Investigating the response of subtropical forests to environmental variation through the study of the *Abies kawakamii* treelines in Taiwan

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This thesis is submitted as a collection of papers. Details of these, including current status are shown below:

Consequences of treeline shifts for the diversity and function of high altitude ecosystems

Arctic, Antarctic and Alpine Research **46**: 829-840

Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region

Global Change Biology **20**: 3756-3766

Climate growth relationship of *Abies kawakamii*: an investigation over the species altitudinal range on Yushan, Taiwan

Not yet submitted

Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline

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How fast is too fast? Rapid forest change leads to community disassembly and reduced diversity in advancing forests

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Summary and Aims

Altitudinal treeline advance represents a sensitive and well-studied example of species response to climate warming. Although a great deal of work has been conducted globally, few studies have considered subtropical alpine treelines and little is known about their structure and function. This research aims to investigate the response of high altitude forests in Taiwan to climate variation by characterising treeline advance in the area, exploring the mechanisms driving the advance, and considering the consequences of advance for the wider community.

The thesis consists of a general introduction to the topic followed by a series of papers, exploring: (1) Possible consequences of treeline shifts for biodiversity and ecosystem function. (2) The advance of the *Abies kawakamii* treeline through aerial photograph analysis. (3) The changes in growth rate of *Abies kawakamii* at treeline and the influence of altitude and temperature on growth. (4) Regeneration patterns at treeline and the importance of microclimate and topographic sheltering. (5) Consequences of the range shift for the wider forest community. The work is then concluded with a general discussion and synthesis.

The main aims of this work are therefore to characterise and understand the pattern and pace of treeline advance and forest structural change throughout the Central Mountain Range of Taiwan. Treeline advance is characterised through the study of repeat aerial photographs and the mechanisms behind the observed shift are explored through the study of two key responses associated with forest advance: tree growth at treeline and seedling establishment beyond treeline. The consequences of treeline advance for the wider subalpine community are investigated through the study of epiphytic lichen communities at treeline sites. This investigation of an understudied region will allow for improved understanding of treeline response at a global scale.

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Chapter 1

General Introduction

Climate change

Climate change has occurred naturally throughout Earth's history, although the unprecedented rate of current change can be attributed to the impacts of anthropogenic greenhouse gas emissions. The amount of CO_2 in the atmosphere increased by more than a third during the industrialised era (Le Treut *et al.* 2007) and other gases such as methane (up by 150% over this period) and nitrous oxide (up by 20%) are also contributing to the warming trend (IPCC, 2013).

Global mean surface temperature has increased since the 19th century, with the first decade of the 21st century being the warmest on record. Global mean surface temperature increased by 0.85°C from 1880 to 2012 and there is evidence that warming has occurred worldwide (IPCC, 2013). Heatwaves have become more frequent throughout Europe, Asia and Australia, the number of cold days and nights have decreased, and the number of warm days and nights increased globally since the 1950s. It is likely that this pattern of increase will continue into the future, with predictions of an increase in global mean temperature in the region of 1.5-4°C for the period 2081–2100 compared to 1850-1900, depending on greenhouse gas emission (IPCC, 2013). Global precipitation will also likely increase, although there will be high regional variability in patterns of both temperature and precipitation, with some areas experiencing decreases in both (IPCC, 2013).

Other associated changes include a rise in global mean sea level; this occurred at a rate of 3.2 mm $year^{-1}$ between 1993 and 2010, and an increase in oceanic CO_2 uptake, leading to ocean acidification (IPCC, 2013). Arctic and Antarctic sea ice has reduced in extent and thickness, glaciers are shrinking globally, and the rate of the reduction in these snow/ice masses is increasing over time (IPCC, 2013).

Climate change impacts on ecosystems and species

There is evidence of widespread and diverse impacts of climate change on species and ecosystems in terrestrial, marine and freshwater environments (Walther *et al.*, 2002; Walther, 2003). For example warming temperatures and increases in CO_2 can increase growing season length (Reyes-Fox *et al*., 2014), net primary productivity (NPP) and plant carbon sequestration (Saxe *et al*., 2001), thus creating negative feedback to climate warming (Fang *et al*., 2014). However melting snow and ice (IPCC, 2007), thawing permafrost (Walter *et al*., 2006), and the expansion of forest and shrubs into tundra ecosystems (Tape *et al*., 2006; Myers-Smith *et al*., 2011) all have the potential to release large amounts of carbon to the atmosphere thus creating positive feedback to warming (Chapin *et al*., 2005). Climate change also has the potential to change nutrient cycling, for example by making nitrogen more available to plants (Rustad *et al*., 2001; Butler *et al*., 2012), so potentially changing plant community composition (van der Wal *et al*. 2005).

Range shifts, such as the latitudinal expansion of shrub species in the Arctic (Sturm, 2001; Myers-Smith *et al*., 2011) and upwards shifts of alpine plants (Grabherr *et al*., 1994; Pauli *et al.*, 1996) are a commonly observed response to warming climate. The individualistic nature of species' response to climate change mean that community level impacts are extremely complex (Huntley, 1990; 1991) and changes in species interactions are likely to occur (Klanderud and Totland, 2005).

Climate change will impose strong selection pressures on populations, and can thus be expected to induce adaptation (Jump and Peñuelas, 2005; Jump *et al.* 2008). Research suggests that species have the potential to adapt to changes in climate, for example Jump *et al.* (2008) found evidence of rapid evolution in response to drought conditions in the shrub *Fumana thymifolia.* Adaptation to warming through changes in phenology and the earlier onset of spring events is widely reported (Parmesan and Yohe, 2003) with earlier dates for egg laying in birds (e.g. Red Grouse in the Scottish Highlands advance of 0.5 days/year (Fletcher *et al*., 2013)), and earlier bud burst and flowering in plants (Cleland *et al.*, 2007) being observed.

Complex and species specific responses to changing climate can lead to changes in temporal overlaps and trophic interactions, for example, winter moth hatching and oak bud burst have become unsynchronised in recent years (Visser and Holleman, 2001), leading to increased moth mortality and decreased body size. Such asynchrony can have impacts further up the food web, reducing food availability for birds (Visser and Both, 2005). Experimental warming treatments lead to changes in plant community composition in Mediterranean (Lloret *et al.*, 2009) and Arctic systems (Walker *et al.,* 2006). Gottfried *et al.* (2012) describe the European wide ‘thermophilization’ of alpine vegetation; a decline in cold adapted species and an increase in those adapted to higher temperatures. Climate change can put species at risk of decline or extinction, for example many coral reefs are dying through bleaching due to raised ocean temperatures (Mumby *et al.,* 2001) and warming is associated with increases in pathogens and the spread of disease, with consequent negative impacts on populations (Harvell *et al.,* 2002).

When species are faced with a change in conditions, several responses can thus occur; local extinction, adaptation to deal with the change *in situ* or migration to new areas that are now more suitable. Of these responses migration to new areas of suitable climate seems to be the most common response, at least among plant species (Huntley, 1991).

Altitudinal treelines

Altitudinal treelines and their upslope migration in response to warming represent sensitive and well-studied examples of species range shifts that are thought to be useful as early indications of climate change response (Smith *et al.*, 2009). Here I follow the terminology of Körner (1998, 2012) so define ‘treeline’ as the rough boundary connecting the highest forest patches within a given slope or slopes of comparable exposure. Some authors refer to this as forest limit, and as Körner states, this would be terminologically most accurate but due to its common usage the term treeline has become the most appropriate way to define this boundary. Given the complex and gradual nature of the change from forest to alpine tundra it is also useful to define ‘tree-limit’, or ‘tree species limit’ (sensu Körner, 1998, 2012) as the extreme upper limit of tree occurrence. The treeline thus represents an ecotone between forest and alpine environments and can take a number of structural forms (Harsch *et al.*, 2009; Harsch and Bader, 2011).

Global treeline patterns and explanations

Climatic conditions vary with altitude, the most important being the reduction in temperature with increasing altitude, or the altitudinal lapse rate. This has strong impacts on organisms existing at high altitudes and is partly responsible for creating the boundaries or transition zones of changing vegetation, of which alpine treeline is an obvious example.

A number of studies have considered patterns and controls on treeline position at a global scale (Wardle, 1974; Körner, 1998, 2003; Jobbagy and Jackson, 2000; Holtmeier, 2003), and consistent patterns can be identified. Treeline tends to be highest in the subtropics, lower at the equator and generally lowers in elevation from the subtropics to the poles. However continentality or the ‘Massenerhebungs’ effect can raise treelines in continental areas such as in parts of North America where treelines often reach elevations comparable to subtropical areas.

Treeline position at a global scale is generally accepted to be related to temperature (Tranquillini, 1979; Körner, 1998; Körner and Paulsen, 2004), and this is why treelines are thought to be such good indicators of climate change and early species responses. For many years the position of treelines in the northern hemisphere was accepted to be related to the mean isotherm of 10°C in the warmest month (Wieser and Tausz, 2007). However more recent research has found this to be a poor predictor of treeline position (Körner, 1998 and 2003). Körner (1998) shows that treeline positon is associated with growing season temperatures of 5.5±7.5°C, and a global study by Körner and Paulsen (2004) provides additional strong evidence of a common thermal driver at a global scale, with treelines consistently associated with a range of soil temperatures (5-8°C, and a mean value of 6.7°C). Trees are more sensitive to low temperatures than lower stature alpine vegetation and shrubs because of limitations imposed by their architecture; the tall life form is coupled to the atmosphere in a way that lower stature vegetation is not and thus suffers more from extreme conditions (Körner, 2003; Wieser and Tausz, 2007).

There are a number of hypotheses regarding the physiological limitations of tree growth and survival at high altitude, related to the low temperatures experienced by trees (Wiser and Tausz, 2007), these include: frost drought and damage (Sullivan and Sveinbjornsson, 2011), mechanical damage caused by wind and ice (Hadley and Smith, 1986), limitations to carbon assimilation (Hoch *et al*., 2002; Hoch and Körner, 2003), cell growth and tissue formation (Körner, 1998, 2003; Wieser, 2002; Hoch *et al*., 2002), the effect of low root zone temperatures on photosynthesis and the availability of nutrients (Steinbjornsson, 1992; Aers, 2002; Karlsson and Weih, 2001), and limitations on reproduction and regeneration (Hattenschwiler and Smith, 1999; Germino *et al.*, 2002, Germino and Smith, 1999).

Treeline advance

If treeline is mainly limited by temperature then we would expect to see widespread responses to warming through an upslope advance of treeline (Grace, 2002). Indeed many studies have found evidence of an upslope migration (Suarez, 1999; Kullman, 2002; Peñuelas and Boada, 2003; Shiyatov *et al.*, 2007; Kharuk *et al.*, 2009; Harsch *et al.*, 2009). For example altitudinal treeline has advanced upslope by up to 35 m in the polar Urals (Shiyatov *et al.* 2007) and by around 70 m in the Montseny Mountains (Peñuelas and Boada, 2003).

The response of treelines to warming through an altitudinal advance is highly variable both between and within study areas (Mamet and Kershaw, 2012; Hofgaard *et al.*, 2013), and a significant number of studies have found treeline to be stable (Hättenschwiler and Körner 1995; Sziecz and MacDonald 1995; Cullen *et al.*, 2001), or to be lagging behind changes in climate (Lescop-Sinclair and Payette 1995; Lloyd 2005). The variability in response is likely due to the fact that treeline is limited on a local scale by a wide range of factors including: slope aspect (Elliott and Kipfmueller, 2010), topographic shelter (Resler *et al.*, 2005), precipitation (Lloyd and Graumlich 1997), soil properties (Hertel and Scoling, 2011; Dai *et al.*, 2013), nutrient availability (McNown and Sullivan, 2013), seed dispersal (Normand *et al.*, 2013), grazing (Cairns and Moen, 2004; Cairns *et al.*, 2007) and disturbance (Dufour-Tremblay and Bordreau, 2011).

Where treelines are not responding to advance through an upslope migration, other structural changes can often be observed, including; changes in growth (Villalba and Veblen, 1997), growth form from krummholz to upright (Lescop-Sinclair and Payette, 1995; Devi *et al.,* 2008; Kharuk *et al.,* 2009, 2010) and increases in forest density (Lescop-Sinclair and Payette, 1995; Sziecz and MacDonald, 1995; Camarero and Gutiérrez, 2004; Liang *et al*., 2010). Increased understanding of the limitations to key processes that are associated with advance, such as tree growth and regeneration, will allow for better prediction of treeline response to warming and understanding of the controls on treeline position at local, regional and global scales.

Tree growth

Many studies report a recent increase in tree growth at high altitudes, generally related to increases in growing season length and temperature (Vallee and Payette, 2004; Bunn *et al*., 2005; Salzer *et al.,* 2009). Climate growth relationships have been found to vary with altitude (Mäkinen *et al.,* 2002; Yu *et al.,* 2013), and to be changing over time as climate warms (D’Arrigo *et al.,* 2008). It is important to fully understand how the growth of trees responds to climate; it allows for accurate prediction of the role of forests in carbon sequestration, an important factor in climate models, and helps to retain the accuracy of climate reconstructions from tree rings. It is also important from a conservation perspective; to understand likely changes in species distributions and to identify species that may be at risk from changing climate. Many studies of tree growth and climate have been conducted in temperate and arctic treelines (Ditmar *et al*., 2003; Bunn *et al*., 2005; Jump *et al*., 2007; Kharuk *et al.,* 2009) but there is a lack of studies conducted in the subtropical zone.

Regeneration

Dispersal, establishment and survival of tree seedlings beyond treeline is crucial for treeline advance (Germino *et al.,* 2002; Smith *et al.,* 2009) and depends on a multitude of factors. Microclimate conditions beyond the treeline must be suitable for seedlings, with high survival and growth rates often associated with the presence of rocks and boulders (Germino and Smith, 1999) and adult trees or other vegetation (Hattenschwiler and Smith, 1999; Mamet and Kershaw, 2013). Facilitative effects and positive feedbacks are common at the upper treeline (Bader *et al*., 2008), although in some cases regeneration can be inhibited by vegetation (Wardle and Coleman, 1992). Shelter can also be provided by topographic features (Resler *et al.* 2006) and establishment success has been linked to aspect and slope exposure (Germino and Smith 1999). Soil temperature (De Lucia *et al*., 1991) and moisture (Cui and Smith, 1991; Moyes *et al.,* 2013) are important for seedling survival as is nutrient availability (Zurbriggen *et al*., 2013) and seedling numbers have been found to be correlated with snow pack depth (Hattenschwiler and Smith, 1999). Many treeline species require a mineral soil for establishment so the availability of suitable sites or the ability to disperse to them can limit regeneration success (Dufour -Tremblay *et al*., 2012).

Although regeneration beyond treeline is common, and does not necessarily lead to advance, or may be associated with a significant time lag before an advance is realised (Lloyd, 2005), it does represent the necessary first step towards treeline advance and merits full investigation. Again, although studies have focused on regeneration and the factors driving seedling patterns at and beyond treeline they are generally concentrated in temperate regions and more knowledge is required of sub-tropical alpine treelines where the driving factors may differ.

Implications of treeline advance

The study of treeline advance provides early insight into species distributional changes, providing essential information on patterns and processes that are likely to be widely applicable in other ecosystems (Smith *et al*., 2009). Advancing treelines have the potential to affect ecosystem processes and community dynamics so it is crucial that we are able to predict patterns of change in these systems (Greenwood and Jump, 2014). Treeline advance and changes in the structure of high altitude forests could provide negative feedbacks to climate by increasing carbon sequestration potential (Wang *et al.* 2013), although the impact of warming on net primary production (NPP) is not straightforward (Hu *et al*., 2010). Little is known about how treeline advance will affect soil carbon storage in alpine sites (although see Kammer *et al.* 2009) and studies of arctic systems show that decreases in net carbon storage can occur when trees invade tundra (Wilmking *et al*., 2006; Hartley *et al*., 2012). More research is required in alpine areas to allow for accurate predictions on changes in ecosystem carbon balance with treeline advance.

Treeline advance could have an impact on alpine species occurring above the treeline by invading alpine grassland and thus reducing their habitat (Moore and Huffman, 2004); given the high endemism rate of alpine areas (Körner, 2012), and the threats already imposed by land use and climate warming (Pauli *et al*., 1996; IPCC, 2007), it is extremely important to understand community scale changes and interactions in high altitude areas. Treeline advance is already leading to reduced diversity in alpine areas (Halloy and Mark, 2003; Moiseev and Shiyatov, 2003; Moen *et al.,* 2004), but few studies look directly at the impacts of treeline advance on associated communities (Smith *et al.,* 2009).

In this thesis I aim to thoroughly characterise the nature of treeline advance in the Central Mountain Range of Taiwan and to explore the mechanisms of advance through the study of tree growth patterns (Chapter 4) and regeneration (Chapter 5). The implications of treeline advance for species and ecosystem function will be explored in detail through a literature review in the following chapter (Chapter 2) and later through a study of the consequences of advance for associated communities using epiphytic/corticolous lichens as study species (Chapter 6).

Study area

This study was conducted on the subtropical island of Taiwan (Figure 1). The island straddles the Tropic of Cancer, and much of it experiences a subtropical climate with typhoons during the summer months and warm winters. However, Taiwan is a mountainous country with more than 200 peaks over 3,000 m a.s.l., contained within its Central Mountain Range, and at high elevations conditions range from temperate to alpine. For example; mean July temperature at around sea level in the capital city Taipei is 28 °C whereas on Yushan (the highest peak in Taiwan at 3952 m) it is 8.5 °C recorded at an altitude of 3844 m.

Two main regions of the Central Mountain Range were studied: Yushan and Taroko National Parks, with research effort concentrated around two main peaks; Yushan and Hehuanshan (Figure 1). Disturbance is generally low throughout the Central Mountain Range with little human development. Populations of grazers/browsers (in this area mainly sambar and muntjac deer and the long haired mountain goat) are at a low density and grazing/browsing seems to have little influence on tree regeneration in the area (S. Greenwood, personal observations of seedling damage). There is no livestock grazing in the area, and no major changes in human settlement or hunting levels over the last c. 100 years (Pei, 1999). The treeline in this region can thus be considered to be natural and not influenced by management.

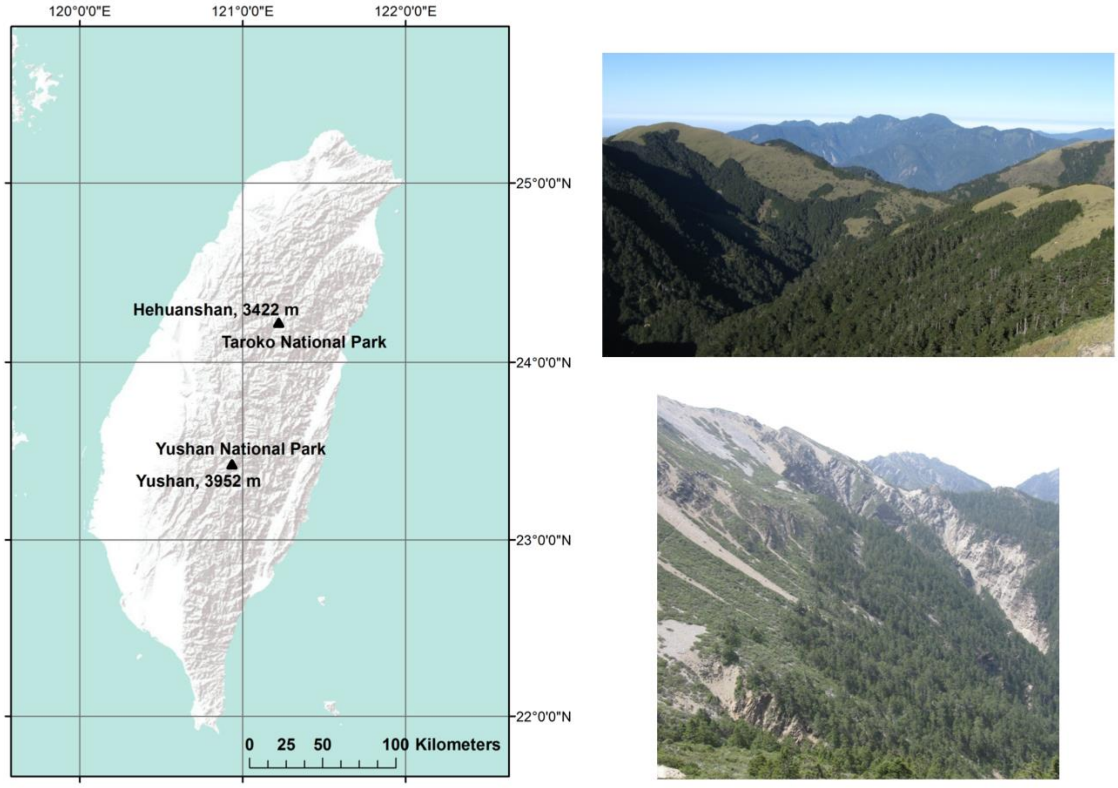

Figure 1: Map of Taiwan showing the two study regions Yushan and Taroko National Parks and the location of the two main peaks where research was carried out: Hehuanshan and Yushan. Typical treeline structure at each of these areas is shown to the right with Taroko (Hehuanshan area) above and Yushan below.

Climate change in Taiwan

Temperatures in Taiwan have increased recently (Figure 2). Jump *et al*. (2012) report a temperature increase of 1.05 ºC compared with 1934-1970 mean values for the Alishan region, an area near to Taroko National park, and Hsu and Chen (2002) predict rises in temperature of between 0.9 and 2.7 ºC over the next thirty years, compared to 1961-1990 mean values.

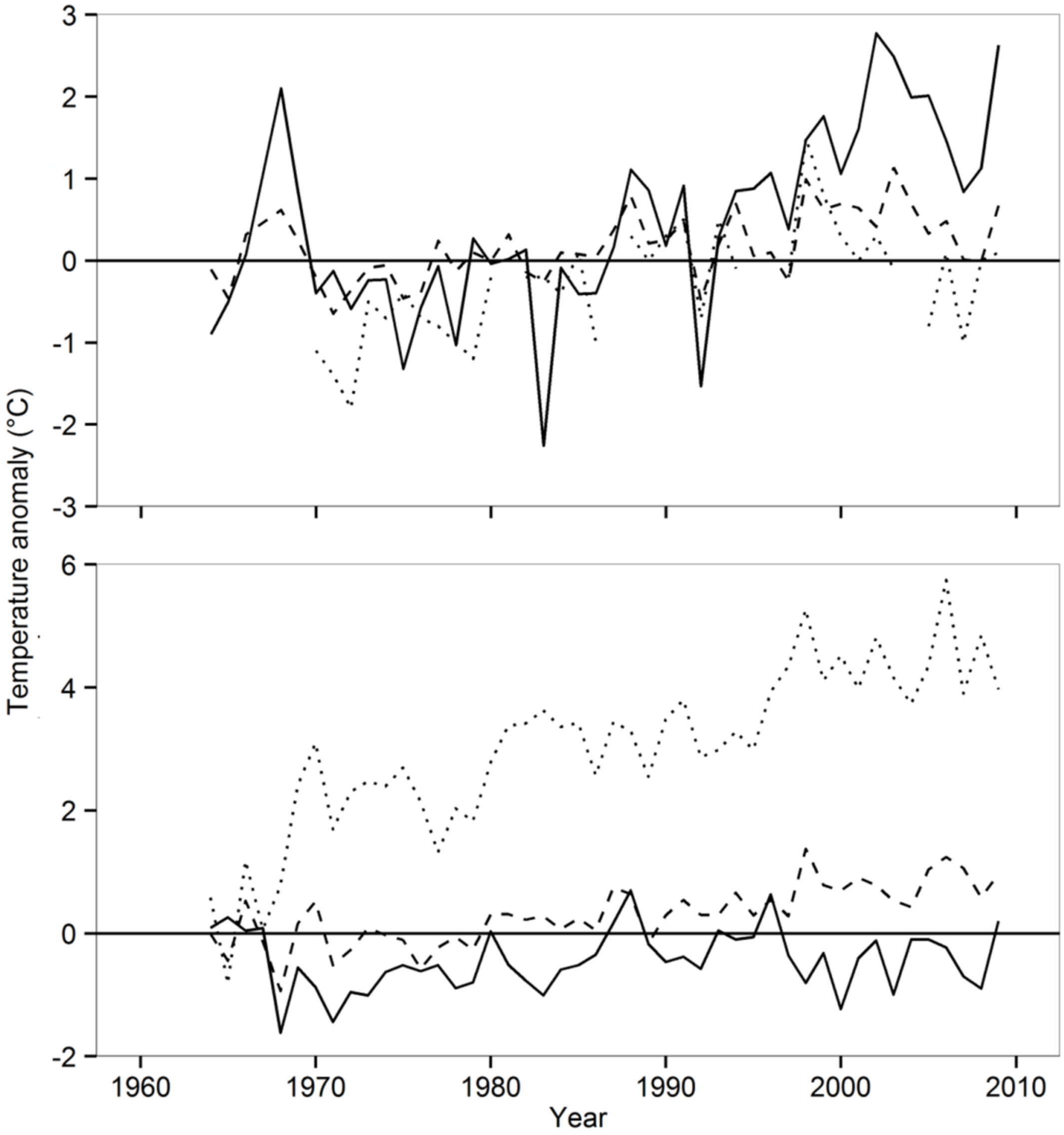

Figure 2: Anomaly data for Yushan (above) and Alishan (below) areas of Taiwan as compared to 1943-1963 mean values. Measurements were made at government weather stations. The following temperature data are shown (all are annual mean values): Maximum temperature (solid line), mean temperature (dashed line), minimum temperature (dotted line). A small number of values are missing from the Yushan dataset.

