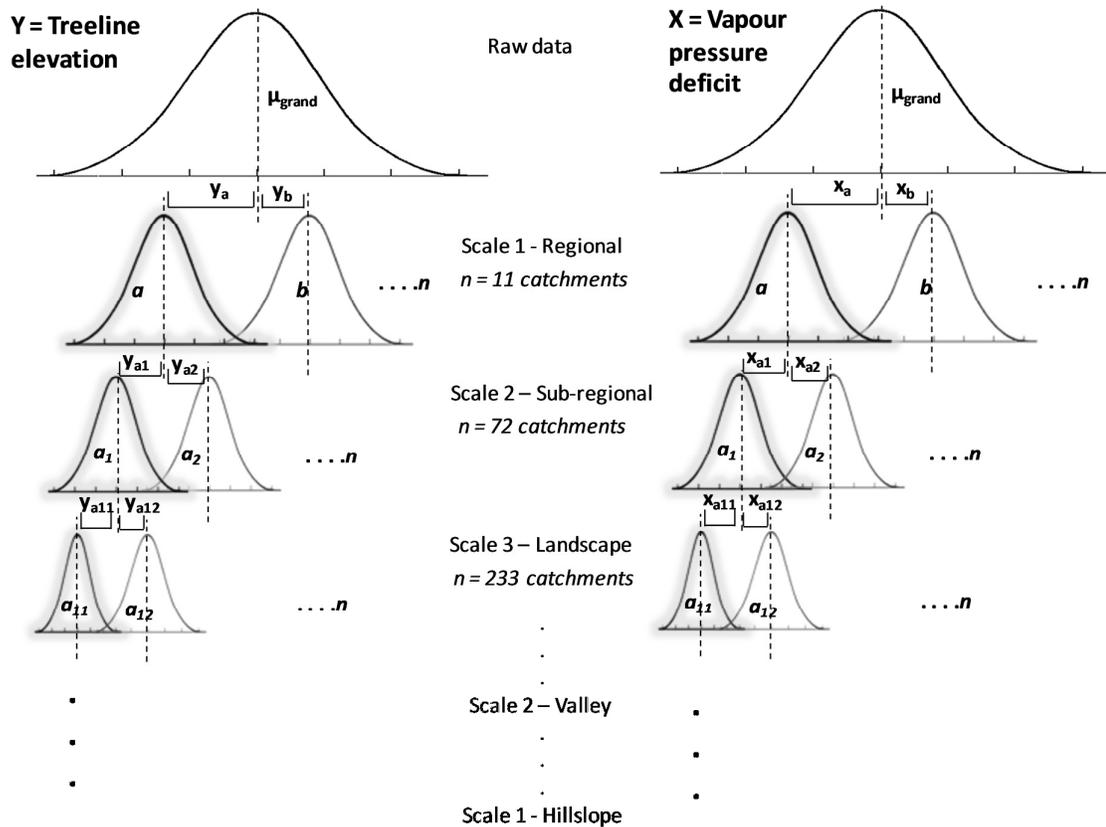


Figure B.2 A conceptual diagram to illustrate the hierarchical structure of the data and the analyses used in Chapter 3.

Hierarchical structuring of the data and random effects coefficients

Figure B.2 first of all illustrates how data for treeline elevation (on the left) and the abiotic factors (VPD shown as an example on the right) used in our analysis are hierarchically structured based on nested river catchments. The bell curves represent conceptually the distribution of data extracted at treeline sample points, spaced at 500m intervals along treelines, within different catchments (spatial units) at different scales. The distribution at the top is for the full dataset (eg. 53,912 data points at treeline). At each scale, the data are partitioned by catchments, which are treated as random effects. At scale 1, for example, the datasets as a whole are partitioned into 11 regional-scale catchments. At scale 2, the data are partitioned into 75 sub-regional-scale catchments, each of which are nested within one of the 11 catchments at scale 1. This structure is repeated across the five scales used in the analysis.

Using the hierarchical structure described above, data for each variable (treeline elevation and each of the eight abiotic factors) were initially modelled using an intercept-only, hierarchical linear model (i.e. random intercept mixed effects model). These models simply represent how the random intercepts produced by the model for each spatial unit (catchment) at each scale deviate from the random intercept of the catchment at the scale above, within which they are nested. These random intercept deviations are termed “random effects coefficients”. For example, in Figure B.2, y_a and y_b are the random effects coefficients that describe the deviation of the treeline elevation intercepts for catchments a and b at the regional scale (Scale 1) away from the overall mean treeline elevation across all of the data (μ). In this case, the intercept for catchment a is lower (ie the random effect coefficient y_a is negative) than the overall treeline elevation mean, while the intercept for catchment b is higher (the random effect coefficient y_b is positive). Similarly, intercepts for treeline elevations within catchments at Scale 2 deviate away from the intercepts for the Scale 1 catchments within which they are nested. For example, the random effects coefficient y_{a1} shows a negative deviation of the treeline elevation intercept for catchment a_1 (which is nested within catchment a) away from the catchment a intercept. Thus, the random effects coefficients at each scale represent the variability in the data for a given variable (eg. treeline elevation, VPD, etc.) at that scale, independent of the other scales.

Regression analyses at each scale

The main aim of our study was to determine to what extent treeline elevation variation was associated with variation in the eight abiotic factors at the five scales of interest. We achieved this by regressing the random effects coefficients for treeline elevation at each scale (as the response variable) against the random effects coefficients for the eight abiotic factors. For example (referring to Figure B.2 above), a vector notation representation of a simple regression between treeline elevation and VPD at Scale 1 would be achieved as:

$$\begin{bmatrix} y_a \\ y_b \\ \cdot \\ \cdot \\ y_n \end{bmatrix} = \begin{bmatrix} 1 & x_a \\ 1 & x_b \\ \cdot & \cdot \\ \cdot & \cdot \\ 1 & x_n \end{bmatrix} \begin{bmatrix} \beta_0 \\ \beta_1 \end{bmatrix} + \begin{bmatrix} \varepsilon_a \\ \varepsilon_b \\ \cdot \\ \cdot \\ \varepsilon_n \end{bmatrix}$$

where y_i are random effects coefficients for treeline elevation at Scale 1, x_i are random effects coefficients for a given abiotic factor (VPD, solar radiation etc.) at Scale 1, and β_0 and β_1 are

the intercept and slope parameters of the regression model. The regression error, $\varepsilon_i \sim \text{iid } N(0, \sigma^2)$.

If the relationship between the random coefficients for treeline elevation and those for VPD at Scale 1 were positive, this would indicate that treeline elevation and VPD both deviate from their overall grand intercepts in a positive way across the catchments at Scale 1, thus suggesting that higher treeline elevations are correlated with higher VPDs at Scale 1. This type of regression was repeated at all other scales to look at scale-dependent relationships between treeline elevation and the eight different abiotic factors. Multiple regression models were constructed in a similar way, with random effects coefficients for multiple abiotic factors regressed against those for treeline elevation. Thus, the regression analyses at each scale are accounting for how variation in treeline elevation is associated with variation in abiotic factors, independent of the other scales.

B.3 Pearson's correlations among random effects coefficients for the eight abiotic factors at each of the five spatial scales.

Scale 1 – Regional

	Solar radiation	Mountain mass index	CTI	VPD	Extreme wind days	PC1 Soil fertility	PC2 Soil moisture	Earthquake intensity
Solar radiation	1	-0.233	-0.664	0.512	-0.155	-0.522	-0.281	-0.593
Mountain mass index	-0.233	1	0.547	0.385	-0.459	-0.324	0.493	-0.298
CTI	-0.664	0.547	1	-0.189	-0.054	-0.004	0.577	0.188
VPD	0.512	0.385	-0.189	1	-0.327	-0.345	0.375	-0.710
Extreme wind days	-0.155	-0.459	-0.054	-0.327	1	0.449	-0.135	0.029
PC1 Soil fertility	-0.522	-0.324	-0.004	-0.345	0.449	1	-0.036	0.529
PC2 Soil moisture	-0.281	0.493	0.577	0.375	-0.135	-0.036	1	-0.248
Earthquake intensity	-0.593	-0.298	0.188	-0.710	0.029	0.529	-0.248	1

*At the regional scale, CTI and Earthquake intensity were omitted as explanatory from multiple regression analyses due to relatively strong collinearity with other variables.