Main species

The main tree species occurring in the subalpine zone (c. 2,000-3,500 m) are *Abies kawakamii* (Figure 3), *Tsuga chinensis*, *Pinus taiwanensis*, *Pinus armandii* var. *masteriana* and *Picea morrisonicola*). At treeline the forests consist of almost monospecific stands of *A. kawakamii* with only a few scattered individuals of *T.chinensis* and some *Pinus* spp. regeneration in lower elevation disturbed sites.

Above treeline the subalpine grasslands of Taroko National Park are dominated by a dwarf bamboo species; *Yushania niitakayamensis* (Figure 3) which grows in dense swathes, often reaching heights of up to 2 m. In Yushan National Park there is unstable bare ground beyond treeline with stands of krummholz Juniper (*Juniperis formosana* and *Juniperus squamata* var. *morrisonicola*) (Figure 4). Other notable alpine species include *Anaphalis morrisonicola*, *Gaultheria itoana, Gentiana arisanensis, Rhododendron pseudochysanthum* and *Rhododendron rubropilosum* var. *taiwanalpina.*

Figure 3: The dominant treeline species *Abies kawakamii* (left hand images) and the dominant alpine grassland species *Yushania niitakayamensis* (right hand images).

Figure 4: Juniper and Rhododendron spp. above treeline on Yushan (left image), *Anaphalis morrisonicola* (above right) and *Gaultheria itoana* (below right).

High altitude treelines in the tropics

Subtropical alpine ecosystems have received far less research attention that their boreal and temperate counterparts and this is particularly true of alpine treelines. Few studies have investigated the response of high altitude tropical treelines to climate change, compared with the wealth of information that exists for Arctic and temperate zone treelines, and very little is known about the ecology of subtropical Asian treelines. Given this lack of understanding of the patterns and processes occurring at treelines in the subtropics, and the lack of information on the community consequences of treeline shifts throughout the world, in this thesis I will characterise the nature of treeline advance throughout the Central Mountain Range of Taiwan (Chapter 3), explore the key processes associated with advance (Chapters 4 and 5) in order to achieve a better mechanistic understanding of what drives treeline advance in the subtropics. After thoroughly reviewing literature on the possible consequences of treeline advance (Chapter 2), I will then investigate the community impacts of advance in the Central Mountain Range of Taiwan (Chapter 6). This research increases understanding of treeline advance in the subtropics, allowing for better predictions to be made at a global scale. The last chapter of this thesis (Chapter 7) will provide a synthesis of the knowledge that this research has provided and will suggest some key directions for future research.

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Chapter 2

Consequences of treeline shifts for the diversity and function of high altitude ecosystems

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Abstract

Treeline advance is reported as a widespread response to rising temperatures yet few studies have considered the impact of treeline advance on the diversity and function of high altitude systems. Evidence suggests that climate change is already having a negative impact on alpine diversity and is modifying functions such as carbon sequestration and nutrient cycling. Treeline advance is likely to further affect diversity and function yet our understanding of the processes involved is limited. Here we review and synthesise literature that assesses the impact of treeline advance into treeless ecosystems. Using published literature, we explore to what extent treeline advance will lead to the displacement of alpine species and the fragmentation of alpine habitats. While large changes will be observed in the ecosystems above the current treeline as trees migrate, it is likely that these newly forested areas will deviate substantially from the established forests from which they have developed. Consequently, at the forest community level we investigate the potential for differential response speeds of typical forest plant species, and the potential for treeline advance to lead to community disassembly. Given that changes in species presence and abundance can alter the functional composition of plant communities, we explore the potential for shifts in tree distribution to lead to changes in carbon storage, nutrient cycling and hydrological properties of ecosystems. Despite typically being intensively studied regions, the likely impact of forest expansion above the current mountain treeline has received relatively little attention and so we identify key knowledge gaps that should act as priorities for future research in mountain systems.

Introduction

Recent and historic changes in species distributions in response to environmental change are well documented in the scientific literature. In recent decades, investigation of the impact of current changes in climate has been a major focus in biogeographical studies (Parmesan and Yohe, 2003; Walther, 2003; Parmesan, 2006). Climate conditions play an important role in determining the limits to species distributions. Consequently, when climatic conditions change rapidly, it is often observed that species distributions can respond rapidly, for example by migration to new areas that have only recently become climatically favourable for survival (Pauli et al., 1996; Lenoir et al., 2008) or through range retraction elsewhere (Beckage et al., 2008; Kelly and Goulden, 2008). These changes in distribution will continue into the future as climate continues to warm (IPCC, 2007; IPCC, 2013).

Upward elevational migration of mountain treelines and latitudinal advance toward the poles (treeline shifts) represent a well-studied and ecologically highly important example of species distributional change occurring across the globe. Many authors have discussed the factors responsible for controlling treeline position and the phenomenon and mechanisms of treeline advance; the majority of alpine and polar latitudinal treelines are showing at least some response to climate change (Harsch, 2009). However, despite the widespread nature of this biotic response to changing climate, little attention has been devoted to gaining an understanding of the impacts that this change in species distribution is likely to have in ecosystems occurring at and above the current tree limit. Forest advance into alpine areas will have profound effects on ecosystem structure and function. Trees are a key structural feature of the landscapes in which they occur and determine the soil and light environment and microclimate conditions experienced by the biotic communities associated with them, and also on the wider climate system through their functional roles in ecosystem processes such as carbon sequestration and hydrology.

Treeline position is strongly dependent on temperature (Tranquillini, 1979; Körner, 1998; Jobbagy and Jackson, 2000, MacDonald et al., 2008), although other factors such as: precipitation levels and drought (Daniels and Veblen, 2004), nutrient availability (Sveinbjornsson et al., 1992), orographic and anthropogenic influences also play a significant role in treeline position (Holtmeier and Broll, 2005; Wieser, 2007). Treelines are, therefore, very sensitive to temperature increases associated with anthropogenic climate change and they can provide early indications of the responses to be expected elsewhere in forest ecosystems. Climate change scenarios for 2100 predict a mean global temperature increase in the range of 0.3-4.8 ºC compared with 1985-2005 mean values (IPCC, 2013).

The response of treelines to warming climate via an upward range expansion is widespread (Suarez et al., 1999; Kullman, 2002; Lloyd and Fastie, 2002, 2003; Moiseev and Shiyatov, 2003; Penuelas and Boada, 2003; Shiyatov et al., 2005, 2007; Baker and Mosely, 2007; Devi et al., 2008; Beckage et al., 2008; Kharuk et al., 2009, 2010), a recent global meta-analysis by Harsch et al. (2009) found evidence for a treeline advance at 52% of studied sites and in cases where no actual advance has been documented (e.g. Masek 2001) treelines are often still responding to climate through changes in growth (Villalba and Veblen, 1997), growth form (Lescop-Sinclair and Payette, 1995) or density (Lescop-Sinclair and Payette, 1995; Szeicz and MacDonald, 1995; Camarero and Gutiérrez, 2004; Liang et al., 2011).

However, rising temperatures at the regional scale will not necessarily lead to treeline expansion. Steep slopes and lack of suitable substrate can be important limiting factors for treeline advance at high altitudes (Batllori et al., 2009(a); Macias-Fauria and

Johnson, 2013). Where appropriate substrates occur, microsite factors determining temperature and soil moisture conditions are extremely important in allowing for the successful establishment of tree seedlings (Cui and Smith, 1991; Gobbi and Schlichter, 1998; Lee et al., 2004; Catorci et al. 2012). Establishment success can also be dependent on the degree of shelter due to microtopographic variation (Resler et al., 2005), surrounding ground level vegetation (Germino et al., 2002; Smith et al., 2003; Bader et al. 2008; Mamet and Kershaw, 2012) and the presence of krummholz (Hättenschwiler and Smith, 1999; Germino, 2001; Batllori et al., 2009(b)), rocks and boulders (Resler et al., 2005). This sheltering effect can result in positive feedback (Bader et al., 2008), whereby establishment of tree seedlings above the treeline promotes further establishment by creating more favourable microclimate conditions (Smith et al., 2003; Bekker, 2005; Resler et al., 2005).

Consequently, there will be considerable variability in the response of treelines to changes in climate at both the local and regional scale (Hofgaard et al., 2013), with some treelines remaining stable and lagging climate changes while others advance (Lloyd, 2005). This variability has important consequences for the diversity and function of ecosystems above the treeline, since rising temperatures in alpine regions will not always be associated with treeline advance. While experimental work assessing impacts of elevated temperatures on alpine and tundra vegetation have been conducted (Chapin et al., 1995; Walker et al., 2006) relatively few studies have looked directly at the impact of treeline advance on the invaded ecosystems. In the following sections of this review, we discuss the consequences of treeline expansion for the structure and function of ecosystems, using evidence from; direct assessments of changes occurring in advancing treeline ecotones, experimental manipulation of ecosystems beyond the treeline, predictions from modelling studies and indirect evidence from other ecosystems. We conclude by outlining important gaps in our knowledge in this area. Specifically we discuss impacts on biodiversity through an investigation of the displacement of alpine communities, alterations to microclimate associated with changes in tree cover and the influence of individualistic responses on community structure. We then move on to explore impacts on ecosystem function, specifically carbon and nitrogen dynamics, hydrology and slope stabilisation (see Figure 1 for a visual summary). We aim for a global discussion of these topics, although most of the literature cited comes from studies of temperate and arctic regions, as this has been where most relevant research has been focused. While we explore the likely impacts of treeline shifts on biodiversity and ecosystem function, it is not our aim to exhaustively review the literature on treeline advance, which has been done previously. For detailed reviews on treeline positions, shifts and their causes see Rochefort et al. (1994); Körner (1998); Harsch et al. (2009); Grace et al. (2002); Körner and Paulsen (2004) and Holtmeier and Broll (2005).

Biodiversity impacts

High altitude areas can be disproportionately important for their biodiversity; high levels of habitat heterogeneity and isolation allow for the development of high levels of species endemism, species richness and the retention of many rare species (Essl et al., 2009; Körner, 2003). However, mountainous areas are very sensitive to the effects of climate change and are also predicted to experience higher than average increases in temperature (Pauli et al., 1996; IPCC, 2007; Dirnböck et al., 2011).

Climate change will have diverse effects on plant communities, for example advancing phenological events, extending growing season length, and altering plant productivity (Peñuelas et al., 2002; Walther et al., 2002; Parmesan and Yohe, 2003; Parmesan, 2006). Changes in climate affect plant distribution (Walther, 2003; Lenoir et al., 2008) and competitive dynamics (Callaway et al., 2002). Changes to plant communities may be particularly evident in mountainous or high latitude regions where the presence or absence of species is often determined by relatively low threshold temperatures (Körner, 2003; Kullman, 2007). The upslope migration of forests can be a threat for many plant species due to out-competition for space or substrate (Grabherr et al., 1994). It is, therefore, probable that the upward migration of vegetation zones will eventually lead to species loss and a reduction in diversity through the removal of specialised species with small niche tolerances and an increase in more widespread species from lower altitudes (Jump et al., 2012).

Displacement of alpine communities

Treeline advance leads to a reduction in the area available for alpine and nival species and can cause the fragmentation of remaining habitat. Forest expansion in the Urals has already reduced the area of alpine grassland and heath by around 10-30% (Moiseev and Shiyatov, 2003) and in the Mediterranean advancing shrub and broom have displaced nival vegetation (García-Romero et al., 2010). In Glacier National Park, Arizona forest encroachment has led to a reduction in diversity; open areas have 4-5 times higher diversity than areas with high tree cover but are much reduced in size as tree regeneration increases (Moore and Huffman, 2004).

A number of predictive modelling studies have come to similar conclusions; General circulation model (GCM) scenarios coupled with ordinal regression models of alpine vegetation responses in Austria show that expansion of *Pinus mugo* is likely to occur at the expense of alpine habitat (Dirnböck et al., 2003). Moen et al. (2004) simulated treeline advance on Swedish mountains using climate predictions and a digital elevation model and found that the predicted degree of treeline advance led to a severe reduction in alpine areas: even a conservative estimate of a 100m rise in treeline position would reduce the occurrence of alpine heath by 41%, the majority of alpine areas remaining would be on scree slopes and boulder areas. Cliffs and rocky areas act as refugia for alpine species during periods of tree expansion, allowing alpine species to persist in areas with forest cover (Bruun and Moen, 2003); such areas could become increasingly important as treelines advance and further reduce alpine habitat. However, open refuges in newly expanding forest that are unsuitable for forest development will be inadequate to maintain the full range of species currently found in alpine areas since they will be dramatically different in terms of both area, microclimate and substrate quality compared with the range of existing alpine habitats.

Accordingly, alpine plant extinctions have been predicted. In New Zealand substantial loss of species is expected under a scenario of a 3 ºC rise in temperature and an associated 500m rise in treeline. Because the already fragmented alpine habitat will be disturbed by treeline advance and 93% of alpine habitat islands will likely be lost (Halloy and Mark, 2003). Dirnböck et al. (2011), combining the distribution of endemic species in the Austrian Alps with a model projecting forest expansion under different climate scenarios, found that even with conservative estimations of climate change, the area of alpine habitat lost to forest was very high, and that areas of high endemism suffered disproportionately.

Ground-level non-vascular plants occurring beyond the treeline, such as lichens and bryophytes may be especially at risk from forest encroachment. They will face increased competition for light resources where elevated temperatures result in increased plant growth and/or the establishment of more competitive species from lower altitudes (Trivedi et al., 2008). For alpine communities dominated by non-vascular plants, such as *Racomitrium* heath, this is likely to result in their out-competition and replacement by faster growing plant species. This affect has already been reported for *Racomitrium* heath in response to changes associated with nitrogen deposition in Scotland (van der Wal et al., 2005). *Sphagnum* spp. occurring above treeline in peat lands in both mountain and boreal areas could also be at risk from forest advance, as can be seen from their response to afforestation by modern management and to past changes in treeline position (Dudova et al., 2012). However, direct out-competition of such communities by forest species is unlikely since they typically occur well beyond the treeline under current conditions.

Trees substantially modify their surrounding environment (Holtmeier and Broll, 2005) and play a critical role in determining the identity of co-occurring plant species. Soil temperatures are lower during summer and higher during winter under tree canopies compared with open sites (Körner, 1998; Jennings et al., 1999; Kammer et al., 2009), and dense canopies can almost completely prevent the penetration of photosynthetically active radiation (PAR) to understory level (Canham and Burbank, 1994). The transmission of light through the forest canopy is the most important factor limiting understory plant diversity and productivity (Hart and Chen, 2006), such that a positive relationship is often found between understory light levels and plant cover and diversity and a negative one with canopy density (e.g. Grytnes, 2000; Doležal and Šrutek, 2002; Coop et al., 2010). Forest development also modifies factors including soil, nutrient content, pH and soil moisture (Augusto et al., 2002) all of which can impact the presence and abundance of understory species. The environmental modifications associated with tree establishment will, therefore, substantially modify plant communities as forest cover expands at high latitudes and altitudes. The influence of tree establishment extends well beyond the forest edge; Hofgaard (1997) found a high turnover of species across the treeline ecotone and both Hofgaard and Wilmann (2002) and Camarero and Gutierrez (2002) found a positive relationship between field layer diversity and distance from the treeline, and a negative relationship with tree cover. The commonality of evidence showing that alpine species are unable to survive below forest cover has important implications for diversity changes associated with treeline shifts and displacement of alpine and nival species is therefore, largely inevitable as treelines migrate upwards.

Increased density in high elevation forest below and at treeline will also lead to changes in microclimate that are likely to drive changes in the composition of existing forest understory communities, as seen in experimental work manipulating the density of managed stands (Thomas et al., 1999; Ares et al., 2010). A higher density of trees throughout the treeline ecotone will reduce light levels and increase sheltering effects, reducing the probability of persistence of alpine species co-occurring in the woodland/grassland mosaics that often occur at high altitudes. However, many treelines were higher during the early Holocene and Hofgaard and Wilmann (2002) found that some species occurring in plant communities above the treeline were indicative of past treeline position. An advance of the treeline was, therefore, less likely to dramatically change the field layer composition in such areas as it was pre-adapted to a higher forest position. Consequently, increased treeline elevation should not be viewed as an indication of the definite loss of species that currently exist in un-forested areas at higher altitudes, though greater ecological information is needed for species in such areas in order to better predict those most likely to be displaced.

Differential migration rates and community disassembly

Species display individualistic responses to climatic change (Huntley, 1991; Pauli et al., 1996; Hansen et al., 2001) and will, therefore, migrate at different rates with climate warming. Such differential responses are detected both within and between plant functional types. Tree species co-occurring in the same forests can show different responses to change (Rabasa et al., 2013), for example in southern Siberia (Kharuk et al., 2009) and the Alps (Motta and Nola, 2001), pine species show a greater response of growth and regeneration to temperature and are beginning to replace larch species as dominant. Similarly, proportions of tree species have been altered in the Northern Urals due to birch showing greater responses than pine or larch (Kapralov et al., 2006) and in in Vermont where northern hardwood species are replacing boreal species that are suffering from high mortality rates as the climate warms (Beckage et al., 2008).

Upslope expansion of species on the sub-Antarctic Marion Island led to community changes because more than half of the species studied were unable to move upslope in pace with climatic changes whereas the remainder demonstrated high migration rates; an average of 1.8 m yr^{-1} change in altitudinal limit (le Roux and McGeoch, 2008). Species responded individualistically to warming and nutrient addition treatments in alpine sites in Norway (Klanderud, 2008); grass species generally responded positively whereas lichen, moss, sedge and many forb species had negative responses (species of large stature responded well but small species showed a decline with treatment), leading to changes in community composition. As Pigott (1978) identified, this interspecific variation in sensitivity to temperature can alter the competitive balance of communities, potentially leading to greater changes in species composition than would be expected based solely on individual species responses.

The migration rate of forest herbs is very different to that of tree species; migration rates of common European forest herbs are around 0.3-0.5 m/yr^{-1} (Brunet and Oheimb, 1998), this contrasts sharply with the much higher rates of around 100 m/yr^{-1} suggested for tree species (McLachlan et al., 2005). Understory plants tend to produce fewer seeds and have slower migration rates than tree species (Roberts, 1989) and are often dispersal limited (Matlack, 1994; Cain, 1998) so it is likely that understory species will not be able to respond quickly to changes in treeline position where advance is occurring rapidly. Non-vascular plants such as epiphytic lichens and bryophytes are also likely to have different migration and colonisation rates from trees. Forest lichens and bryophytes have been shown to be very sensitive to forest disturbance (Johansson, 2008) and to have low growth and establishment rates. The negative impact of disturbance could be due to dispersal limitations (Sillet et al., 2000), establishment limitation (Kuusinen and Siitonen, 1998), or because of high sensitivity to microclimate (Sillet et al., 1994). Dispersal ranges and colonisation rates are very variable among lichen species, and those with low colonisation rates require more stand continuity (Ruete et al., 2014). Studies suggest that lichen epiphytes can be slow to respond to changes in forest conditions (Johansson et al. 2013), with current lichen distributions often reflecting past, rather than current forest conditions (Ellis and Coppins, 2007, 2009).

The logical consequence of individualistic species responses is that community composition will change, and new assemblages will form. There is evidence of this from Quaternary migration rates, inferred from isochrones (Huntley, 1991) and isopoll maps (Huntley, 1990) showing that past compositional changes in forests led to the formation communities with no modern analogue. Edwards (2005) also provides evidence from early Holocene (13,000 - 10,000 Y BP) fossil pollen, showing that during this time, the structure and functioning of communities was very different from that of assemblages found in the same areas today. Studies of fossilised packrat middens in the south western US (Van Devender and Spaulding, 1979), together with macrofossil investigations of the tree flora of the Swedish Scandes (Kullman, 1998) and forest composition in the Pacific Northwest (Sea and Whitlock, 1995) during the early

Holocene confirm the generality of these findings of community breakup and change in response to past warming periods.

Consequences of response lags for biodiversity.

Both modelling (Chapin and Starfield, 1997; Bugmann and Pfister, 2000) and dendroecological studies have suggested that a lag of at least several hundred years is likely to occur between a change in climatic conditions and the subsequent development of forests at higher altitudes or latitudes. This lag is thought to be due to limitations in seed availability and establishment probability, disturbance events and variations in tree growth rates. Furthermore, this lag varies both spatially and temporally due to local site conditions such as the presence of permafrost, krummholz or high wind exposure (Lloyd, 2005). The critical factor that will determine how a lag in the response of vegetation to climate will affect biodiversity and community composition is the difference in response rate between different species and vegetation types. If, due to greater seed production and higher dispersal distances, trees respond more rapidly to increased temperatures than alpine plants the likelihood of survival of many alpine species will be low. However, evidence exists that forests may be less responsive to interannual changes in climate because of the buffering effect of the canopy (Lenoir et al., 2008) and are often more influenced by long-term climate trends rather than inter-annual variation. In contrast, alpine vegetation is responsive to these short term changes (Kullman, 2007) and is therefore likely to be able to respond faster, although more variably to climatic change. The lag in treeline response to climate is likely to have positive implications for the survival of alpine communities, at least in the short term, as they might show increased response rates compared with forest understory communities and be able to migrate to areas of suitable habitat before they are displaced by advancing treelines.

Ecosystem function and services

High altitude ecosystems also play crucial roles in many functions that will be impacted both directly as temperatures rise, but also indirectly as plant species and life forms from lower altitudes migrate upwards and increase in abundance. High altitude forests provide important ecosystem services, including carbon sequestration and storage (Peng et al., 2009; White et al., 2000), slope stabilisation and erosion prevention (Stoffel et al., 2006; Schönenberger et al., 2005), and they play key roles in water and nutrient cycling (Dirnböck and Grabherr, 2000). There is already a large body of evidence to suggest that the response of forests to climatic change will have an impact on associated ecosystem functions (Saxe et al., 2001), although relatively little research has been conducted on the specific impacts of treeline advance in alpine systems. In the following sections, we discuss the likely consequences of treeline advance for some of the fundamental processes in which forests are involved.