Scale 2 – Sub-regional

	Solar radiation	Mountain mass index	CTI	VPD	Extreme wind days	PC1 Soil fertility	PC2 Soil moisture	Earthquake intensity
Solar radiation	1	-0.219	0.116	0.101	0.266	-0.021	0.197	-0.395
Mountain mass index	-0.219	1	-0.036	0.169	-0.218	-0.007	<.001	0.116
CTI	0.116	-0.036	1	0.225	-0.027	0.026	0.121	-0.24
VPD	0.101	0.169	0.225	1	-0.13	-0.223	0.081	-0.464
Extreme wind days	0.266	-0.218	-0.027	-0.13	1	0.223	-0.047	0.031
PC1 Soil fertility	-0.021	-0.007	0.026	-0.223	0.223	1	0.352	0.318
PC2 Soil moisture	0.197	<.001	0.121	0.081	-0.047	0.352	1	-0.108
Earthquake intensity	-0.395	0.116	-0.24	-0.464	0.031	0.318	-0.108	1

Scale 3 – Landscape

	Solar radiation	Mountain mass index	CTI	VPD	Extreme wind days	PC1 Soil fertility	PC2 Soil moisture	Earthquake intensity
Solar radiation	1	-0.202	0.093	-0.011	0.137	-0.139	0.008	-0.134
Mountain mass index	-0.202	1	0.135	0.231	-0.125	0.023	0.027	0.06
CTI	0.093	0.135	1	0.285	-0.14	0.033	0.192	-0.149
VPD	-0.011	0.231	0.285	1	-0.092	-0.11	0.03	-0.516
Extreme wind days	0.137	-0.125	-0.14	-0.092	1	0.133	-0.047	0.037
PC1 Soil fertility	-0.139	0.023	0.033	-0.11	0.133	1	0.485	0.179
PC2 Soil moisture	0.008	0.027	0.192	0.03	-0.047	0.485	1	0.031
Earthquake intensity	-0.134	0.06	-0.149	-0.516	0.037	0.179	0.031	1

Scale 4 – Valley

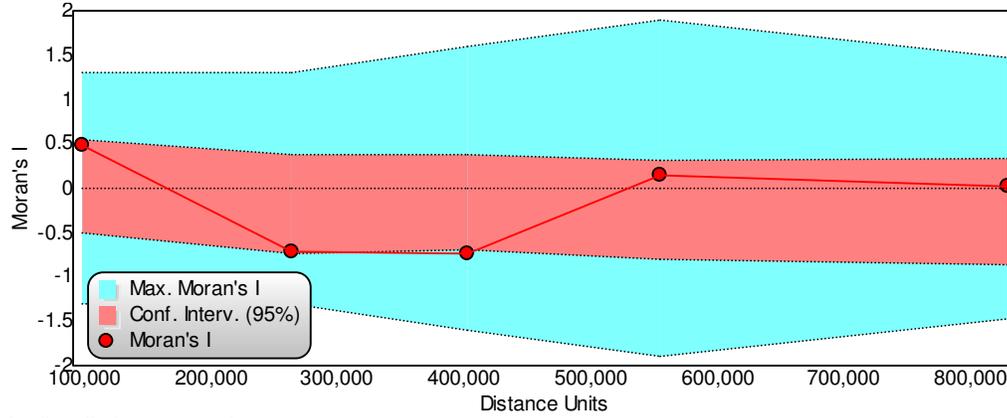
	Solar radiation	Mountain mass index	CTI	VPD	Extreme wind days	PC1 Soil fertility	PC2 Soil moisture	Earthquake intensity
Solar radiation	1	-0.068	0.034	0.016	0.286	0.024	0.013	-0.094
Mountain mass index	-0.068	1	0.007	0.172	0.174	-0.042	-0.032	0.036
CTI	0.034	0.007	1	0.151	0.032	0.012	0.074	-0.011
VPD	0.016	0.172	0.151	1	-0.106	-0.062	0.019	-0.343
Extreme wind days	0.286	0.174	0.032	-0.106	1	-0.088	-0.062	<.001
PC1 Soil fertility	0.024	-0.042	0.012	-0.062	-0.088	1	0.11	0.165
PC2 Soil moisture	0.013	-0.032	0.074	0.019	-0.062	0.11	1	-0.02
Earthquake intensity	-0.094	0.036	-0.011	-0.343	<.001	0.165	-0.02	1