Carbon sequestration and storage

Given the fundamental dependence of processes such as photosynthesis, respiration and soil decomposition rates on temperature and CO_2 concentrations (Saxe et al., 2001; Xu et al., 2012), climate change will modify plant photosynthetic assimilation rates, and hence growth and production as CO_2 concentration and temperature continue to rise (Griffis et al., 2003; Kallarackal and Roby, 2012). However, indefinite increases in productivity are not expected since studies show that the response of plant productivity to rising CO_2 saturates (Nabuurs et al., 2013). Forests are major carbon stores both in plant biomass and in soils (Hyvönen et al., 2007) and rising temperatures in high altitude forests could result in increased CO_2 sequestration, growth and plant biomass (Devi et al., 2008; Fan et al., 2009). In a recent meta-analysis, Lin et al (2010) report that biomass increased in all plant types with warming but that woody species show the greatest response. As rising temperatures drive tree range expansion and increases in woody biomass at and above the current the treeline, carbon accumulation at treeline will increase, although such increases may be accompanied by carbon release from low altitude forests and the overall balance remains unclear (Zierl and Bugmann, 2007). There is, however, considerable evidence that increased growth and biomass at many treelines is increasing their ability to act as carbon sinks e.g. Lopatin et al. (2006) in Russia, Tømmervik et al. (2009) in Norway, and from the many recent studies of increased tree growth, density and forest expansion (Devi et al., 2008; Kharuk, 2009; Kullmann, 2002; Villalba and Veblen, 1997). Modelled changes in vegetation and NPP in China under various climate warming scenarios show that a replacement of alpine vegetation by forest trees and shrubs occurs alongside overall increases in net photosynthesis (Wang 2013), although such changes are expected to be highly spatially variable.

Increased growing season temperatures can combine with an increase in growing season length due to warmer spring and/or milder winter temperatures to increase net ecosystem production (NEP) (Griffis et al., 2003; Barr et al., 2007). However, the relationship between growing season and NEP can be complicated at high altitude. For example, there was a negative correlation between growing season length and NEP in subalpine forests in the Western US due to a decrease in water availability because of decreased snow fall and earlier snow melt (Hu et al. 2010). Similar results have been reported by other authors, including transitory increases in productivity that are then offset by higher temperatures and/or low water availability later in the season (Monson et al., 2002; Angert et al., 2005; Delpierre et al., 2009). The impact of growing season and temperature changes on carbon sequestration at the treeline will therefore be influenced by other factors and is likely to vary between regions.

Increased temperature is also likely to elevate soil respiration, which represents a major component of the carbon cycle. A meta-analysis by Rustad et al. (2001) found that an increase of temperature in the range 0.3-6ºC would increase soil respiration by as much as 20%, with the largest increases occurring in forested systems. This has major implications for carbon sequestration and ecosystem carbon balance (Sjögersten and Wookey, 2002). Soils in colder regions, such as treeline and alpine areas are especially sensitive to warming (Sjögersten et al., 2011). The response can be due to the direct effect of temperature on microbial activity; experimental warming of alpine soils in Switzerland led to a greater microbial use of older soil organic carbon, potentially reducing long term C storage (Streit et al., 2014). Indirect effects of changes in ecosystem properties and functions can also be important; such as the change across the forest ecotone when treelines advance with subsequent changes in microenvironment and litter inputs.

Changes in vegetation cover at the treeline have been shown to have an impact on soil carbon storage and on the quality of soil organic matter (SOM). Kammer et al. (2009) found that tundra soils contained significantly more carbon in organic layers, but less in the mineral horizon compared with forest soils. Total stocks of carbon did not vary significantly so treeline advance was likely to have little impact on soil carbon pools. Soil respiration rates were found to vary across the mountain birch forest tundra ecotone in Abisko, Sweden (Sjögersten and Wookey, 2002), with higher rates occurring in forest soils, and in tundra soils transplanted to forest sites, than in tundra sites. Consequently, an expansion of forest into tundra in response to warming could lead to increased soil respiration, at least initially (Rustad et al., 2001), potentially reducing the impact of higher carbon storage in plant biomass.

Evidence of this offsetting of carbon sequestration exists from a study of forest expansion into tundra in NW Alaska (Wilmking et al., 2006) where it was found that conversion of tundra into forest led to a net loss of ecosystem carbon; increases in soil respiration completely offset the increase in above ground biomass. This effect was also reported by Hartley et al. (2012) who found that soil carbon stocks were lower in mountain birch forest than in nearby tundra sites, by an amount that offset the increase in above ground biomass, and that the establishment of birch led to a loss of soil carbon in tundra.

These studies are in agreement with simulations conducted by Peng et al. (2009) who modelled the effects of climate change on forest C dynamics in north-eastern China. However, Steltzer (2004) proposed that expansion of spruce into tundra would lead to increases in the carbon storage of the system due to the higher NPP values of forest compared with tundra and because of the possibly lower decomposition values, given the lower litter quality of trees and the cooling effect of shading. This study found that soil carbon accumulated under spruce trees as the trees age. Although in contrast with the findings of the studies above, the work of Steltzer (2004) suggests the need for observational and experimental timescales that are long enough to fully capture the range of processes that can occur during natural stand development.

The relationship between tree cover and soil carbon storage may be very different depending on whether altitudinal or latitudinal treeline advance is considered; in the case of latitudinal expansion trees are invading tundra sites with a high proportion of carbon contained within soils (Tarnocai et al., 2009), conversely, in altitudinal treelines the soils of the invaded alpine areas tend to be thinner with lower carbon content (Michaelson et al., 1996; Körner, 1998) and, because trees tend to preferentially regenerate on mineral soils in these areas, it is probable that tree expansion into alpine zones will increase the carbon content. Due to the importance of carbon storage in high latitude tundra sites, the majority of studies investigating the impacts of treeline advance on carbon dynamics have been concentrated in these systems; more studies in alpine ecosystems are needed to explore the impact of treeline advance on soil carbon properties and the balance between carbon sequestration and emissions. Increased focus on mountain systems will allow us to better identify how altitudinal and latitudinal treelines differ in this respect.

Nitrogen content and availability

Soil decomposition rates, and the amount of SOM, affect nitrogen availability (Spargo et al., 2011) and because nitrogen is frequently limiting to plant growth in high latitude/altitude areas (Rustad et al., 2001), it is important to consider how its availability may be affected both by climate change and by treeline advance. It is clear that increasing temperatures can directly alter nutrient cycling and potentially increase availability (Butler et al., 2012; Rustad et al., 2001) but the effects of climate warming on N cycling are likely to be complex. For example, recent evidence suggests that warming leads to increases in the amount of N fixed by cryptogams in arctic areas (Lett and Michelsen, 2014) but that reduced snow-cover could reduce rates of decomposition and release of N from plant litter (Wu et al., 2014). It is also possible that an advance of treeline could have more impact than warming on N availability (Sjögersten and Wookey, 2005).

Forest soils at the mountain birch-tundra treeline in Fennoscandia had significantly higher ammonification and mineralisation rates, and higher N availability than did tundra soils so the expansion of birch forest in the study areas could have significant impacts on N cycling (Sjögersten and Wookey, 2005). Similar results have been obtained by Davis et al. (1991) in Fennoscandia and Sveinbjörnsson et al. (1995)

in Alaska, where ammonium concentrations were found to be higher within the forest areas than at the treeline and krummholz zones, though Hartley et al. (2012) provide a counter-example.

Plants from lower altitudes tend to have lower N contents (Reich and Oleksyn, 2004) so the upslope migration of lower altitude plants as temperatures rise could decrease the N inputs from plant litter. However, the concentration of N in shrubs growing within a forest was found to be higher than those from tundra sites (Kaarlejärvi, 2012), so the converse could be true, with treeline advance leading to an increase in plant N levels. Lower N levels in needles and soil have been found at Arctic treeline sites, and attributed to lower microbial activity at low temperatures (McNown and Sullivan, 2013). N availability reduced with elevation at Patagonian treelines and there was a change in microbial communities from bacteria to fungal dominated. Changes in forest cover and composition influence both microbial communities and N availability through litter inputs (Thebault et al., 2014).

Lower nutrient availabilities at the approach to, and beyond treeline have been hypothesised to account for the increase in fine root biomass that has been observed at treeline compared with lower elevation forest (Hertel and Scholing, 2011), such that increased nitrogen availability through vegetation and temperature change at the treeline would likely lead to alterations in biomass partitioning. A positive feedback mechanism whereby warming increased tree establishment, which then increases nitrogen content and subsequent tree establishment is possible (Sjögersten and Wookey, 2005; Sundqvist, 2011).

Evidence is mixed on the likely effects of treeline advance for N cycling and availability. As with C dynamics most research has focused on latitudinal treelines; current evidence suggests that for N similar patterns of change will be observed at advancing altitudinal and latitudinal treelines, and N tends to be limiting at both (Rustad et al., 2001; Thebault et al., 2014). However there is little direct evidence of the effect of altitudinal treeline advance, and since C and N are closely linked, because N is stored in soil organic matter (Thebault et al., 2014), more research is required to fully understand the impacts of altitudinal treeline advance on N availability and mineralisation.

Hydrology

Mountain areas are extremely important in terms of controlling the volume and quality of water provision; plant cover and associated soil properties have a major influence on this service (Dirnböck and Grabherr, 2000). Plant cover can reduce flood flow but also increases infiltration into the soil and water table and hence will augment low flow and provide water supply throughout the dry season (Dirnböck et al., 2003). Treeline advance into previously treeless areas has the potential to significantly impact downslope hydrology since the development of krummholz and montane forest in grasslands increases the water absorption and retention capacities of soils (Dirnböck and Grabherr, 2000). Furthermore, the impacts of forests on hydrological properties can have implications for human societies because the degree of forest cover has been shown to affect sediment load and therefore water quality (Douglas et al., 1992). However, afforestation may lead to reductions in stream flow due to reduced runoff and reduced but more predictable water availability downstream (McVicar et al., 2007). In areas where water supply is already limited this could produce major problems yet our current understanding of the impact of treeline advance on hydrology, especially in mountain areas is limited by lack of direct research.

Slope stabilisation and avalanche/rock fall prevention

Mountain forests also play a highly important role in slope stabilisation and the prevention of landslides and avalanches (Bebi et al., 2001), and the anthropogenic lowering of the treeline due to land use in regions such as the European Alps is believed to have led to increased avalanche risk (Li and Yang, 2004). Modelling of avalanche risk based on forest cover found that the risk of extreme events depends on degree of forest cover and forest structural features (Teich and Bebi, 2009), with avalanche risk being significantly reduced by the presence and high cover of structurally complex undisturbed forest. Wehrli et al. (2006) combined a forest dynamic model (ForClim) with a model of rock fall risk (RockFor) in order to investigate the role of forests in preventing rock fall, and the degree to which this was affected by forest dynamics. It was found that high stand density, as well as high regeneration improved the ability of forests to protect against small rocks but that forest were limited in their ability to prevent the damage caused by large rock displacement. Model simulations by Dorren et al. (2005) produced similar results; an absence of forest would lead to a greater impact of rock fall events whilst an increase in tree density improved the protective function of forested areas.

Conclusion

Treelines are advancing upward and toward the poles in response to rising temperatures worldwide (Harsch et al., 2009). Whilst these changes in distribution and the reasons for them are relatively well investigated, much less attention has been focussed on the impacts of treeline advance for ecosystems beyond the current treeline. Research discussed herein suggests that the upward migration of forests will have major consequences for biodiversity (Figure 1), eventually leading to reductions in alpine diversity (Moore and Huffman, 2004; Halloy and Mark, 2003). However, this process is highly unlikely to occur as a simple replacement of one ecosystem by another. Rather, newly formed communities are likely to lack historical precedent, retaining some components of former vegetation types due to differential migration rates of individual species and variation in their tolerance of shading in the forest understory. Evidence from assessments of responses to past periods of temperature change indicates that species have responded to environmental fluctuations in the past in a similar way, with the breakdown of communities and formation of novel assemblages (Edwards et al., 2005; Van Devender and Spaulding, 1979). Such changes, and the possible impacts that they will have on the surrounding communities represent a natural continuous process since treeline position and vegetation composition are dynamic. However the current rate of climatic warming is unprecedented (IPCC, 2013) and is therefore likely to drive larger and more variable impacts on species migration and community response compared to that which has occurred in the past. In addition to impacts on diversity across the treeline ecotone and in the alpine zone above, ecosystem functions will be affected in a multitude of ways (Figure 1) such as alterations to net ecosystem productivity and carbon storage (Griffis et al., 2003; Rustad et al., 2001), nutrient cycling (Sjögersten and Wookey, 2005) and hydrology (Dirnböck and Grabherr, 2000). However, at present there is insufficient information available, particularly from mountain regions to make reliable predictions on the direction and magnitude of effects in most cases. Mountain regions present a particular challenge in this respect as their varied topography can result in ecosystems showing a wide diversity of responses in a relatively small area.

Future research

From a biodiversity perspective, knowledge is particularly lacking in the diversity of recently colonised areas of high altitude forest compared to long established areas and in the migration rates of forest understory and epiphytic species. Given the importance of alpine areas for biodiversity, and because of the high endemism rates, more field-based research on the impacts of treeline expansion on alpine species survival and migration is required. An important aspect of such research should be the determination of the balance between competition and abiotic factors such as habitat availability and climate in determining the presence or absence of key species. Given the highly heterogeneous landscapes of mountain regions, such knowledge would allow us to substantially improve local scale modelling of species distributions to better forecast species loss or retention.

In terms of ecosystem function, research is required to assess the spatial heterogeneity of impacts of treeline advance for carbon and nutrient cycling. The imbalance in our understanding of tree invasion into arctic and alpine areas is particularly important to redress given feedbacks of such changes in vegetation and soil properties to the global climate system. Furthermore, in order to better predict the effects of forest expansion on ecosystem carbon storage, a better understanding of the relationship between above and below ground processes is required across the alpine treeline ecotone.

Treeline inertia in response to climate could modify the degree of feedback that occurs with climate and this phenomenon produces significant uncertainties in models attempting to simulate the consequence of treeline advance for climate feedbacks. Further field research on rates and time courses of treeline advance in arctic and alpine areas will contribute vital information that can reduce this uncertainty.

The advance of treelines into previously treeless ecosystems will continue as the climate continues to warm. The consequences of such advance for biodiversity and ecosystem function will be felt over ever-greater areas. To date, the majority of investigations of the consequences of treeline advance have been focused on northern tundra ecosystems, which seems intuitively sensible given both the expanse of tundra and boreal forest, with a consequently large potential to influence climate, and the far larger predicted rate of treeline advance (distances of km rather than tens of meters) compared with alpine sites. However given that mountain ecosystems cover a major proportion of the Earth’s surface (somewhere between 20-24% of total land surface) (IPCC, 2007), it is essential to ensure that data availability on ecosystem response to change in high altitude and high latitude regions is comparable. On the broadest scale, an assessment of the comparability of such data from altitudinal and latitudinal systems is lacking, and is necessary if we are to fully understand the interactions between spatial scale and heterogeneity and ecological processes over altitudinal and latitudinal gradients (Jump et al 2009). A clear understanding of the potential for data transferability between these systems would be highly advantageous for more accurate modelling of ecosystem responses to current and future environmental changes.

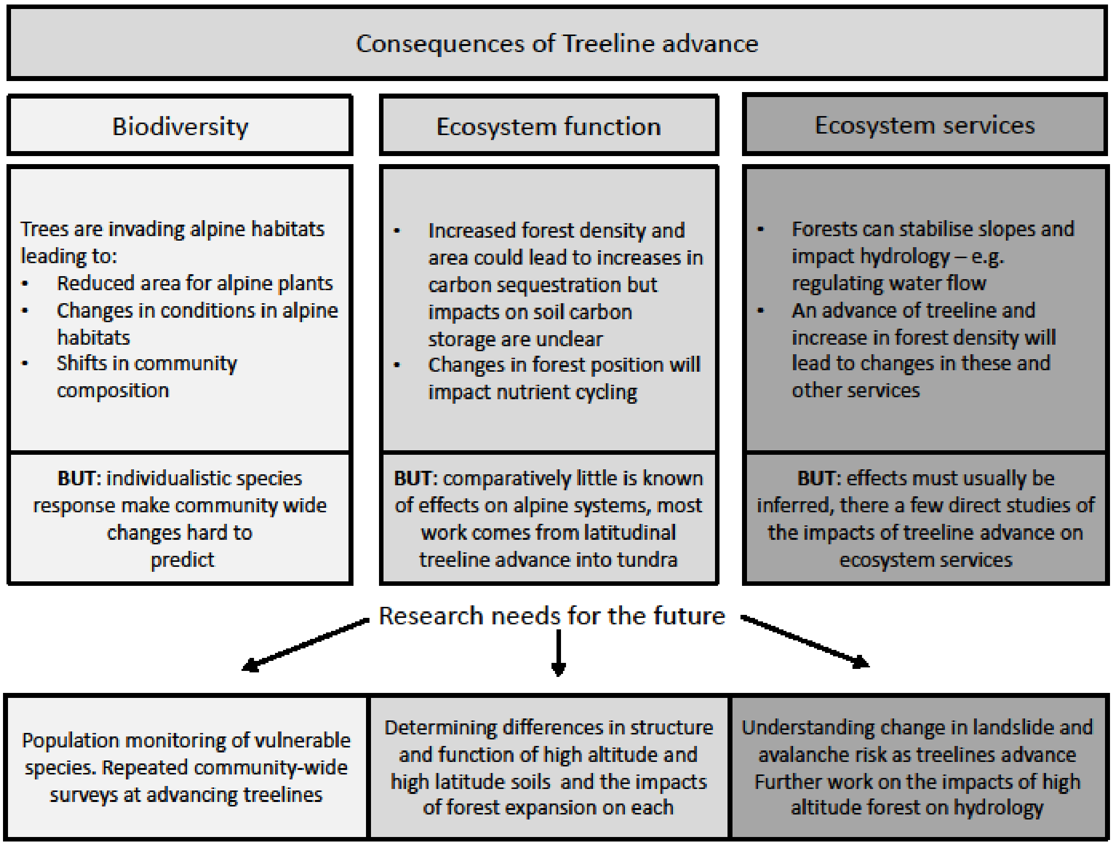

Figure 1: Summary of key points and research needs.

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Chapter 3

Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region

Title: Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region

Running title: Complex subtropical treeline advance

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Abstract

Altitudinal treelines are typically temperature limited such that increasing temperatures linked to global climate change are causing upslope shifts of treelines worldwide. While such elevational increases are readily predicted based on shifting isotherms, at the regional level the realised response is often much more complex, with topography and local environmental conditions playing an important modifying role. Here, we used repeated aerial photographs in combination with forest inventory data to investigate changes in treeline position in the Central Mountain Range of Taiwan over the last 60 years. A highly spatially variable upslope advance of treeline was identified in which topography is a major driver of both treeline form and advance. The changes in treeline position that we observed occurred alongside substantial increases in forest density, and lead to a large increase in overall forest area. These changes will have a significant impact on carbon stocking in the high altitude zone, while the concomitant decrease in alpine grassland area is likely to have negative implications for alpine species. The complex and spatially variable changes that we report highlight the necessity for considering local factors such as topography when attempting to predict species distributional responses to warming climate.

Introduction

Anthropogenic climate change has resulted in unprecedented rates of warming across the globe with temperatures rising by around 0.25 ºC per decade in the period 1979 to 2012 (Collins *et al*., 2013). Particularly high levels of warming are expected in mountain regions (Beniston *et al.*, 1997; Grace *et al*., 2002; Fischlin *et al*., 2007).

As climate warms, the geographical distributions of species are changing in response to the spatial shift of their typical climate-space (Parmesan, 2006; Fischlin *et* *al*., 2007). Range shifts have occurred as a consequence of past changes in climate (e.g. MacDonald *et al*., 2000) and are occurring in many plant and animal taxa in response to modern climatic changes (Parmesan *et al*., 1999; Parmesan, 2006; Walther, 2003; Chen *et al*., 2011). Mountain plants are particularly vulnerable to changes in climate (Pauli *et al.*, 1996; Klein *et al*., 2004) because they are very sensitive to warming temperatures and often have limited habitat available for upward migration (Pauli *et al.*, 2003). Alpine areas are often high in endemics, so the possibility of species extinction is high (Jump *et al.*, 2012) should habitat be lost to competitors migrating from lower altitudes.

Altitudinal range shifts of forests trees are widely reported as lower range edges contract and upper ones expand (Peñuelas and Boada, 2003; Beckage *et al*., 2008; Kharuk *et al*., 2009). Treeline advance is common at high altitude in response to warming because trees are typically growth-limited by low temperature at their upper range edges (Tranquillini, 1979; Körner, 1998; Körner and Paulsen, 2004). However an advance is by no means a universal response; many treelines that experience warming temperatures show no change in position (Hättenschwiler and Körner, 1995; Harsch *et al*., 2009). Environmental variability between sites is high (Lloyd and Fastie, 2003) and some forests will be unable to respond to warming through an upslope advance due to extremely steep slopes or unsuitable substrate (Macias-Fauria and Johnson, 2013). Furthermore, there is often a time lag between climatic change and forest response because it can take some time before improved conditions for tree growth to lead to successful recruitment beyond current limits due to factors including limited dispersal or poor soil conditions (MacDonald *et al*.,1998; Rannow, 2013).

The structure of treelines can be highly variable, and this can affect how they respond to climatic changes (Harsch *et al*., 2009). Some sites show an abrupt change from forest to grassland or sub alpine shrubland, in others the transition is smooth

(Wiegand *et al*., 2006) or diffuse (Harsch and Bader, 2011). Although an upslope shift in response to warming temperatures is common, many factors control treeline position at a local scale. Studies that consider the complexity in the form and response of treelines and how this varies spatially are required to fully understand treeline advance, and to enable us to more accurately predict forest responses to environmental change, and their wider implications.

Previous studies have identified topography as playing a potentially important role in determining treeline patterns and behaviour (Butler *et al*., 2003; Danby and Hik, 2007; Macias-Fauria and Johnson, 2013). Huang (2002) shows the importance of topography for controlling the spatial pattern of *Abies kawakamii* throughout the Central Mountain Range of Taiwan; forest stands establish preferentially in sheltered sites at high altitude. Models of treeline advance in the Canadian Rockies (Macias-Fauria and Johnson, 2013) show that treeline advance is spatially complex and occurs only on moderately steep slopes.

By not accounting for the spatial variability of treeline advance, we risk erroneous prediction of the implications for associated biodiversity, carbon sequestration and other ecosystem services. While the variable response of high altitude forests to climate warming has been identified from studies in Europe (Kullman, 1993; Peñuelas and Boada, 2003; Camarero and Gutiérrez, 2004) and North America (Rochefort *et al*., 1994; Beckage *et al*., 2008; Suarez *et al*., 1999), there is a lack of knowledge on tropical and subtropical treeline advance. Studies in Far East Asia are poorly represented in the scientific literature and the dynamics of high altitude sub-tropical forest ecosystems represent a major gap in ecological knowledge. Tropical mountainous regions have been identified as being particularly vulnerable to climate warming (Fischlin *et al*., 2007), making further study of these areas of very high importance.

It is important to understand the process of treeline advance, and to be able to predict future changes. The invasion of trees into alpine habitats may have negative consequences for alpine plants that are already potentially threatened by climate warming, leading to a reduction and fragmentation of available habitat and likely species losses (Halloy and Mark, 2003). Treeline advance also has implications for the regional carbon economy; an increase in forest area could mean more carbon stored in tree biomass, while advance of trees into grassland habitats will also alter below ground carbon stocks (Hartley *et al*., 2012).

While many existing reports of treeline shifts are based on comparing historical and recent photographs from a pedestrian vantage-point (e.g. Peñuelas and Boada, 2003; Elliott and Baker, 2004; Danby and Hik, 2007; Hagedorn *et al*., 2014), repeat aerial photography and satellite imagery offer an excellent resource for the study of treeline shifts over wide areas (Shugart *et al*., 2001; Hofgaard *et al*., 2013). By comparing images from different time periods, the degree and nature of treeline advance can be quantified and spatial variability explored in a way that is not possible using comparison of photographs of single sites. This large-scale information can also be paired with forest inventory data to provide detailed information on changes in treeline position and forest dynamics (Beckage *et al.*, 2008; Mathisen *et al.*, 2014).

The Central Mountain Range of Taiwan includes extensive areas of mountain forest and subalpine grassland. Anthropogenic disturbance is generally low in the area and the ecotone between forest and grassland, the treeline, is readily discernable from aerial photographs spanning a period from the 1940s to 2001. The treeline and grassland beyond have low grazing pressure from native mammals, with no domesticated livestock grazing in the area. Hunting pressure from aboriginal peoples is low and is not believed to have changed over recent decades (Pei, 1999 and references contained within). Furthermore, unpublished dendroecological work by the authors shows no evidence of widespread fire or changes in fire frequency in the area and the forests are not used for fuel wood extraction.

Here we explore spatial and temporal changes in the treeline of the Central Mountain Range (Figure 1). Our aim was to examine the highly spatially variable treeline advance within the region and identify how realised shifts correspond to those predicted from upward isotherm movement due to regional warming. To do this, we combine information from aerial photography and forest inventory data, allowing us to assess changes in treeline position, maximum elevation of forest and changes in forest density together with the influence of topographic features such a slope, aspect and sheltering.

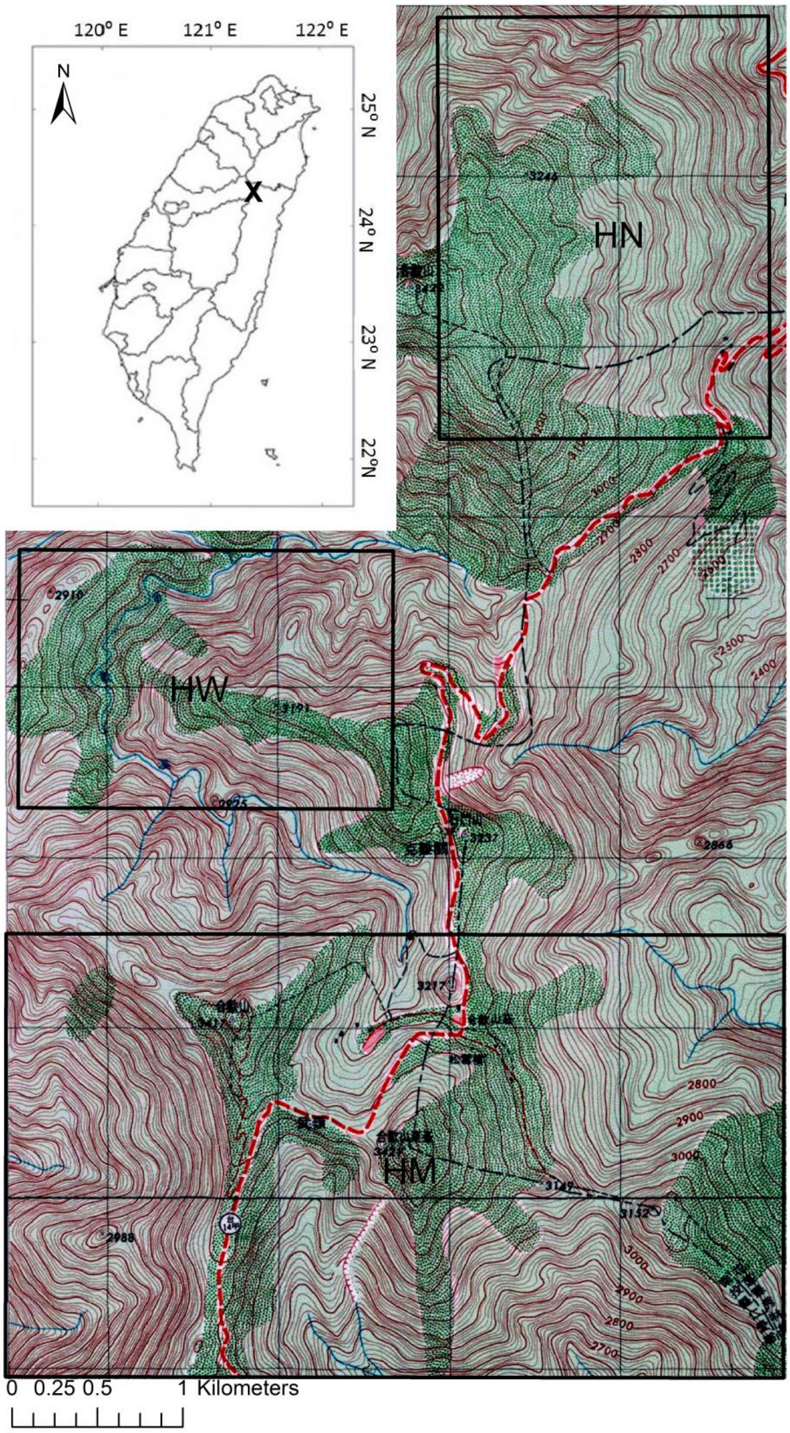

Figure 1: Location of the study area Hehuanshan (black cross) in the island of Taiwan (inset) and location of the aerial photographs (black outlined boxes (HN: Hehuan North Peak region, HW: Hehuan West Peak region, HM: Hehuan Main Peak region)) within this area on a topographic map (1:25,000 scale).

Materials and methods

Study area

The island of Taiwan straddles the Tropic of Cancer and has more than 200 mountains over 3,000 m a.s.l., concentrated within the Central Mountain Range (Guan *et al*., 2009). The main tree species at treeline is *Abies kawakamii*, an endemic fir that grows in almost monospecific stands at the very highest elevations. Treeline position varies but reaches about 2,800-3,000 m. Above treeline, the bamboo *Yushania niitakayamensis* dominates the subalpine grasslands. This dwarf bamboo is tall and dominant, limiting ground cover forbs. Throughout the alpine grassland there is low density shrub cover of *Juniperis* and *Rhododendron* spp. and species such as *Gentiana arisanensis* can be seen where bamboo cover is sparse. Although the majority of the island experiences subtropical climate at low elevation, at high elevation conditions grade through temperate to alpine.

Following Körner (1998 and 2012) we use ‘treeline’ to represent the rough boundary or line that connects the highest forest patches occurring on slopes of similar exposure and ‘tree-limit’ to describe the upper limit of trees reached by outpost individuals. The treeline thus represents an ecotone or transition zone between forest and alpine tundra.

The *Abies kawakamii* treeline is spatially heterogeneous with five broad classes of treeline identifiable from aerial photographs and forest inventory plots: abrupt static treelines, abrupt advancing treelines, diffuse advancing treelines, infill sites (where the treeline over a small section is lower than that surrounding it and the forest is now infilling) and island sites (where a small patch of trees occurs clumped together beyond the treeline). These island sites tend to include old trees and are either stable or increasing in area. Similar variation in treeline structure has been identified by other authors (Harsch and Bader, 2011). Where the treeline is abrupt, tree density is high and forest trees are tall right to the boundary with alpine vegetation, there is then a sudden change as forest ends and alpine tundra or grassland emerges. In diffuse or smooth boundary treelines there is a gradual decrease in tree height and density with altitude and the forest- tundra transition occurs over a wide area.

Temperatures in Taiwan have increased over the last decades. Jump *et al*. (2012) report a temperature increase of 1.05 ºC for the Alishan area compared with 1934-1970 mean values, while Hsu and Chen (2002) predict rises in temperature over a thirty-year period of between 0.9 and 2.7 ºC, compared to 1961-1990 mean values.

Rectification of aerial photograph data

Three sets of repeat aerial photographs were used in these analyses (Figures 1, 2, Table 1 and supporting information Figures S1, S2). Images from 1963/4 and 1975 were already ortho-rectified, and the 2001 images were ortho- and geo-rectified with the Transverse Mercator (TWD1997) projection. The older images were geo-rectified to the 2001 images with a spline function. More than 60 ground control points (GCP's) were selected for each image pair. The images from the 1940s were not ortho-rectified, and since no information on camera or sampling was available, the same process had to be followed for these images without correcting for topology. Exact error varies across the photographs and between sets but is generally less than 5 m, and never more than 10 m for the images from 1963/4 and 1975, and generally less than 10 m for the images from 1948. A digital elevation model (DEM) (resolution of 30 m) and topographic map (1:25,000) (National Land Survey and Mapping Centre, Taiwan (Jingjian Version)) were also used and all analyses were conducted using ArcMap 10 (ESRI 2011, Redlands, CA).

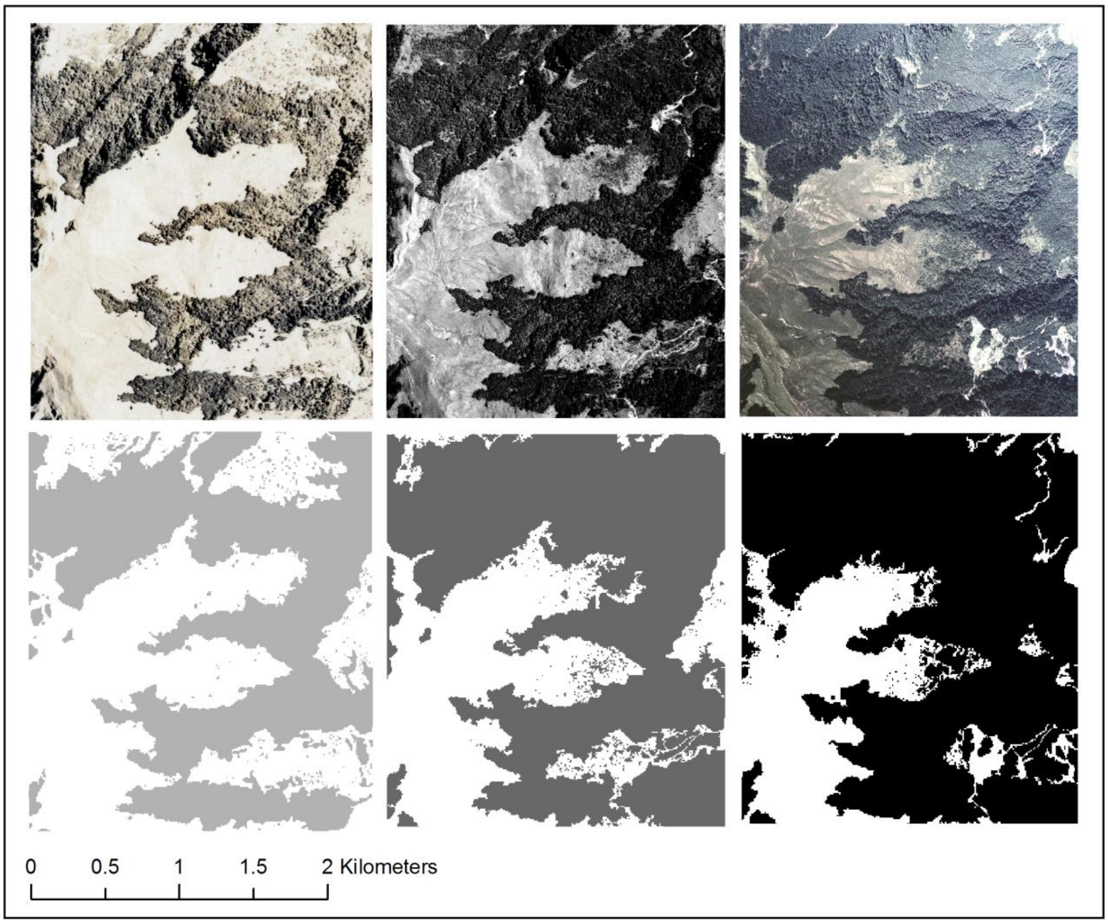

Figure 2: Forest and grassland extent in the Hehuan North Peak region of the Central Mountain Range of Taiwan. Upper panels show aerial photographs and lower panels the raster layer of forest cover for each photograph respectively. Images from left to right are from 1948, 1964 and 2001.

Changes in treeline position and forest density

Supervised classification with training samples was attempted but the effects of complex topography, shading and insufficient resolution of the images made results of this automated process inaccurate. Polygons were, therefore, manually created to classify forest and subsequently converted to raster format for further analyses. The forest raster layer was multiplied by a 30 m resolution DEM, giving an elevation value for each pixel of forest cover for each year that could then be compared to see how maximum, minimum and mean elevation of forest had changed between years.

Changes in treeline position in terms of metres on the ground were calculated by measuring the distance between treelines for each year. Line and point data were created manually and DEM elevation data was extracted to allow for 3D analysis, thus accounting for the effects of topography. Sample points (100 per image) were randomly selected along treelines. The distance was measured between these random points on the older treelines to the nearest points on the newer treelines.

In order to have a measure of forest change that was independent of the small error in rectification of photographs, we measured treeline position within photographs and compared this position between images. Easily identifiable set points (52 per image) were located on high areas and ridges in each image set. The distance between treeline and these set high points was measured for each photograph. Distances between years for each image could then be compared. This analysis was not possible for the oldest photographs (those taken in the 1940s) as the resolution did not allow for identification of points beyond treeline.

To quantify variability in treeline response, we compared changes in elevation from four subsamples of 50 m x 100 m for each of the three main treeline forms described for the study area (abrupt static, abrupt advancing, diffuse advancing) using Hehuan North and West Peak images (Table 1). To assess temporal changes in forest density, we compared photographs from 1963/4 and 2001. Three 300 x 500 m subsamples per photograph were taken from Hehuan North and West Peak images. Subsamples were selected randomly but had to include an area of treeline as well as forest. All trees within these samples were marked with points and a density analysis was performed.

Table 1: The years of capture, total area and resolution of the images for each region covered.

Region	Area (ha)	Years of image capture			Resolution (m)		
Hehuan North Peak	633	1948	1964	2001	1	0.3	0.3
Hehuan West Peak	331	1948	1963	2001	1	0.3	0.3
Hehuan Main Peak	1476	1975	2001		0.3	0.3	

Impacts of topography

Data from the forest classification and elevation analysis was used to explore the effects of aspect and slope on the establishment of new trees. For Hehuan North and West Peak images (Table 1) the 1948 forest polygon layer was subtracted from 2001 forest polygon layer leaving only newly established trees, this polygon layer was then converted to a point dataset.

Aspect and slope were derived from a 30 m resolution DEM and elevation, slope and aspect were all added to the point data. A point dataset was also created for the entire available area of each image, and then randomly sampled using the sample function in R (R core team, 2013). Differences in the proportions of trees establishing across different aspects and slopes were investigated using Kolmonogrov-Smirnov tests in R.

Inventory data were collected along belt transects (20 m by 60-120 m) from forest interior to treeline in static and advancing (diffuse and abrupt) treelines. Thirty three transects were recorded, split evenly between the three forms. All trees were measured for diameter at breast height and the position of trees in each transect was mapped and tree density calculated. To explore the relationship between sheltering and treeline form/advance, these data were then analysed alongside a topographic sheltering index taken from Huang (2002), according to the following equation:

$$\boldsymbol{S_{ij} = \frac{\sum_{k=1}^{8} \frac{W_k}{d_k}}{STD(d'_k)}}$$

Where:
S_{ij} = Topographic shelter index
W_k= weight in cardinal compass direction (k)
d_k= distance in cardinal compass direction (k)
STD (d'_k) = standard deviation of scaled distances from point to ridge in all 8 directions
d'_k= scaled distance = (min (d_k))(max (d_k) − min (d_k))$^{-1}$

Subsamples were also used to explore the variation in and relationship between treeline form and advance. Samples of 50 m x 100 m were taken and changes in elevation of treeline were compared using raster elevation data. The samples were selected using visual examination of the aerial photographs in order to include four samples each of three main treeline forms described in the study area (abrupt static, abrupt advancing, diffuse advancing). ANOVA in R was used to test for differences in sheltering and advance with treeline form.

Results

Shifts in forest distribution and extent

Raster classification and DEM analysis of forest cover generally show that maximum and mean elevation of forest increased over time in the study areas (by up to 27 m and 12 m respectively between 1940 and 2001, Table 2). However, this was not the case for the Hehuan Main Peak region, where no overall change in treeline elevation was found. Measured changes are subject to the aforementioned rectification errors of 5-10 m. Forest area increased throughout the study area; for example in the Hehuan North Peak region forest area increased by 141 ha over the full study period. However, the pattern of change in forest area was variable across both space and time (Figure 3). In the Hehuan North Peak region there was a large increase in forest area between 1948 and 1964, while in the West Peak region a small decrease in area from 1948 to 1963 was followed by an increase from 1963 to 2001. Measurement of the difference in treeline position between years shows that treeline is advancing (Table 3). The change is spatially variable on both local (within image) and regional (between images) scales and in some cases is affected by very rapid infilling in otherwise treeless areas below the local treeline. Results of the analysis based on measurements of treeline position from set points on ridges (Table 4) demonstrate an upward shift of the treeline of between 25.8 and 10.5 m for the Hehuan North and West Peak regions respectively.

Table 2: Temporal changes in forest elevation in the Central Mountain Range of Taiwan, calculated based on manual forest classification of aerial photographs and subsequent raster multiplication with a 30 m resolution DEM.

Region	**Year**	**Highest elevation of tree cover**	**Mean forest elevation**	**Lowest point of tree cover**
Hehuan North Peak	1948	3330	2858	2428
	1964	3338	2863	2428
	2001	3357	2870	2428
Hehuan West Peak	1948	3256	2982	2700
	1963	3264	2981	2700
	2001	3264	2989	2708
Hehuan Main Peak	1975	3409	2915	2408
	2001	3405	2916	2408

Table 3: Changes in treeline position between years of image capture based on comparing the distance between treeline for each year, for two regions of the Central Mountain range of Taiwan. Values shown are means with one SE.

Region	Mean distance 48-60s (m)	Mean distance 60s-2001 (m)	Mean distance 48-2001 (m)
Hehuan North Peak	16.5±1.9	37±8.1	56.7±10.1
Hehuan West Peak	10.7±1.1	8.8±0.7	14.7±1.4

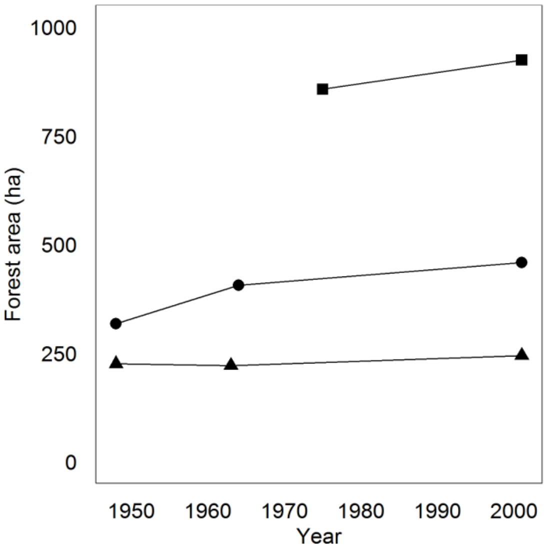

Figure 3: Temporal changes in forest area in three regions of the Central Mountain Range of Taiwan: North Peak (circles), West Peak (triangles) and Main Peak regions (squares).

Table 4: Temporal changes in treeline position based on comparing within image point locations from aerial photographs of the Central Mountain Range. Values shown are means with one SE.

Region	Mean distance 1960s (m)	Mean distance 2001 (m)	Change (m)
Hehuan North Peak	153.1±8.5	127.3±8.7	25.8
Hehuan West Peak	37.2±2.5	26.7±2.1	10.5

Tree establishment patterns and impacts of topography

Analysis of the slope and aspect values associated with trees established between 1948 and 2001 shows that trees did not establish at random within the available space. Count data plots reveal that trees established more frequently at east, north east and south east aspects in Hehuan West and North Peak regions and also at north west aspects in Hehuan West Peak region, at moderate slope steepness and at mid-range elevation values (Figure S3 in supporting information).

Kolmogorov-Smirnov tests show that the frequency of slope (D = 0.15 (North Peak Region) and 0.06 (West Peak Region), $p < 0.001$ for both image sets) and aspect (D = 0.23 for North Peak and 0.07 for West Peak, $p < 0.001$ for both) values of new establishment is independent of the available habitat area. Trees reached higher mean elevation at south west and south aspects (Figure 4).

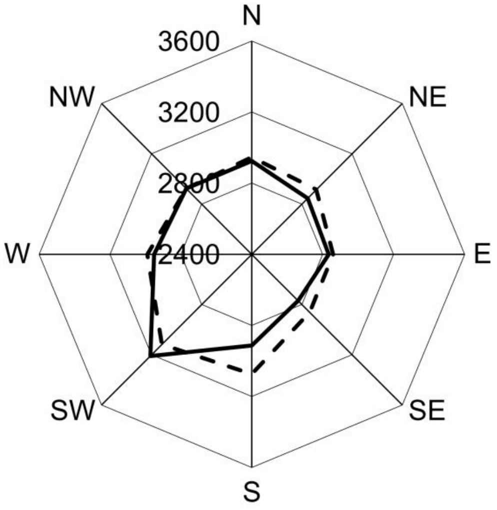

Figure 4: Mean elevation (in metres) of newly established *Abies kawakamii* trees above treeline at each aspect for two regions of the Central Mountain Range of Taiwan. Hehuan North Peak is represented by a solid line, Hehuan West Peak with a dashed line.

Size class distributions of trees at each treeline form (Figure S4 in supporting information) largely confirm patterns identified from aerial photograph data for different treeline forms. Abrupt static treelines have few young trees at the treeline. Abrupt advancing treelines have many young trees concentrated at high density (a mean of 1991 trees/ha) at the treeline. Diffuse treelines also have many young trees but these are distributed over a wider area due to a greater degree of advance, and there are also a great number of older outpost trees forming the tree-limit. Overall density is lower; a mean density of 566 trees/ha was found across the treeline to the tree-limit. An ANOVA of topographic sheltering and treeline form/advance type shows that treeline advance form varies significantly with topographic shelter (F = 4.38, p = 0.03, df = 24). Shelter is significantly higher in diffuse treelines and lower in static treelines (Figure 5).

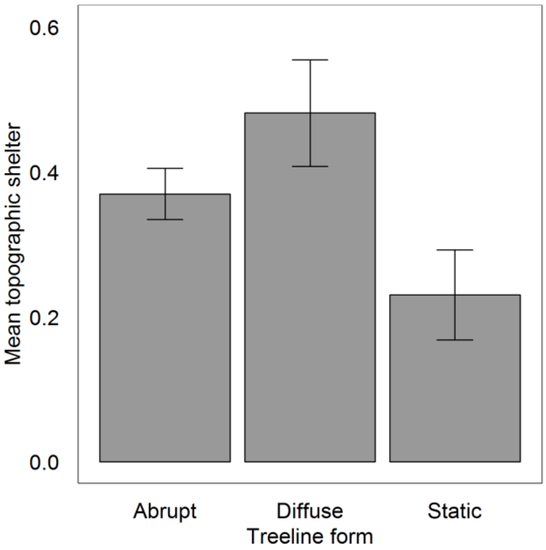

Figure 5: Mean topographic sheltering score (± 1SE) associated with principal treeline structures in the Central Mountain Range. A higher topographic sheltering score is associated with more sheltered areas.