Scale 4 – Hillslope

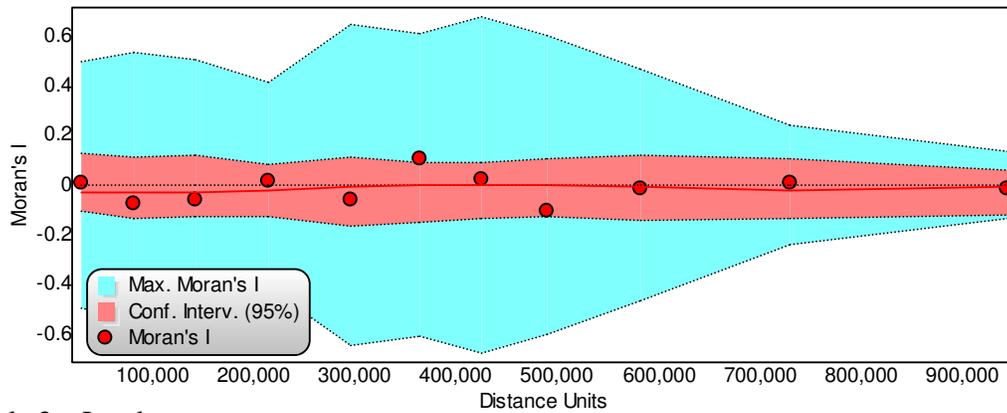
	Solar radiation	Mountain mass index	CTI	VPD	Extreme wind days	PC1 Soil fertility	PC2 Soil moisture	Earthquake intensity
Solar radiation	1	0.008	-0.016	-0.055	0.459	0.062	-0.058	-0.077
Mountain mass index	0.008	1	0.012	0.099	0.072	-0.021	-0.005	<.001
CTI	-0.016	0.012	1	0.135	0.123	0.019	0.038	0.029
VPD	-0.055	0.099	0.135	1	-0.221	0.151	0.021	-0.115
Extreme wind days	0.459	0.072	0.123	-0.221	1	-0.102	-0.086	-0.022
PC1 Soil fertility	0.062	-0.021	0.019	0.151	-0.102	1	-0.053	0.063
PC2 Soil moisture	-0.058	-0.005	0.038	0.021	-0.086	-0.053	1	-0.023
Earthquake intensity	-0.077	<.001	0.029	-0.115	-0.022	0.063	-0.023	1

B.4 Moran's I correlograms, used to assess the presence of spatial autocorrelation in the residuals of the top-ranked multiple linear regression models at each of the five scales in Chapter 3.