Subsamples from the Hehuan North and West Peak areas show a large variation in the degree of advance based on treeline form (Figure 6). Diffuse treelines shifted upslope by an average of 33 m over the period 1963/4 to 2001 whereas the two abrupt treeline forms showed little or no change in elevation. ANOVA results show the change in elevation to vary significantly depending on treeline form (F = 17.77, p < 0.001, df = 9).

Temporal changes in forest density

Density analyses show that forest density is generally increasing, especially close to the treeline. In many areas large increases in density of around 800 tress/ha can be observed between 1975 and 2001 (Figure 7 and Figure S5 in supporting information). These large increases tend to occur at, and just below treeline. The pattern of density change is complex, however, and although an overall increase can be observed there is considerable variation in response on a small scale, with some areas even showing small decreases in density.

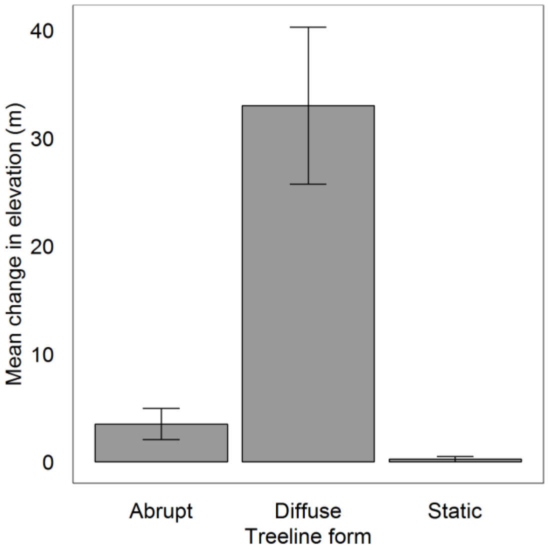

Figure 6: Mean change (± 1SE) in elevation of the treeline in the Central Mountain Range between years 1963/4 and 2001 for the principal treeline structures identified within the area.

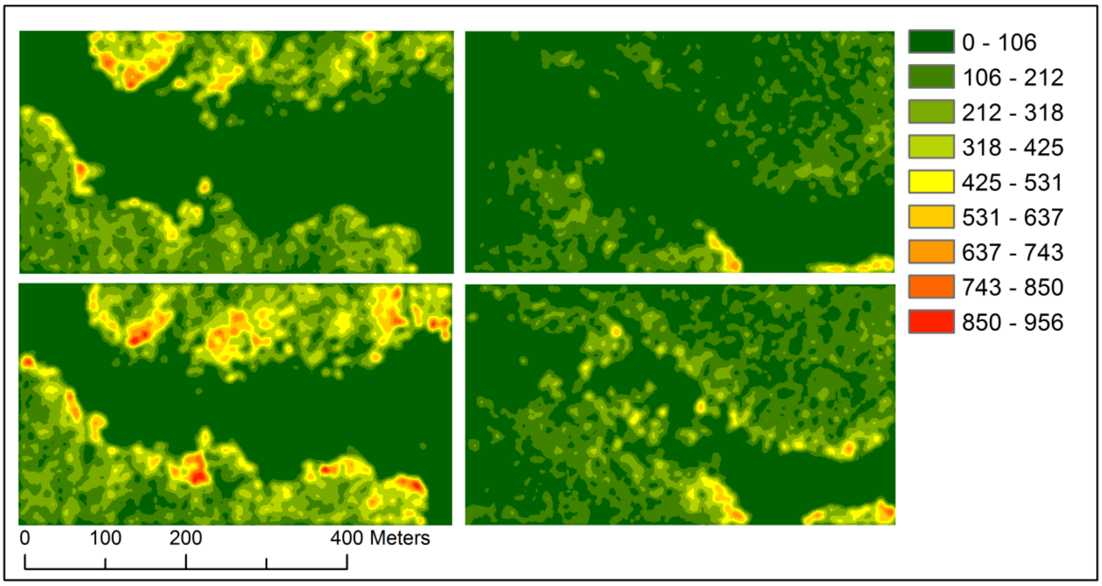

Figure 7: Changes in tree density from 1964 to 2001 from locations immediately below the treeline of the Central Mountain Range. Images are in pairs; top two images are from 1964, bottom two are the same subsamples from 2001. Density values are shown in trees per ha, rounded to the nearest tree.

Discussion

Repeat aerial photography ground-truthed with plot-level forest inventory data demonstrate that the *Abies kawakamii* treelines in the Central Mountain Range of Taiwan are shifting upwards in elevation over recent decades, although the response is highly spatially variable. Treeline responses to increased temperature are typified by both upward movement and increased density or 'infilling' below the existing treeline (Szeicz and MacDonald, 1995; Taylor, 1995; Kharuk *et al*., 2010). Here, both responses are reported from this previously poorly understood ecosystem. One of the defining features of the migrational response of the treelines of the Central Mountain Range is the high level of variability on the regional (between photograph sets) and local (within photograph sets) scale owing to the topographically varied landscape. Furthermore, the magnitude of elevation change reported here is small compared to that described by other authors (e.g. Kullman, 2007; Moen *et al*., 2004). However, it is important to recognise that this change in altitudinal treeline position, when combined with the reported density increases has led to a large increase in forest area with potential impacts on both the carbon stocking potential of forests and the area of alpine grassland above the treeline.

We report upward changes in elevation up to a maximum of 27 – 33 m between 1948 and 2001 (Table 2 and Figure 6). Guan *et al.* (2009) calculated altitudinal temperature lapse rates for Taiwan to be 0.5 ºC 100 m $^{-1}$. Given this change in temperature with elevation, and the rise in temperature reported for this region (Jump *et al*., 2012), we would expect the treeline to have risen by around 200 m in elevation between 1934 and 2001 if it was tracking the change in isotherm position. The response that we report is, therefore, markedly lower than the response predicted from climatic changes alone. Treeline advances reported in the literature are highly variable; whilst some treelines are highly responsive to warming (Devi *et al*., 2008), others show a marked lag behind isotherm movement (Szeicz and MacDonald, 1995). Disparities between isotherm movement and treeline position highlight the complex interaction of ecological and physical factors that are responsible for realised shifts in treeline position. A more mechanistic understanding of the drivers of treeline movement based on a modelling approach that integrates climate, treeline and landscape data with information on treeline and alpine species ecological traits (e.g Dullinger *et al*., 2004; Wallentin *et al*., 2008) will be highly useful to refine future predictions of treeline movement and their implications.

Time-lags are known to occur between warming and forest response (MacDonald *et al*., 1998) and so it may take some time before a response of advance can be identified. This can be due to limited seed production and dispersal (Dullinger *et al*., 2004), establishment limitations such as poor soil conditions (Lloyd *et al*., 2002) and competition from alpine species (Holtmeier and Broll, 2007). It is possible that competition with the dominant alpine grassland species *Yushania niitakayamensis* is limiting the degree of advance at high altitudes in the Central Mountain Range. This dwarf bamboo grows in extremely dense swards, and in many areas reaches heights in excess of 2 m (S. Greenwood unpublished data). A competitive limitation of treeline advance has been found by other studies; Dullinger *et al*. (2003) found evidence for competition with grass species preventing the expansion of *Pinus mugo* in the Austrian Alps, although alpine plant cover can also have an important facilitative effect on establishment beyond treeline (Mamet and Kershaw, 2013).

Topography (aspect, slope, sheltering) influences treeline behaviour in Taiwan (Figures 4, 5 and 6). The steep and highly variable topography of the Central Mountain Range might explain why treeline has not been able to advance as much as would be predicted based on increased temperature. Whilst advance has occurred in sheltered sites, those with exposed aspects and extremely steep slopes limit treeline advance. It is also important to consider geology since the bedrock throughout much of the Central Mountain Range is unstable and given to landslides on steep slopes. This issue will undoubtedly limit treeline advance in many areas, especially on steeper exposed slopes. The need for accounting for local factors such as water availability, soil quality and topographic features is recognised (Butler *et al*., 2003; Danby and Hik, 2007) and it is likely that these local factors partly drive variability in treeline form and response at small scales. In this example, the variability of response and form is evident; areas where a large advance has taken place are associated with a diffuse treeline form and occur most often in sheltered sites, with moderate slope values, in agreement with spatial patterns identified in the Ural Mountains (Hagedorn *et al*., 2014) and Canadian Rockies (Macia Fauria and Johnson, 2013).

Harsch *et al*. (2009) report that treeline form is related to advance, with 80% of diffuse form treelines showing a response to warming. We report similar results here in that although many areas of abrupt treeline were shown to have advanced, the degree of advance was much less than in the diffuse form treeline areas. On Hehuanshan, topography is a major driver of treeline form and advance pattern, with treeline reaching higher elevations in sheltered valleys where a diffuse treeline form predominates. Further work in the area, such as studies of seedling patterns and how these are related to topography and microclimate could allow us to begin to derive a mechanistic understanding of the importance of topography and sheltering effects on treeline form and advance, as would a more detailed understanding of the importance of substrate conditions. For example, Holtmeier and Broll (1992) found that the influence of microtopography on soil formation and properties was a major driver of treeline formation in the Colorado Range and seedling establishment patterns seem to be affected by wind and snow accumulation in the central Rocky Mountains (Hättenschwiler and Smith, 1999) but, to date, little work has been conducted in the sub-tropics where the driving mechanisms may differ.

In this study, changes in treeline position led to large increases in forest area (Figure 3) and also in forest density (Figure7). These changes could produce negative feedbacks to climate warming through increased carbon sequestration (Saxe *et al*., 2001). Modelling studies suggest greater carbon accumulation potential of alpine forests with warming (Zierl and Bugmann, 2007. However, such effects will vary between regions; Hu *et al*. (2010) identify that winter warming and a longer growing season might lead to a decrease in overall carbon sequestration in the Colorado Rocky Mountains due to the negative effects of earlier snowmelt on summer water balance yet it is unlikely that such effects will be seen in Taiwan, where summer water availability does not limit tree growth at high altitude. Forest expansion has been found to increase soil respiration and cause a net loss of ecosystem carbon in tundra sites (Wilmking *et al.*, 2006; Hartley *et al*., 2012), however, the upslope advance of alpine treelines could lead to increased carbon accumulation (Steltzer, 2004) because alpine soils tend to have much lower levels of carbon (Michaelson *et al*., 1996). The relationship between treeline advance and carbon balance is thus complex, with many interconnected variables and possible feedbacks and future studies that consider both above and below ground processes would be highly valuable.

The upslope migration of forest has implications for the biodiversity of the local area. Several modelling studies predict a large reduction in alpine grassland, with a reduction in alpine species richness as treeline advances (e.g. Halloy and Mark, 2003; Moen *et al*., 2004; Dirnböck *et al*., 2011) and in many areas this can already be observed. In the Urals, alpine grassland and heath has already been reduced by between 10-30% (Moiseev and Shiyatov, 2003) while in Arizona, diversity has been reduced by a decrease in open areas (Moore and Huffman, 2004). However, the increased elevation of closed forest is often much less than that of tree limit and so the impacts on alpine vegetation will be less (Kullman, 2010). This is likely true in the region investigated here where the diffuse treeline form shows most upslope migration and will change conditions in the alpine grassland less than the advance of closed forest. Refugia also exist within the alpine habitat; trees may be unable to establish on cliffs and bare, rocky areas, thus allowing for the persistence of alpine plants (Bruun and Moen, 2003). The topographic influence on advance, found here and in other studies (Kullman and Oberg, 2009; Macias-Fauria and Johnson, 2013) has implications for biodiversity, as many areas will remain free from new forest cover, thus allowing alpine plants to persist in exposed sites that are unsuitable for tree establishment (Danby and Hik, 2007; Kullman and Oberg, 2009).

Given the complexity of response found here, and the large potential impacts of changes in treeline position and forest density, a more integrated understanding of the factors driving spatial and temporal variation in treeline advance in the sub-tropics is required. The influence of topography and microclimate for regeneration beyond the treeline is understudied and this crucial stage in advance merits further investigation. Little is known about the true impacts of forest advance for forest and alpine diversity at treeline; given that advance is a key response to warming climate it is crucial that we gain a better understanding of the possible impacts on alpine diversity in these often highly bio-diverse regions.

Recent changes in treeline position in the Central Mountain Range are highly variable and strongly mediated by topography. Small shifts in elevation have, however, resulted in large increases in forest area and have been accompanied by increased forest density. These changes will have a potentially large impact on carbon stocking at high altitudes and on the biodiversity of the spatially limited and endemic-rich ecosystems above the treeline.

Compared with their temperate and boreal counterparts, tropical and subtropical mountains are typically poorly understood. The work that we present here provides a vital first step toward addressing this inequality by documenting change and detailing the topographical variation that is of crucial importance in modifying the forest response to recent climatic changes. However, more extensive field-based research into changes in ecosystem structure and function is needed if we are to develop a more mechanistic understanding of both how these systems are likely to respond to climate change and of the implications for ecosystem function, biodiversity and dependent human populations.

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Supporting information

Figure S1: Aerial photographs of the Hehuan West peak region.

Figure S2: Aerial photographs of the Hehuan Main Peak region.

Figure S3: Frequency of establishment of new trees at each aspect, elevation and slope in the Hehuan North Peak and West Peak Regions.

Figure S4: The change in tree numbers recorded along transects from forest interior to treeline for each treeline form.

Figure S5: Changes in tree density between 1963 (top) and 2001 (bottom) in subsamples immediately above treeline in the Hehuan North and West Peak Regions.

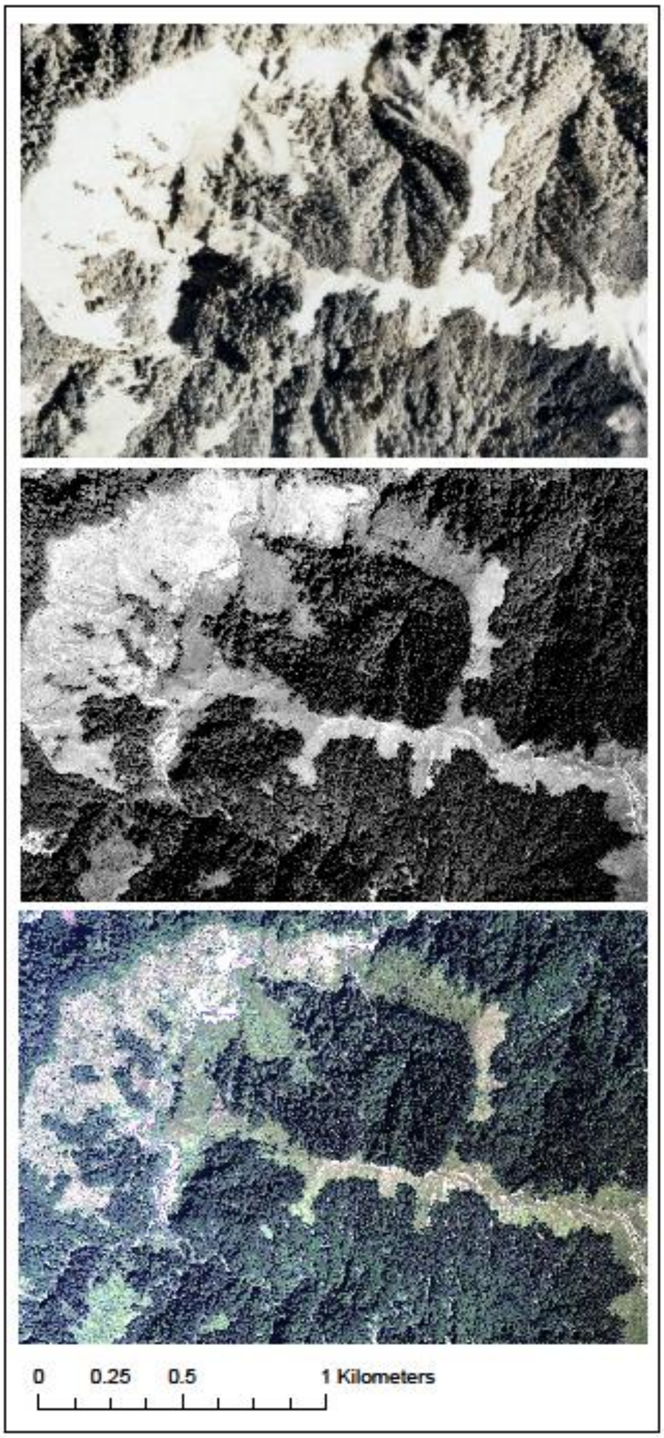


Figure S1**:** Aerial photographs of the Hehuan West Peak region in 1948 (top), 1963 (middle) and 2001(bottom).

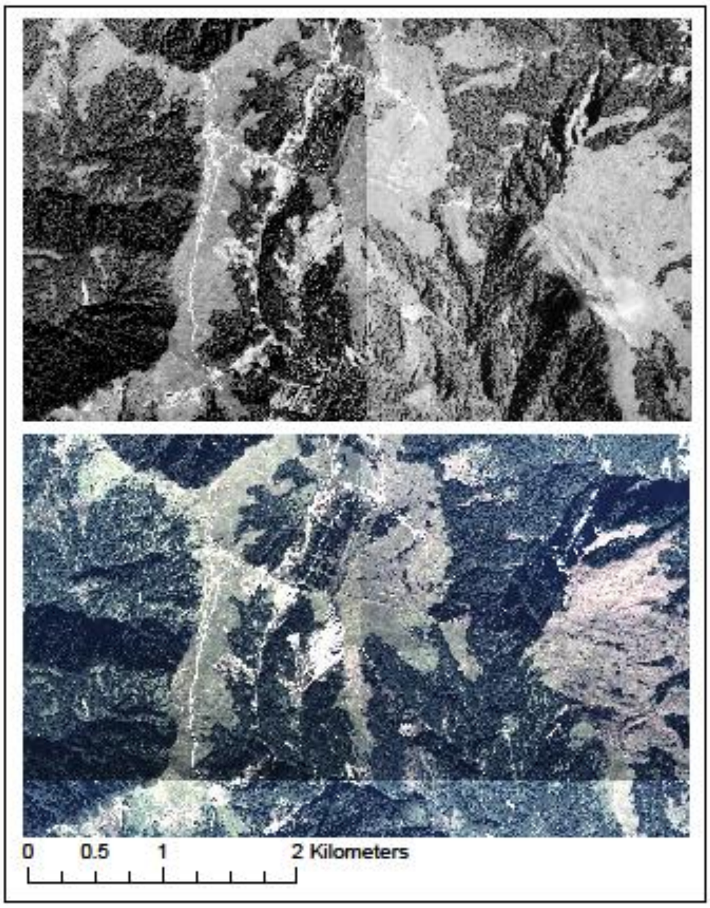


Figure S2: Aerial photographs of the Hehuan Main Peak region in 1975 (top) and 2001 (bottom).

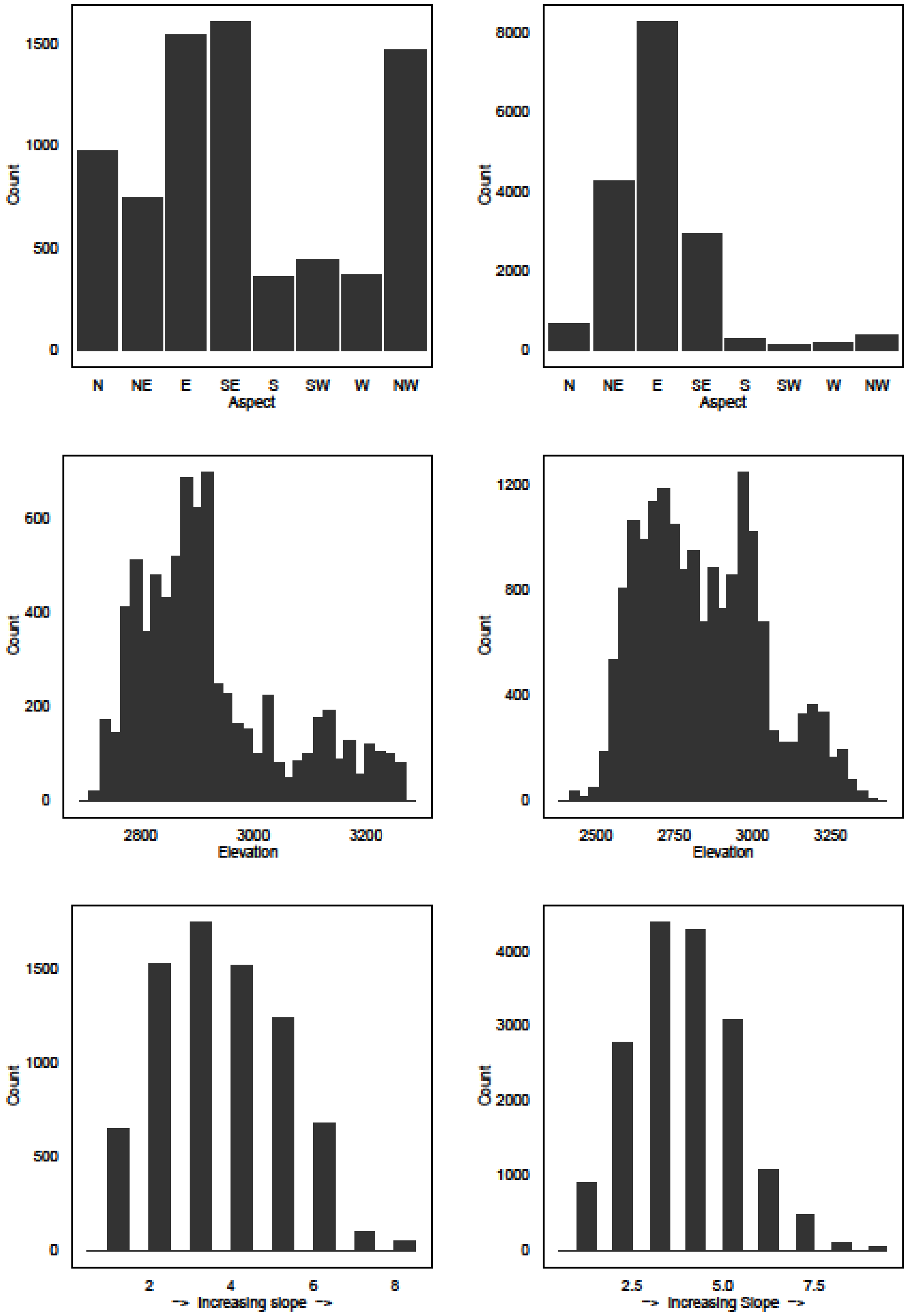
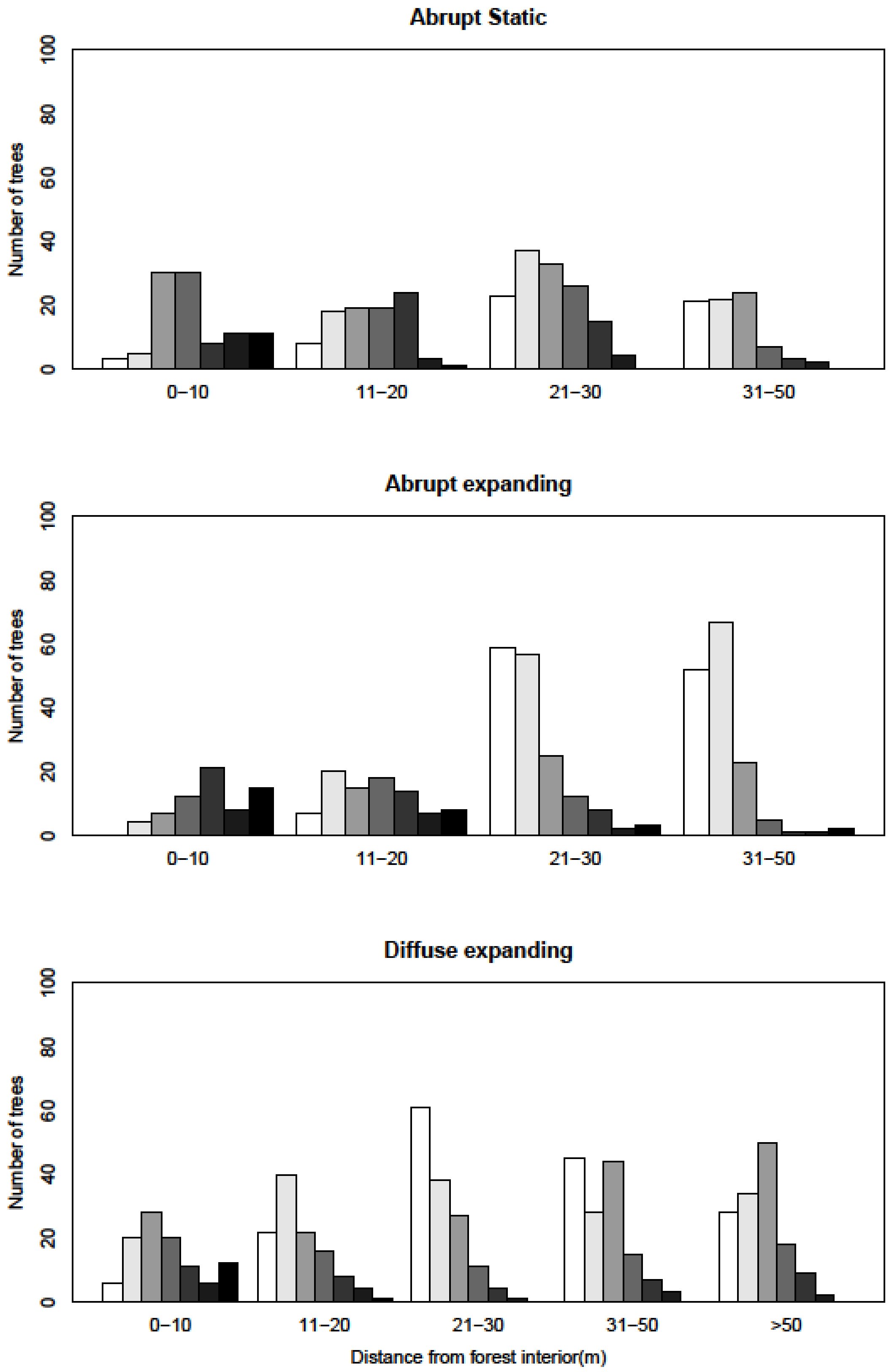


Figure S3: Frequency of establishment of new trees at each aspect, elevation and slope in the Hehuan West Peak (left) and North Peak (right) Regions.



Abrupt Static

Abrupt expanding

Diffuse expanding

Figure S4: The change in tree numbers recorded along transects from forest interior to treeline for three treeline forms in the Central Mountain Range of Taiwan. Transects were 20 m wide by 50-120 m long. Bar colours represent tree size with white through grey to black as follows: <10cm (white), 10-20cm, 21-30cm, 31-40cm, 41-50, 51-60, >60cm (black).

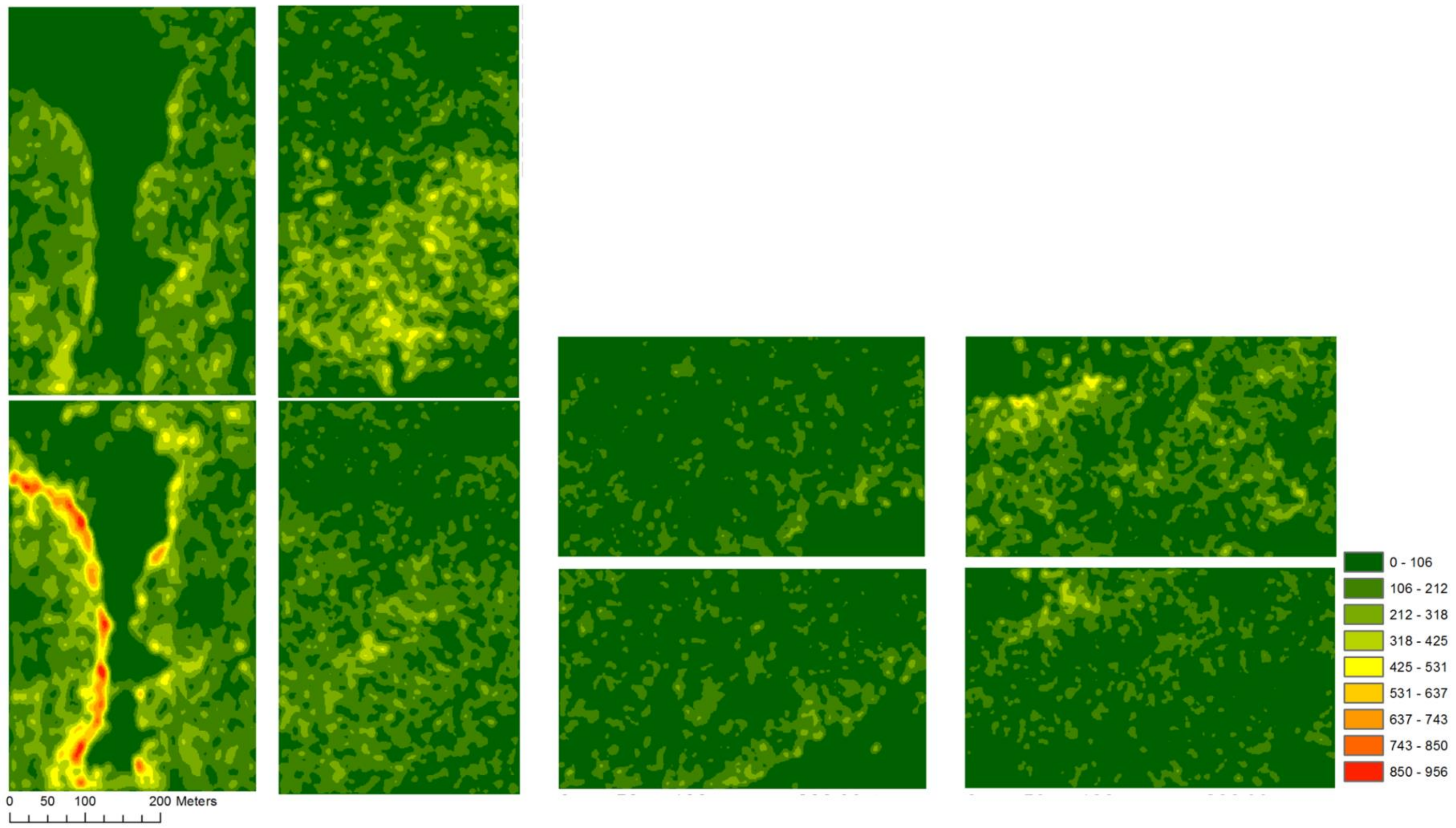


Figure S5: Changes in tree density between 1963/4(top) and 2001(bottom) in four subsamples immediately above treeline in the Hehuanshan West and North Peak Regions. Density values are shown in trees per ha, rounded to the nearest tree.

Chapter 4

Climate growth relationship of *Abies kawakamii*: an investigation over the species altitudinal range on Yushan, Taiwan

Title: Climate growth relationship of *Abies kawakamii*: an investigation over the species altitudinal range on Yushan, Taiwan

Running title: Tree growth and altitude

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Abstract

Tree growth is affected by climate, and individuals occurring at the limit of a species distribution are known to be particularly sensitive to climatic drivers such as temperature at the upper altitudinal limit. Recent climate warming has been found to be leading to changes in growth at the upper altitudinal limit of many tree species. In order to describe the climate growth relationship of *Abies kawakamii* (Taiwan fir) and its spatial and temporal variation we sampled trees throughout the range of this species on Yushan, Taiwan. Some variation in climate response was apparent in populations from different altitudes, as was increased growth in recent years, especially of younger trees in populations from both the upper and lower limit of the species altitudinal range on Yushan. It is important to understand the drivers of change in tree growth so that we are better able to predict forest response to change and its potential feedback to future climate warming.

Introduction

Tree growth is affected by climate and past climate variability is recorded in annual growth rings. Dendrochronological techniques allow tree ring series to be developed and for past climates to be reconstructed from this information (Graumlich *et al*., 1993; Briffa *et al.,* 1995; Villalba *et al*., 1998; Esper *et al*., 2002; Frank and Esper, 2005; Yang et al., 2010). In fact, tree rings are one of the most commonly used climate proxies (Alftine and Malanson, 2004). It is also possible to use these techniques from an ecological perspective and, when climate information is available for an area, to investigate the relationship between climate and tree growth. By sampling populations across the species range and by using long lived individuals it is possible to determine spatial and temporal trends in relation to climate, for example to determine the factors responsible for range limits (Mäkinen *et al*., 2002) or investigate how climate has affected growth over time (Kharuk *et al*., 2009), and how this climate growth relationship varies throughout the range of a species (Mäkinen *et al*., 2001; Piovesan *et al*,. 2005; Jump *et al*., 2007). This information is of value not only for understanding the ecology of tree species, how they respond to their environment and are likely to react to climatic change, but is also necessary to retain the accuracy of climate proxies obtained from tree ring data and to aid predictions of ecosystem and carbon budget response to warming climate.

The factors limiting to tree growth are known to vary throughout the range of a species (Fritts, 1965; Mäkinen *et al*., 2002; Savva *et al*., 2006; Yu *et al*., 2013). Studies of the altitudinal treeline often conclude that temperature is the most limiting factor at the species upper range limit (Tranquillini,1979; Körner, 1998; Jobbágy and Jackson, 2000; Mäkinen *et al.*, 2002, Körner and Paulsen, 2004; Zhang *et al.*, 2010), with precipitation limitations common at lower edges (Mäkinen *et al.*, 2002; Dittmar *et al.*, 2003; Jump *et al.*, 2007; Zhang *et al.*, 2010), although both these climatic factors can be limiting at the upper treeline in very arid sites (Graumlich, 1993; Takahashi *et al.*, 2003; Wang *et al.*, 2004). Since temperature is limiting to growth at the upper treeline it is likely that a response to warming will be evident in trees growing at high altitude sites. A number of authors have discussed increased tree growth in relation to climate change at species upper limits (Briffa *et al*., 1995; Vallee and Payette, 2004; Bunn *et al.*, 2005; Salzer *et al.*, 2009) but there has been a lack of work in subtropical regions, with most work concentrated in temperate regions of the Northern hemisphere.

Increased tree growth could produce a negative feedback to climate warming (Saxe *et al.*, 2001) as more carbon will be sequestered, this is particularly true if forests are also expanding through altitudinal treeline advance and increased forest density, as reported in many studies (Harsch *et al*., 2009). In order for modelling studies to accurately predict changes in climate, whilst accounting for the role forests in global carbon budgets, detailed understanding of tree growth and its relationship with climate is required.

The relationship between tree growth and climate can be temporally variable (Biondi, 2000; D'Arrigo *et al*., 2008; Oberhuber *et al*., 2008; Zhang *et al*., 2010), with for example a weakening of temperature response over time (Jacoby and D'Arrigo, 1995). A high degree of temporal instability in tree growth climate relationships will have consequences for the reconstruction of past climates from tree rings and for the modelling of growth response to climate and its wider consequences for climate feedbacks (D'Arrigo *et al*., 2008), as previously discussed. It is therefore useful for tree ring data to be obtained and studied for a wide range of species over as great a geographical coverage as possible for us to better understand the climatic drivers of tree growth and how they may vary spatially and temporally.

Abies kawakamii or Taiwan fir is a treeline species endemic to the subtropical island of Taiwan. It is the dominant treeline species throughout much of the Central Mountain Range and has an altitudinal range of 2,500-3,800 m (Huang, 2002). At its upper limit it grows in almost pure stands, throughout the lower part of its range it is interspersed mainly with *Tsuga chinensis* and *Pinus taiwanensis*. Evidence from aerial photography suggests that these high altitude forests are responding to climatic changes that have occurred during the last 50 years with range spread and increases in forest density evident (Greenwood *et al*., 2014).

Here we aim to create a dendrochronology for *A. kawakamii* for each of three populations sampled at different altitudes across the range of the species and to use this to: determine the climatic factors important for its growth, to analyse how growth rates of *A. kawakamii* have changed over time in response to climate and to investigate how this response varies throughout the altitudinal range of the species. We test a number of hypotheses, namely that (1) growth rates have increased in recent years in response to climatic warming, (2) the largest change in growth has occurred at highest altitudes where the species is most temperature limited and (3) climatic factors affecting growth vary throughout the range of the species; growth rates will be most tightly correlated with temperature at the highest altitude site.

Ring widths of *A. kawakamii* are expected to decrease near the upper and lower range limits compared to within the forest interior (Fritts, 1965; Makinen *et al*., 2002). At the lower range limit growth is more likely to be related to moisture limitations, at the upper limit to temperature. Growth will be most highly correlated with climatic factors near range limits and will show greatest changes in response to climate in these areas (Makinen *et al*., 2002), with increased growth rates at the upper limits and then eventually reduced sensitivity as climate warms further and temperature is no longer limiting. It is also probable that this increase in growth rate will occur alongside an advance of treeline due to increased regeneration at the species upper limits as these two processes respond in similar ways to climate (Szeicz and MacDonald, 1995; Gervias and MacDonald, 2000; Jump *et al*., 2007).

Study area

Yushan national park is situated in the south east of Taiwan, within the Central Mountain Range and contains 30 of the islands tallest peaks. Of these Yushan, or Mt Jade is the highest, reaching an altitude of 3,952 m a.s.l. The National Park contains a number of vegetation types ranging from subtropical broadleaf forest at the lowest altitudes to *A. kawakamii* dominated coniferous stands, bamboo grasslands and Juniper stands at the highest altitudes. Above treeline on Yushan there is large amount of bare ground and unstable bedrock but krummholz juniper grows beyond treeline in certain areas. Coniferous stands are common at high altitudes in Taiwan, for although the island is in the subtropical zone, at high altitudes the climate becomes temperate to alpine and the cold, humid conditions provide ideal growing conditions for coniferous trees.

Yushan is Taiwan's largest national park, with a total area of 105,000 ha. This area was selected for the present study due to the long altitudinal gradient on which to study undisturbed stands of *Abies kawakamii* (the treeline reaches around 3,600 m (Figure 1)) and because long-term climate data are available from a nearby meteorological station (Table 1). Within the national park there are a large variety of climatic zones: at lower altitudes the climate and vegetation is subtropical but as altitude increases conditions range from temperate to alpine. At 2,500 m annual average temperature is around 10°C, but at 3,500 m it is 5°C. Precipitation and humidity are high in the area: mean humidity is 80% at high altitudes, Mean annual precipitation is around 2,502 mm, with the bulk of rainfall (78%) occurring in the months May to October, during the typhoon season (eng.wra.gov.tw).

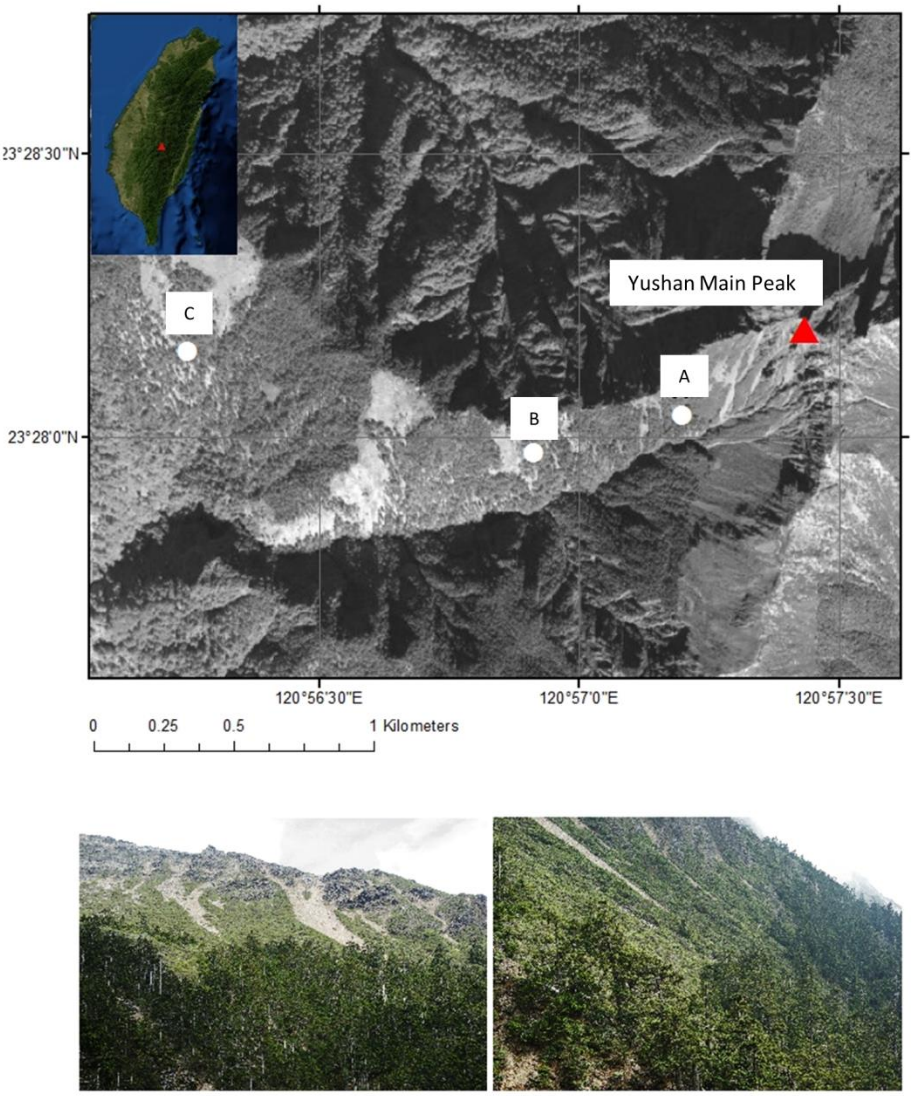

Figure 1: Map of area showing location of Yushan national park in Taiwan (inset on left) and of study sites (A at 3,600 m, B at 3,400 m and C at 3,150 m). The main summit peak of Yushan is shown with a red triangle. Images of the upper altitudinal limit of *Abies kawakamii* on Yushan are shown below the map.

Materials and methods

The study was conducted across the altitudinal range of *A. kawakamii* on Yushan main peak, with 3 study populations sampled at altitudes of approximately: 3,150 (site C), 3,400 (site B) and 3,600 m a.s.l (site A) (Figure 1).

Tree core data

Two cores per tree were taken at a height of 1.3 m from 30 healthy, canopy dominant trees in each study area. Cores were taken perpendicular to the prevailing slope direction. In addition diameter at breast height (DBH) was recorded for each cored tree. Cores were air dried at room temperature for several weeks, stored in paper straws and then returned to the University of Stirling where they were prepared for analysis using standard dendrochronological techniques. Cores were mounted on wooden mounts and then sanded with increasingly finer grits of sandpaper until a fine polish was achieved and individual cells were apparent under the microscope. Cores were then scanned using a flatbed scanner; jpeg images were used to count and measure the rings with the program Coorecorder (cybis.se). Cores were visually cross dated using Cdendro (cybis.se) and cross dating was checked with COFECHA (Grissino-Mayer, 2001). Cores were initially paired by tree and mean values created to produce one ring width file per tree. Where the two cores from one tree did not correlate, these cores were left as individuals and later checked against a mean value sample of all paired cores that showed high agreement (R^2 >0.5). Any cores with poor agreement that were difficult to cross date were not included in the site chronologies and cores identified as being a poor match by COFECHA were removed. The final numbers of cores/trees included in the final site chronologies can be seen in Table 2.

Statistical analyses

Ring width series were standardised and detrended in order to remove the age related growth trend and to amplify the low frequency climatic signal. The detrending methods used were a negative exponential and a cubic smoothing spline; these were applied using the dplR library (Bunn et al., 2012) in R studio (R Core Team, 2014). Final chronologies for each site were then built and tested for correlation with climate data (Table 1). Correlation and response function analyses were run for ring width indices against a number of climate variables (see Table 1 for climate variables). Moving window analyses were then used to check for temporal stability in the correlations with climate data. Bootstrapped response function, correlation and moving window analyses were run using the BootRes package in R (Zang and Biondi, 2013). Correlation analyses use Pearson estimates and significance of both response function and correlation analyses are calculated based on 1,000 random samples; significance at the $p=0.05$ level is when absolute values exceed half the difference between the 97.5th quantile and the 2.5th quantile (Biondi and Waikul, 2004).

Response function and correlation analyses were run for the following mean monthly data: mean minimum temperature, mean maximum temperature, mean temperature, total precipitation and precipitation duration; monthly data from the current and previous year are used. This is standard procedure in dendroecological research, because previous years conditions are known to affect current year tree growth (Oberhuber et al., 2008 and references within). I ran the response function and correlation analyses from previous year June through to current year September.

Climate data

Climate data are available for the Yushan area from 1952 to present. A climate station is situated at 3,858 m on the north Peak of Yushan. This climate station is one of the key stations within Taiwan (Table 1). Temperature and precipitation were analysed for trends over time using mean annual temperature values and total annual precipitation values.

Table 1: Information on the climate data available from Yushan North Peak climate station.

Distance from study site (km)	**Altitude (m a.s.l.)**	**Location lat/lon**	**Period covered**	**Climate variables recorded**	**Mean value**	**Percentage of missing data**
c. 5 km	3,858	23° 29′ 21″ N 120° 57′ 06″ E	1952-2009	Mean air temp	4.0	2.8 % (data are missing from Jan 1967- Aug 1968 for all climate variables
				Mean min air temp	0.6	
				Mean max air temp	9.1	
				Precipitation (mm/month)	256.7	
				Precipitation duration (hrs/month)	104.5	

Results

Climate

Mean annual temperature has increased over the period 1952-2009 (Figure 2); a linear regression analysis gave an R^2 value of 0.1 and a p value of 0.06 (close to significance). However when the analysis was run for only post-1970 temperature data, a significant change was detected ($R^2 = 0.3$, $p < 0.001$). For total annual precipitation linear regression analyses gave non-significant p values.

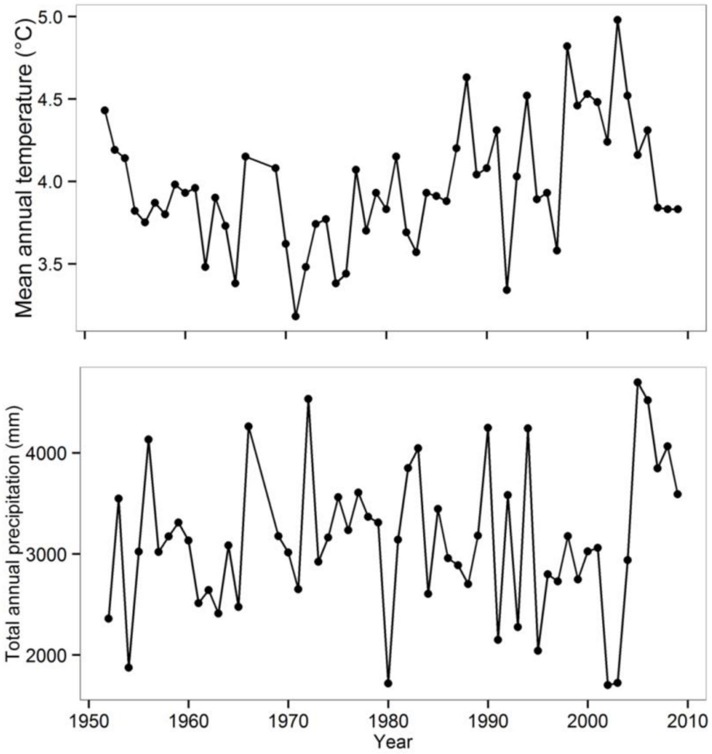

Figure 2: Mean annual temperature (top) and total annual precipitation (below) on Yushan from 1952-2009.