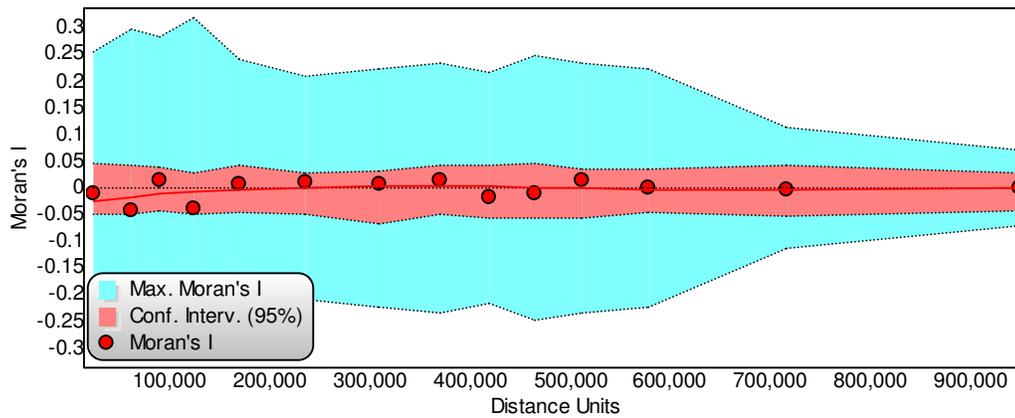
Scale 1 – Regional



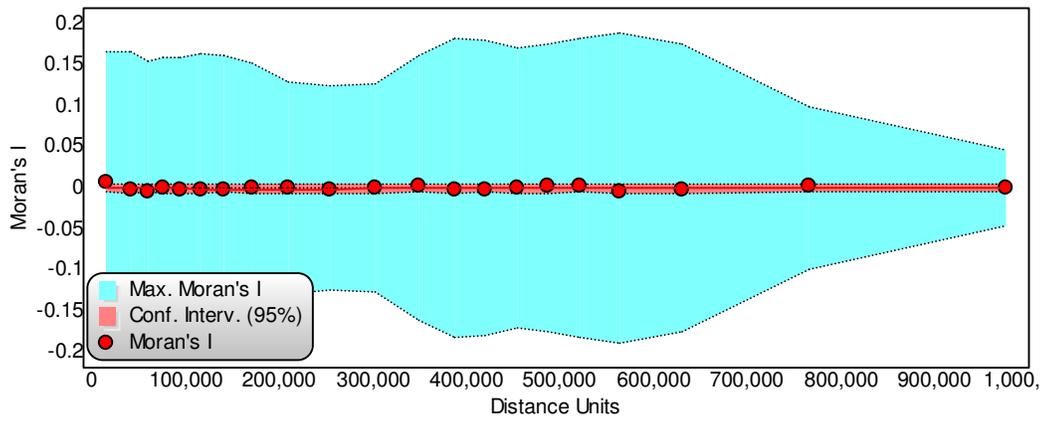
Scale 2 – Sub-regional



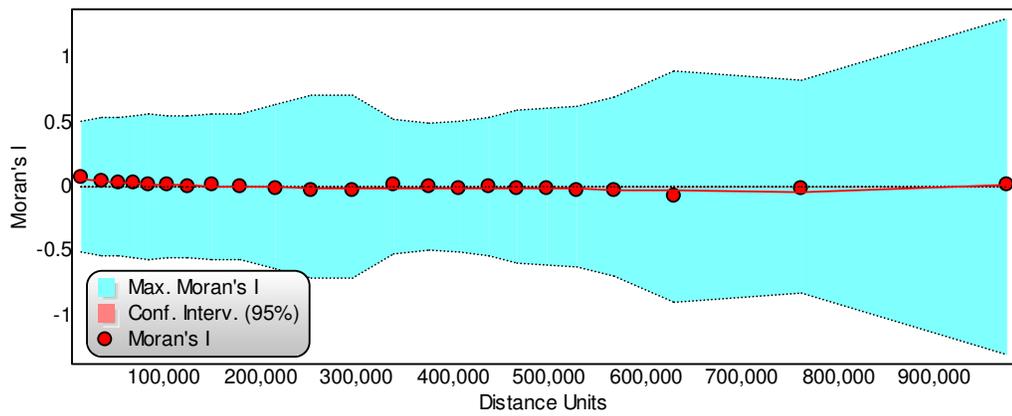
Scale 3 – Landscape



Scale 4 – Valley



Scale 5 – Hillslope



Appendix C

Chapter 4 Appendices

C.1 Observed versus TAPM-generated time series for January and July, 2001-2007 at Ruapehu weather station. Each figure depicts data for a given year.