Chronology summary statistics

Two chronologies were successfully built from the tree core samples (Figures 3, 4, Table 2); one at the highest (A) and one at the lowest (C) sampling elevation. The mid-range elevation cores did not cross-date to a degree that made chronology building possible. For the highest elevation site (A) the quality of the full chronology was fairly poor; an EPS (expressed population signal, an accepted statistic to describe the quality/strength of a chronology) value above the threshold of 0.85 suggested by Wigley (1984) was only obtained when the chronology was cut to 1900 and after. However the chronology post 1952, on which the response function analyses with climate data were run yielded an acceptable EPS value of 0.88. The rbar (mean inter series correlation value) is also low for the highest elevation site (A). The lowest elevation site (C) produced a better quality chronology with an acceptable EPS for all time ranges and a higher mean inter series correlation (Table 2).

Table 2: Chronology sampling information and statistics. Rbar (mean inter series correlation) and EPS (expressed population signal, a measure of chronology strength) values are shown for the full chronologies (top row for each site) and for shortened chronologies to post 1952 (the date from which climate data is available).

Chronology	**Sampling Lat/Lon**	**Sampling altitude (m a.s.l)**	**No. cores/trees**	**rbar**	**EPS**
A	N 23° 28′ 04″	3,557-	40/23	0.26	0.77
	E 120° 57′ 13″	3,663		0.24	0.88
C	N 23° 28′ 07″	3,145-	40/23	0.44	0.91
	E 120° 56′ 12″	3,197		0.43	0.92

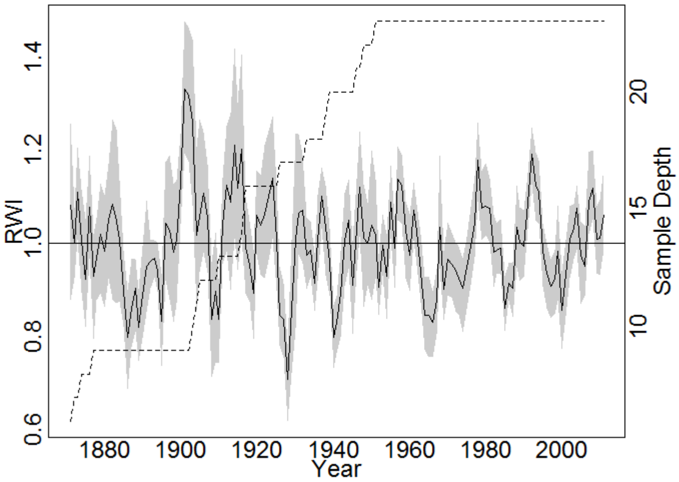

Figure 3: Chronology produced from detrended ring widths of *Abies kawakamii* tree cores for the highest elevation site ((A) 3600 m) on Yushan, Taiwan. The dotted line shows the sample depth over time and the grey shading indicates the 99% confidence interval. RWI= Ring width index (mean standardised ring width)

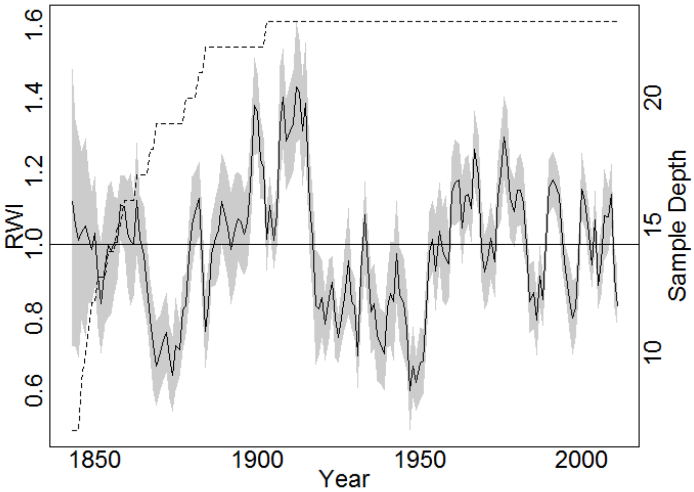

Figure 4: Chronology produced from detrended ring widths of *Abies kawakamii* tree cores for the lowest elevation site ((C) 3150 m) on Yushan, Taiwan. The dotted line shows the sample depth over time and the grey shading indicates the 99% confidence interval. RWI= Ring width index (mean standardised ring width)

Response of tree growth to temperature and precipitation

Correlation and response function analyses (Figures 5 and 6) show significant coefficient values with the same climate predictors, with a small difference in the magnitude of response. Responses were generally stronger in the lower altitude site. Ring widths at the highest altitude site have a significant ($P<0.05$) positive response to previous July mean temperature (CoefC = 0.42, CoefR = 0.21), previous September minimum temperatures (CoefC = 0.39, CoefR = 0.26) and current February minimum temperatures (CoefC = 0.14, CoefR = 0.25) and a negative response to current year January precipitation (CoefC = -0.32, CoefR = -0.20) (Figure 5). At the lowest elevation site significant positive responses were found to precipitation duration of the current May (CoefC = 0.30, CoefR = 0.24) and maximum temperature of previous (CoefC = 0.45, CoefR = 0.33) and current June (CoefC = 0.44, CoefR = 0.26) (Figure 6).

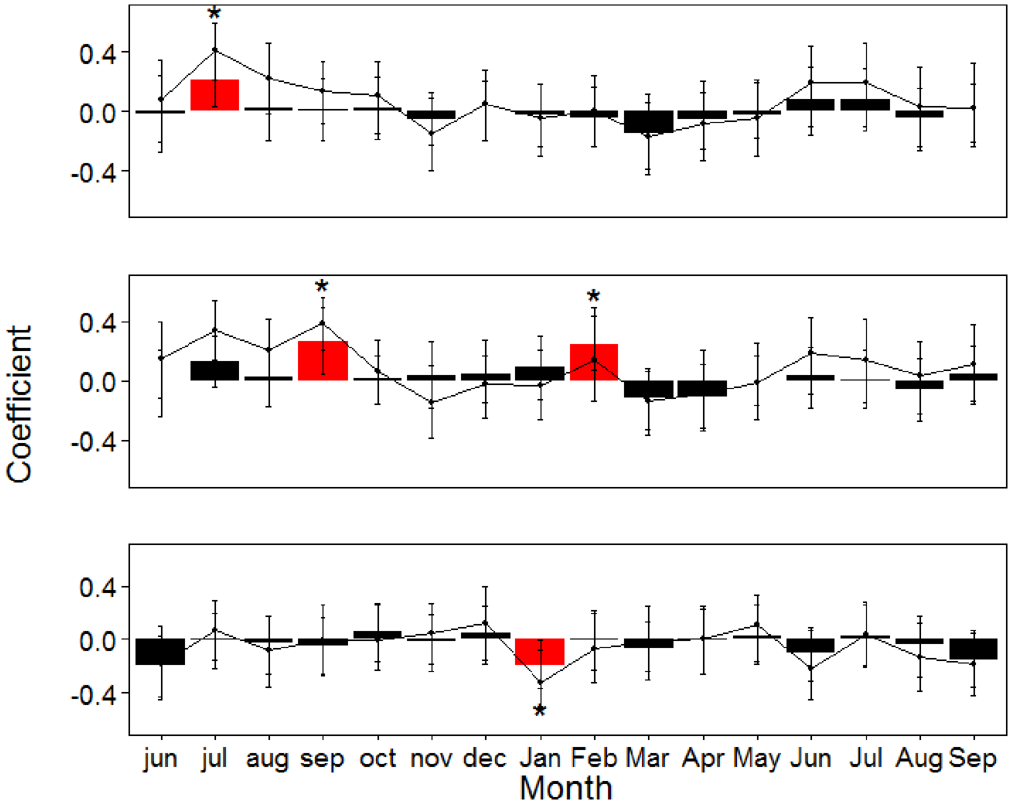

Figure 5: Response functions (bars) and correlations (points) of *Abies kawakamii* chronologies and monthly climate variables (Mean temperature (top), mean minimum temperature (mid) and total precipitation (bottom)) for the highest elevation sampling site on Yushan, Taiwan (3600 m a.s.l.). Lower case letters indicate previous year responses and upper case current year. Red bars indicate significant response functions ($P<0.05$) and the error bars represent 95% quantiles determined by 1000 bootstrapped samples. Significant correlations are shown by an asterisk above/below the data.

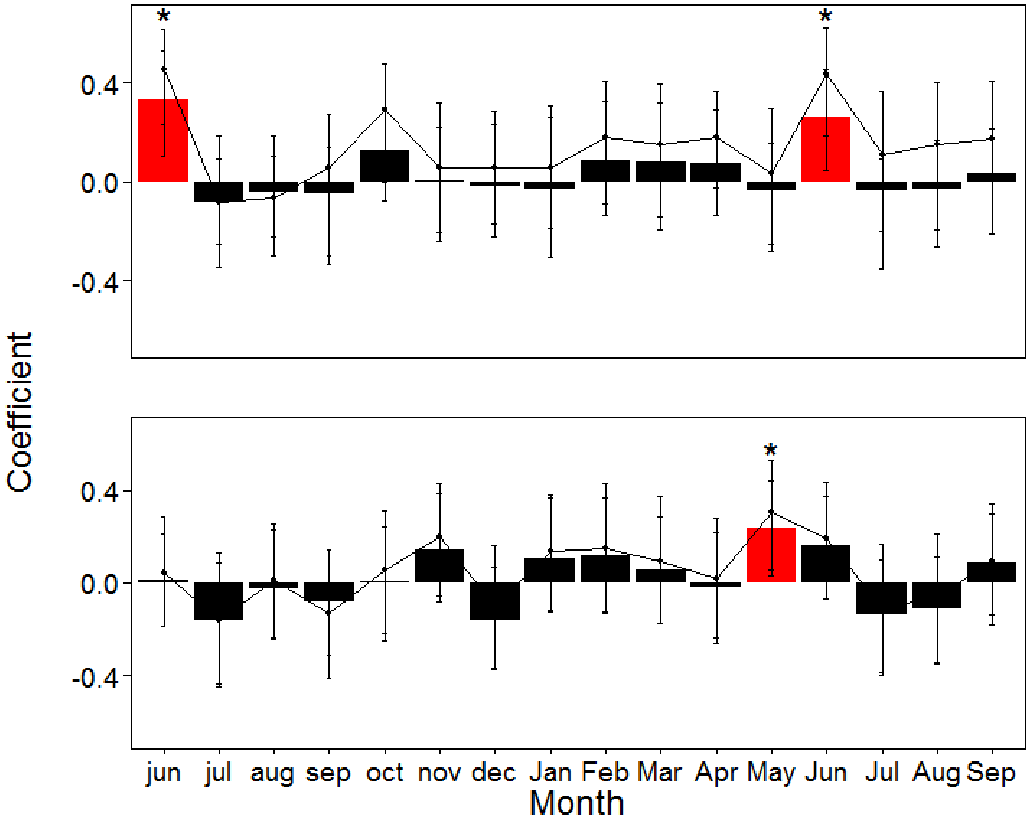

Figure 6: Response functions (bars) and correlations (points) of *Abies kawakamii* chronologies and monthly climate variables (Mean maximum temperature (top) and precipitation duration (bottom)) for the lowest elevation sampling site on Yushan, Taiwan (3150 m a.s.l). Lower case letters indicate previous year responses and upper case current year. Red bars indicate significant response functions (P<0.05) and the error bars represent 95% quantiles for the response function coefficients, determined by 1000 bootstrapped samples. Significant correlations are shown by an asterisk above the data.

Changes in tree growth

Tree growth has increased in recent years in both sites, especially for younger trees (Figure 7). Tree growth is much higher at the lowest elevation site, but the pattern of increased growth of younger trees post 1952 is similar at both sites.

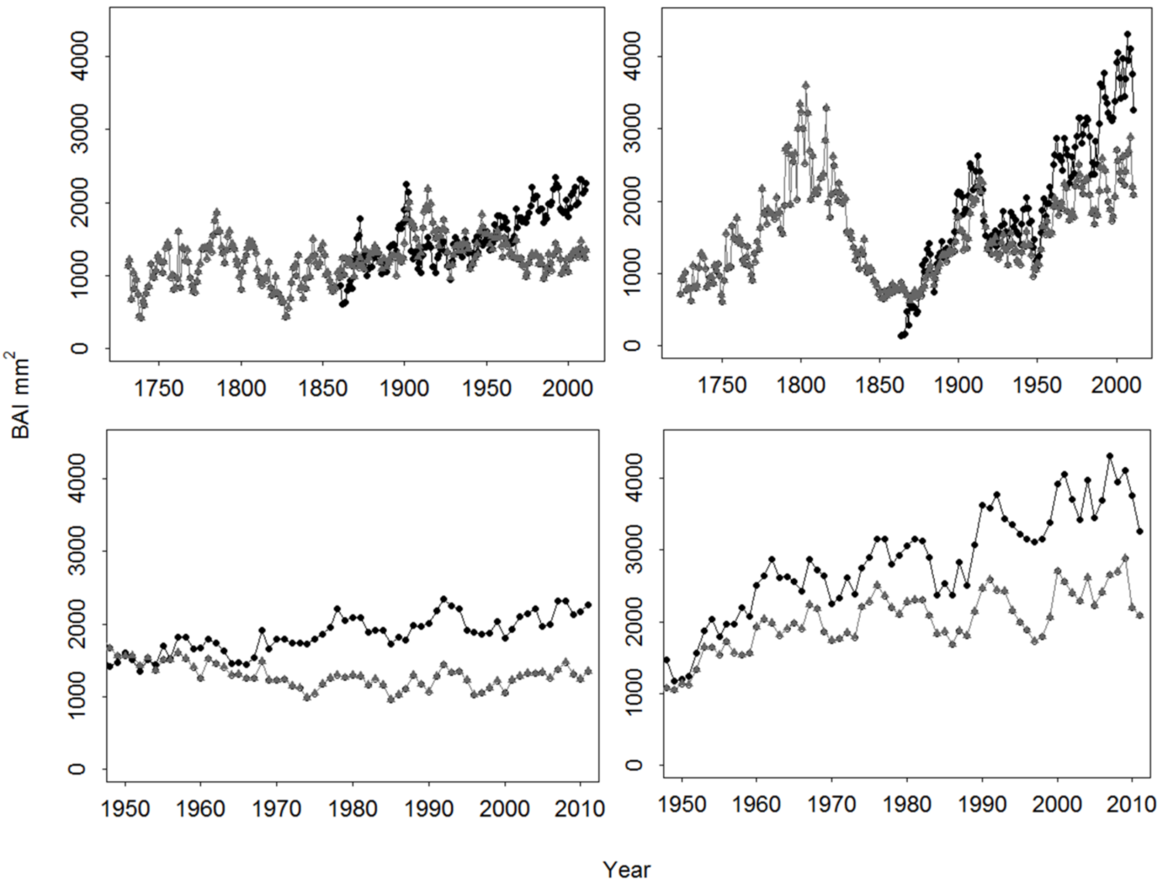

Figure 7: Basal area increment (BAI) of *Abies kawakamii* at site A at 3600 m (left hand images) and Site C at 3150 m (right hand images) on Yushan, Taiwan. Trees less than 150 years are indicated by black circles, those more than 150 years by grey triangles. The upper plots show BAI for the whole length of each of the chronologies, the lower plots are cut to post 1950 to be relevant to climate data availability and to highlight recent changes in growth.

Temporal stability of climate relationships

The response of growth to climate at the highest elevation site seems to have remained stable over the period 1952-2010; moving window correlation analyses show little change in the strength and direction of correlations over time. In contrast, at the lowest elevation site the relationship between climate and tree growth has changed over time for a number of climate variables (Supporting information, Table S1). The response of growth to current January, July, August and September air temperature has changed from positive to negative over time as has the response to precipitation of current

March. For these the only one that has significant values for the correlations is September air temperature. This and other significant correlations that have also reduced over time are shown in Figures 8 (temperature) and 9 (precipitation).

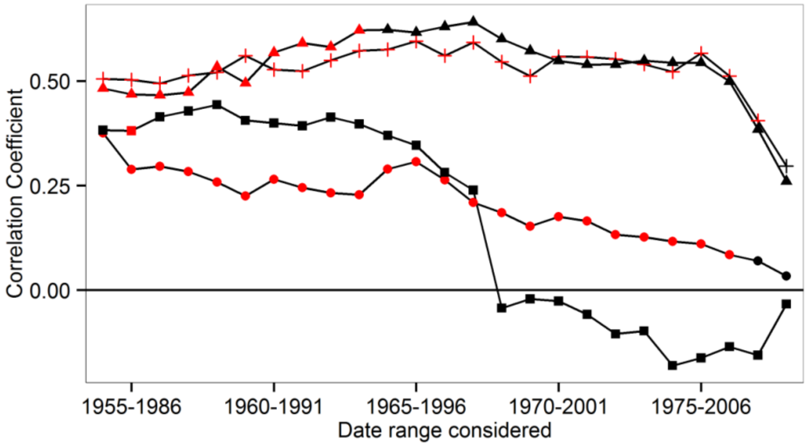

Figure 8: Temporal stability of the climate growth relationship for *Abies kawakamii* at 3,150 m on Yushan for monthly temperature variables: mean maximum air temperature of current April (circle), current June (triangle), current September (square) and previous June (cross). Significant correlations are indicted with red points.

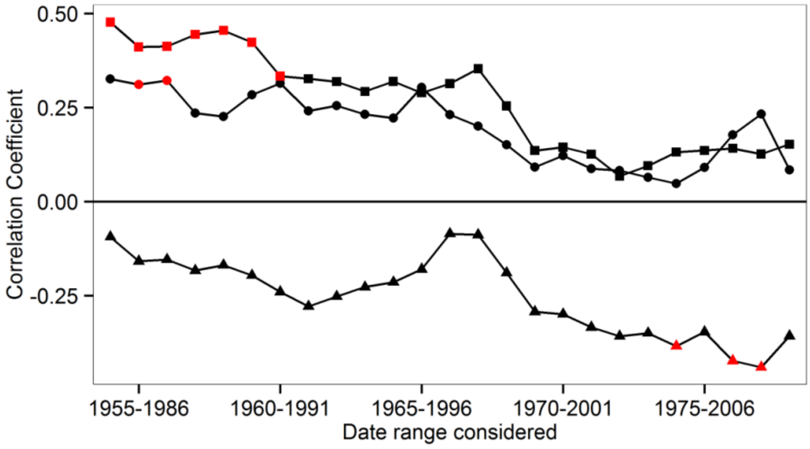

Figure 9: The temporal stability of the climate growth relationship for *Abies kawakamii* at 3,150 m on Yushan for precipitation variables: precipitation duration of current January (circle), July (triangle) and May (square). Significant correlations are indicted with red points.

Discussion

Our tree core samples did not produce a particularly high quality chronology for the highest elevation site on Yushan, although for the lowest elevation site the chronology quality was higher, and over the threshold EPS value throughout the whole of its time span (Table 2). The lower quality chronology produced for Site A suggests a poorer common climatic signal, as does the weak response to temperature which we would expect to be strong at the species altitudinal limit (Tranquillini,1979; Körner, 1998; Jobbágy and Jackson, 2000; Mäkinen *et al.*, 2002, Körner and Paulsen, 2004). This could be due to problems with sampling such as the collection of younger individuals with a weaker climate signal (studies suggest that trees > 200 years have a stronger climatic signal (Carrer and Urbinati, 2004; Szeicz and MacDonald, 1994)). Cores could also have been collected over too wide a geographical area. However, trees were selected from a range of ages in both populations (age span of upper site: 60- 280, of lower site: 108-288), although the mean estimated tree age was higher for the lower altitudinal site (118 (A) vs 162 (C)), and this could have led to the weaker common climatic signal in site A. The geographic area over which the samples were collected was also the same although complex topography; a particular feature of the treeline sampling site could lead to variations in microsite that could create long term variation in the long term signal between trees, thus weakening climate signals (Wilmking *et al*., 2005; Driscoll *et al.*, 2005).

We found some evidence for differences in climate sensitivity dependent on altitude in *A. kawakamii*; although both the upper and lower populations show some correlations with both precipitation and temperature variables (Figures 5 and 6), the nature of the relationship between growth and precipitation/temperature varies between the populations. At the upper altitudinal site there was more evidence of a positive relationship with temperature; tree growth increased with mean and minimum temperatures, although growth at the lower site also responded positively to maximum temperate of previous and current June. There was a difference in the response to precipitation depending on altitude; at the upper altitudinal site tree growth displayed a negative response to winter (January) precipitation, whereas in the lower site there was a positive response to spring (May) precipitation duration. The negative response to January precipitation could be due to deleterious effects of snowfall on the start of the growing season. The timing of snow melt is known the affect growing season (Sutinen *et al.*, 2009) and Vaganov *et al.* (1999) show that increased winter precipitation reduces tree growth and the response of tree growth to increased growing season temperatures in Siberian treelines. Precipitation is generally low in the winter on Yushan, but as average temperatures are below 0 °C (cwb.gov.tw) precipitation is likely to fall as snow and may lie for some time period. Research in the Western US has found that lower levels of snowfall/earlier snowmelt lead to reduced growth rates later that year because of reduced water availability during summer months (Hu *et al.*, 2010), however, this would depend on water being limiting during the summer, which is unlikely in the subtropical climate on Yushan where typhoon rains affect even the high altitude areas. However the positive response of growth to current May precipitation in the lower altitude population could indicate some level of water limitation. Other recent work has found a strong effect of altitude on climate response (Yu *et al.,* 2013). *Fagus sylvatica*, for example has been found to have a positive response to increased temperature at its upper range limits, but a negative response at its lower limits, with precipitation limiting growth at lower altitude sites but being of little importance at higher altitude (Jump *et al.,* 2007). A similar variation in response with altitude has been found in north east China for *Pinus koraiensis* (Yu *et al*., 2013) and in the Alps for *Larix decidua* and *Picea abies* (King *et al.,* 2013).

Lower growth rates of trees at higher altitude sites are also commonly reported (Liang *et al*., 2010), as is increased growth in response to warming climate (Kharuk *et al.,* 2009; Salzer *et al*., 2009). Recent increases in growth are usually associated with only the upper limits of a species distribution (Salzer *et al.*, 2009); in the case of *A. kawakamii* on Yushan, we found increased growth of trees in both upper and lower populations (Figure 7). We also found that younger trees (<150 yrs) had a stronger response than older trees (>150 yrs), this is in contrast to the results of Carrer and Urbinati (2004), who found that older individuals of *Larix decidua* and *Pinus cembra* were more sensitive to climate.

The weak correlation and response function results in the upper population could be explained partly by the poor substrate conditions occurring at and beyond treeline. The slopes on Yushan are extremely steep and the bedrock is unstable, with poor soil formation (see images of upper treeline in Figure 1). Perhaps rather than being limited by climate at its upper limit on Yushan the treeline is driven, at least partly, by substrate conditions. Other authors have found a local limitation of treeline by substrate, exposure and slope (Butler *et al*., 2003; Danby and Hik, 2007; Macias-Fauria and Johnson, 2013), and topography has been found to be influencing treeline position in other areas of the Central Mountain Range of Taiwan (Greenwood *et al*., 2014). In the Hehuanshan Range of Taiwan, bamboo occurs above the treeline in most areas, rather than the krummholz juniper and bare ground as found commonly on Yushan. It is possible that further dendroecological work in the Hehuanhsan area could yield different results and perhaps a stronger common climatic signal. However work in here would be limited by a shorter and less reliable climate data series. Issues with the climate data could also be limiting the climate response results; Wilson and Luckman (2003) note that if mean values are used in areas with a large difference between day and night time temperatures this could lead to poor correlations because trees are likely to be most limited by day time temperatures.

The climate growth response is stable over time in the upper altitudinal population but there is some temporal instability at the lower altitudinal site (Figures 8, 9, Table S1). Figures 8 and 9 show the change in correlations between growth and climate over time for several temperature and precipitation variables that were significant at some point over the investigation period. The trend is one of decreased correlation with temperature and precipitation. Other studies have found evidence of temporal changes in the climate response of growth (Briffa *et al*., 1995; Biondi, 2000; D'Arrigo *et al*., 2008). However it is important to remember, as noted by Zang and Biondi (2013) that some the changes in growth-climate relationships could be due to inconsistencies in the climate data; data quality is likely to improve over time and this could affect results.

Few studies of tree growth response to climate exist for tropical and subtropical areas; although the climate on Yushan is temperate-alpine at the highest elevations some of the climate-growth response could be driven by the influence of subtropical weather. Precipitation is high throughout the spring and summer, which could explain why the lower limit shows only a little evidence of a positive correlation with precipitation.

Conclusion

We have created chronologies for two sites at the upper and lower limit of *A. kawakamii* distribution on Yushan, Taiwan. We have found evidence of increased growth in recent years, especially among younger trees, although this occurred in both the upper and lower populations. This increased growth has implications for carbon sequestration and could provide a negative feedback to climate warming. Some variation in climate response was discovered, although both upper and lower populations responded to both temperature and precipitation variables. The upper population shows stable responses over time whereas the lower population shows weakening responses. Problems with chronology quality, and with cross dating of the mid-elevation samples have led to limited data availability for this analysis and make future dendroecological work in this area necessary to fully disentangle the climate growth response of *A. kawakamii* and how it varies throughout its range.

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Supporting Information

Table S1: Correlation coefficients from a moving window correlation analysis of tree ring and climate data for the lowest elevation Site (C) on Yushan Taiwan. Significant correlations at a 0.05 significance level are shown (indicated with*).

Date range	**Max air prev Jun**	**Max air prev Oct**	**Max air prev Nov**	**Max air prev Dec**	**Max air curr Feb**	**Max air curr Apr**	**Max air curr Jun**	**Max air curr Sep**	**Prec duration curr Jan**	**Prec duration curr May**	**Prec duration curr Jul**
1954-1985	0.50*	0.40*	0.11	0.11	0.36*	0.40*	0.48*	0.38	0.33	0.48*	-0.09
1955-1986	0.50*	0.37*	0.05	0.13	0.43*	0.29*	0.47*	0.38*	0.31*	0.41*	-0.16
1956-1987	0.49*	0.36*	0.03	0.12	0.42*	0.30*	0.47*	0.41	0.32*	0.41*	-0.15
1957-1988	0.51*	0.36*	0.10	0.18	0.35	0.28*	0.47*	0.43	0.24	0.44*	-0.18
1958-1989	0.52*	0.35	0.11	0.15	0.33	0.26*	0.53*	0.44	0.23	0.45*	-0.17
1959-1990	0.56*	0.34*	0.10	0.16	0.33	0.22*	0.50*	0.41	0.28	0.42*	-0.20
1960-1991	0.53*	0.31	0.033	0.11	0.26	0.26*	0.57*	0.40	0.31	0.33*	-0.24
1961-1992	0.52*	0.29	0.07	0.08	0.20	0.24*	0.59*	0.39	0.24	0.33	-0.28
1962-1993	0.55*	0.30	0.04	0.11	0.20	0.23*	0.58*	0.41	0.25	0.32	-0.25
1963-1994	0.57*	0.31	0.07	0.08	0.20	0.23*	0.62*	0.40	0.23	0.29	-0.23
1964- 1995	0.58*	0.31	0.12	0.04	0.22	0.29*	0.62*	0.40	0.22	0.32	-0.21

1965-1996	0.59*	0.30	0.05	0.05	0.17	0.31*	0.62	0.35	0.30	0.29	-0.18
1966-1997	0.56*	0.31	0.08	0.14	0.16	0.26*	0.63	0.28	0.23	0.31	-0.06
1967-1998	0.59*	0.33	0.06	0.14	0.18	0.21*	0.64	0.24	0.20	0.36	-0.09
1968-1999	0.55*	0.36	0.13	0.09	0.07	0.18*	0.60	-0.04	0.15	0.25	-0.20
1969-2000	0.51*	0.26	0.05	0.01	0.02	0.15*	0.57	-0.02	0.09	0.14	-0.29
1970-2001	0.56*	0.27	0.03	0.04	0.06	0.18*	0.55	-0.03	0.12	0.14	-0.30
1971-2002	0.56*	0.26	0.03	0.05	0.08	0.17*	0.54	-0.06	0.09	0.13	-0.33
1972-2003	0.55*	0.27	0.01	0.07	0.02	0.13*	0.54	-0.11	0.08	0.07	-0.36
1973-2004	0.54*	0.27	-0.01	0.02	0.04	0.13*	0.55	-0.01	0.06	0.09	-0.35
1974-2005	0.52*	0.25	0.05	-0.01	0.04	0.12*	0.54	-0.18	0.05	0.13	-0.38*
1975-2006	0.57*	0.28	0.09	0.01	0.00	0.11*	0.54	-0.16	0.09	0.14	-0.35
1976-2007	0.51*	0.19	0.06	-0.02	0.06	0.08*	0.50	-0.14	0.18	0.14	-0.42*
1977- 2008	0.41*	0.28	-0.01	0.02	0.03	0.07	0.38	-0.16	0.23	0.13	-0.44*
1978-2009	0.30	0.09	-0.02	-0.02	0.04	0.03	0.26	-0.03	0.08	0.15	-0.36

Chapter 5

Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline

Title: Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline

Running title: Temperature, sheltering and establishment

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Key words: *Abies kawakamii*, alpine forest, microclimates, micro-topography, regeneration, subtropics, Taiwan, treeline advance

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Research paper

Title: Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline

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Questions: An advance of high-altitude treelines has been reported in response to warming climate throughout the globe. Understanding local controls on the establishment of seedlings above the treeline is essential for predicting wider patterns of treeline response from a process-based perspective. Here we investigate patterns of seedling establishment in relation to microsite conditions in an advancing treeline ecotone in the subtropics using climate data recorded at the plant-relevant scale. We sought to determine which temperature factors were of importance, what the effect of sheltering was on establishment and if the response varied with seedling age.

Location: The *Abies kawakamii* treelines of the Central Mountain Range of Taiwan at elevations ranging from 2,800 to 3,275 m a.s.l.

Methods: Seedlings were monitored in plots covering a range of treeline structural forms over a period of two years. Temperatures were recorded at plant-relevant height (5 cm) above ground and depth below ground with data loggers. Micro-topographic sheltering (at a 10 m scale) and surrounding vegetation were measured. The influence of the above variables on seedling numbers and growth was investigated using generalized linear models and linear mixed effect models respectively.

Results: Soil temperatures had more influence on seedling numbers than air temperatures, whilst air temperatures were positively associated with subsequent seedling growth. Establishment patterns were found to have a strong relationship with micro-topographic sheltering, with more sheltered areas having elevated seedling numbers. Early growth rate has significant implications for subsequent plant performance since smaller seedlings were more sensitive to both temperature and micro-topography than larger seedlings.

Conclusions: Air and soil temperatures and micro-topography determine spatial patterns of seedling establishment. Our results suggest that establishment above the treeline is likely to continue as the climate warms, although advance will not be spatially uniform due to the modifying influence of topography. This variability has important implications for the persistence and extinction of alpine plant communities occurring above treeline in topographically complex systems.

Key words: *Abies kawakamii*, alpine forest, microclimates, micro-topography, regeneration, subtropics, Taiwan, treeline advance

Nomenclature: (Hayata) Tak. Itô

Running head: Temperature, sheltering and establishment

Introduction

Mountain treelines are increasing in elevation in many areas across the globe in response to ongoing climatic warming (Harsch et al. 2009). Such changes in species distribution are driven by changes in plant recruitment, yet studies of treeline advance typically focus on adult trees (Smith et al. 2009). Conditions experienced by seedlings are different from those experienced by larger individuals so establishment will respond to climatic changes differently from the growth of older trees. Consequently, it is important to understand the conditions necessary for successful establishment of young seedlings at the treeline if we are to better predict spatial and temporal responses of treelines to changing environmental conditions (Germino et al. 2002; Smith et al. 2003; and Smith et al. 2009).

Microclimate conditions across the treeline ecotone are very different from conditions below the canopy of a developed forest. For expansion to occur, seedlings must either be able to tolerate the conditions beyond treeline or exploit micro-topographical features that provide a microclimate more favourable for growth. The presence of rocks, boulders, or surrounding vegetation can improve conditions for seedlings (Smith et al. 2003; Resler et al. 2005; Resler 2006) by reducing exposure to excess light and day time temperature, increasing night-time temperatures and providing shelter from high winds. Significantly more conifer establishment has been found to occur above the treeline at sites where some form of shelter is provided (Resler et al. 2005). Facilitation by surrounding vegetation is also noted in many alpine areas (Choler et al. 2001; Germino et al. 2002; Batlorri et al. 2009), although the importance of facilitation will vary depending on the species involved, the degree of cover and the harshness of the environmental conditions (Callaway et al. 2002; Bansal et al. 2011). Similarly, topography and the effects of landscape features on the degree of exposure experienced by seedlings could potentially affect establishment patterns (Huang 2002; Kharuk et al. 2010).

For very small seedlings, temperature is likely to be more important than wind exposure because seedlings of low stature have not yet broken through the ground level boundary layer. The reduction in wind speed provided by this layer, although providing a benefit in terms of reduced abrasion and wind damage can pose a threat by preventing convection and causing temperatures to become much lower at night and higher during the day than ambient air (Germino et al. 2002), thus leading to photoinhibition in conditions of low temperature and high light (Germino and Smith 1999) and damage to photosynthetic machinery at high temperature. Germino and Smith (2001) found that surrounding vegetation could increase seedling survival by reducing the amount of sky exposure and mediating temperature changes between night and day. Soil temperatures are also important for seedling growth, but tend to have a different relationship with vegetation cover to that of air temperatures. Many studies document increased soil temperatures at high altitudes beyond the canopy cover of forest (Holtmeier and Broll 1992; Wieser et al. 2010), this could be a mechanism by which treeline is able to advance beyond forest limits by encouraging establishment beyond the canopy. Wind speed is likely to become critical at the point when saplings break through the boundary layer; the presence of dwarfed or krummholz individuals at many treelines throughout the world is evidence of the negative impacts of exposure to wind and associated ice abrasion. High wind speeds can cause physical damage and desiccation and will depend on both macro and micro-topographic features that can act to reduce wind speeds and provide shelter or cause increased turbulence (Resler 2006).

The importance of temperature in determining treeline position on a wide scale has been investigated by many authors (Tranquillini 1979; Körner 1998, 2003; Jobbagy and Jackson 2000) and it is generally agreed that temperature plays a primary role in treeline position, although the details of this relationship vary between sites. The mechanisms by which temperature controls treeline position are widely discussed; some studies provide evidence for temperature limitations on photosynthesis (Bansal and Germino 2008; Wieser et al. 2010) or for the prevention of the utilisation of photosynthetic products for growth (Körner 1998; Hoch and Körner 2003).

For many years treeline position was considered to be controlled by the 10 ° C isotherm of the warmest month but this has been found to have little predictive power on a global/regional scale (Körner 1998). Körner and Paulsen (2004) found the position of treelines on a global scale to be related to soil temperatures, with treelines occurring at growing season mean soil temperatures of between 5.4 and 7.8 ° C. Low soil temperatures could inhibit root growth and prevent utilisation of the products of photosynthesis (Körner 2003) or reduce root activity, lowering water potential and stomatal uptake of CO_2 thus lowering net photosynthesis (Day et al. 1991; Wieser et al. 2010). Increased soil temperatures have been found to increase germination from the alpine soil seed bank in some species, although responses are variable (Hoyle et al. 2013).

Whilst characterising patterns of treeline advance at a landscape scale are important for understanding the generalised response of the ecotone to a changing environment, predictive power can be significantly increased if we are able to link such broad-scale changes with a more developed understanding of seedling establishment at the local scale. It is, therefore, important to consider how microclimate affects regeneration, since it is the conditions experienced by individual seedlings at this scale that will determine establishment patterns and, ultimately the wider patterns of tree occurrence and treeline advance. Whilst wider scale data from meteorological stations are commonly used to study responses to climate, microclimate recordings can provide data with higher biological relevance (Graae et al. 2012).

In this study we sought to determine the relative importance of temperature and sheltering for tree seedling establishment in the Central Mountain Range of Taiwan and to understand the impacts on treeline form and advance. Accordingly, our work was guided by the hypotheses that (1) Temperature (air and soil) is the main factor driving treeline position in the region with low temperatures limiting seedling establishment. (2) Micro-topography will modify seedling distribution patterns with more seedlings establishing in sheltered sites. (3) Seedling occurrence will be associated with the presence of sheltering individuals such as adult trees and shrubs, with more seedlings being present in plots where adult trees and shrubs occur. (4) Smaller seedlings will be more sensitive to temperature and sheltering than larger seedlings.

Materials and methods

Study Site

This work was conducted in the Hehuanshan area of the Central Mountain Range of Taiwan (Figure 1) at c. 24° 08-09’ N and 121° 15-16’ E. The climate of Taiwan is warm and humid, with seasonal typhoons occurring during the summer months. These bring high wind speeds and large volumes of precipitation. Although Taiwan is crossed by the Tropic of Cancer, temperate and alpine conditions occur at high-altitude sites, thus supporting the existence of cold-adapted conifer stands (Lui 1971). At high altitudes these stands consist mainly of *Abies kawakamii*, *Tsuga chinensis* and *Pinus taiwanensis*. The area consists of complex topography with a maximum altitude of 3,560 m. The dominant treeline species is *A. kawakamii* (Taiwan fir) and above the treeline the bamboo grasslands are dominated by *Yushania niitakayamensis*, a bamboo species that grows in dense swathes up to 2 m high, with occasional cover by shrubs such as *Juniperis formosana*, *Rhododendron pseudochrysanthum* and *Rhododendron rubropilosum.*

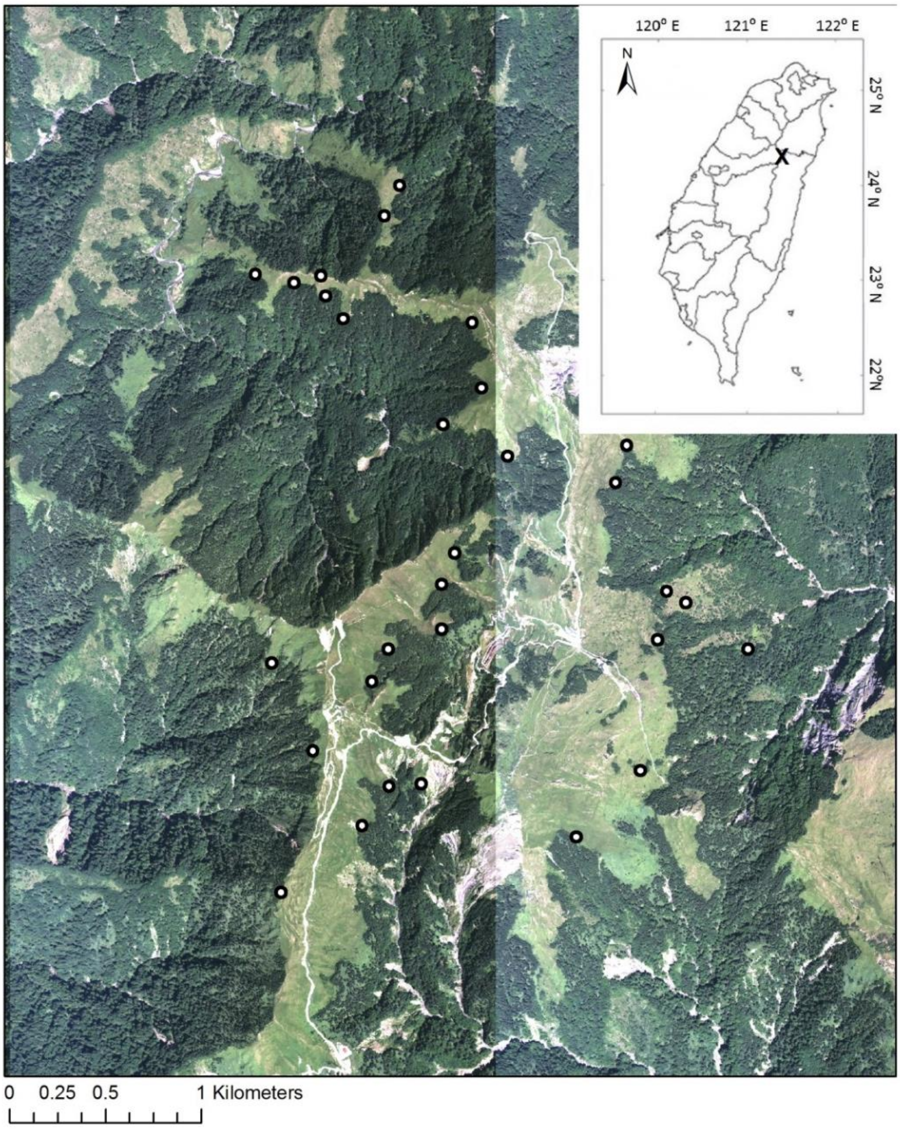

Figure 1: The location of the 30 plots within the study area (white circles) and the location of the study area within Taiwan (inset, study area marked with cross).

The treeline in the study area shows considerable variation in its structural form. Aerial photograph analysis and forest inventory work (data not shown) have identified five main categories of treeline structure, from static non-advancing treelines through to diffuse low-density advance over a broad area (Table 1). Similar treeline forms have been found to occur in other treelines worldwide (Harsch and Bader 2011).

Table 1: Treeline structural forms identified to be occurring throughout the Central Mountain Range of Taiwan with a description of the appearance and structure of each form.

Treeline Structural Form	**Description**
Diffuse advancing	Evidence of advance over time and a gradual decrease in tree density with altitude; although a limit of closed forest can generally be identified, many trees will occur upslope beyond this in a diffuse manner with trees at low density over a wide area.
Abrupt advancing	Evidence of upslope advance occurring; regeneration at high density over a short distance.
Forest infill	Areas of forest below treeline where forest density was previously very low, or where gaps in the forest had persisted over many years but in recent times have begun to infill.
Lower limit of upper treeline	Areas where the treeline is significantly lower over a small area.
Static	Areas of treeline where no advance can be identified and the trees at the forest edge are large and old, these edges tend to be abrupt in structure.

Microclimate data collection

Thirty study plots of 5 x 5 m were set up in April 2011; sampling effort was evenly distributed between the five treeline forms (Figure 1), field work areas were picked randomly within these forms from aerial photographs and plots were then selected randomly when at these areas. At the time of plot selection two iButton Thermochron DS1921G (Maxim Integrated Products, Inc) data loggers were placed in each plot to measure air and soil temperatures; one at a height of 5 cm above the ground (attached by cable ties to a plastic stake set in the ground, and allowed to hang freely and perpendicular to the ground surface), and one buried in the soil at a depth of 5 cm. The below ground iButtons were attached to a small mount with a brightly coloured string that protruded from the soil surface and allowed for easy identification and retrieval. The above ground height was chosen based on prior measurements of seedling in order to accurately represent the height of recently established seedlings in the area and similarly, the depth below ground was based on measurements made on seedling rooting depths from destructive sampling of a small number of seedlings prior to set up. The above ground loggers were angled in such a way as to avoid direct exposure to midday sun, and sheltered by the high density cover of *Y. niitakayamensis* to avoid exposure to direct sunlight and associated overheating. The data loggers were set up to record 6 times over a 24 hour period at intervals of 4 hours at: 00:00, 04:00, 08:00, 12:00, 16:00, 20:00 (UTC+08:00 hrs). Sites were visited periodically (5 times in total including set up and end of study) during the study period (April 2011 to March 2013) to download data and reset loggers for further recording periods. Data logger temperature data were compared with the recordings from a nearby meteorological station (Alishan at 23° 30' 37.42″ N 120° 48' 18.39″ E and 2,413 m a.s.l.) to check for consistency and long-term records were examined to see if the years of the study were typical.

Seedling and habitat data collection

All *A. kawakamii* seedlings present in each plot were recorded. This was the only tree species found to be regenerating in the plots. Here we classed any trees at or under the height of 50 cm as seedlings. Plots were searched thoroughly for a period of approximately 1 hr in order to standardise search effort across plots. Plots were mapped and positions of all seedlings recorded. The height of each seedling was measured, age was estimated through bud scar counts and notes were made on the condition of seedlings to assess changes in health over time. Seedlings were measured over the study period so that survival rates and growth rates could be calculated. Growth rates (cm cm^{-1} yr^{-1}) were calculated non-destructively as relative height growth based on measurements made at the beginning and end of the growing season each year and survival rates are expressed as the percentage of seedlings surviving in the plots over the study period.

The distance from the plot centre to forest edge (treeline) and any trees occurring beyond the treeline were measured (in elevation and m on ground) and aspect, slope, elevation, presence of shrubs (% cover) and adult trees in the plot were recorded. Surrounding vegetation height was measured and calculated as the mean of 6 random points within each plot. In spring 2013, after two years, data loggers were removed and final recordings were made of the seedling numbers, size and condition within each plot.

A measure of sheltering on a small scale (referred to here as micro-topographic sheltering) was calculated using ground measurements and records of elevation collected with a handheld GPS unit (Garmin GPS Map 62s). Elevation was recorded at a distance of approximately 10 m from the centre of each plot, in each cardinal compass direction. The elevation at the centre of the plot, where the data loggers were located was then subtracted from the elevation at each compass direction giving an elevation difference (sites surrounded by higher elevations would be regarded as sheltered, and those surrounded by lower as exposed). An average of all the elevation differences was taken to give one value of micro-topographic shelter per site. Elevation differences in the north, north east and north west directions were given double weight because prevailing wind direction tends to be from the north west in this area (Huang 2002).

Statistical analysis

All analyses were performed using R version 0.98.501 (R core team 2013). Analysis of variance (ANOVA) and Tukey post-hoc comparison tests were used to test for differences in habitat between the different treeline forms. To test for differences in seedling numbers between treeline forms two glms, one including treeline form, and one not were compared with ANOVA (Crawley 2005). Age class distribution plots were used to explore whether distinct patterns of seedling establishment or especially favourable years for establishment could be identified. Package ggplot 2 (Wickham 2009) was used to produce all figures in R.

Generalized linear models (glm) with a negative binomial error distribution and log link function (glm.nb function in the MASS package (Venables and Ripley, 2002)) were used to explore the relationships between seedling numbers and habitat variables. The poisson distribution was originally used in the models as it is considered to be suitable for modelling count data (Zeileis et al 2008), however over dispersion (as suggested by the ratio of residual deviance to residual degrees of freedom and tested with the dispersiontest function of the AER package (Kleiber and Zeileis 2014)) called for the use of a negative binomial distribution (Crawley 2005). Models were run for all seedlings and then for seedlings split by size into two groups: seedlings up to 20 cm and seedlings more than 20 cm, these were analysed separately in order to see if size influenced the sensitivity of seedlings to habitat variables. Models originally included all variables and explanatory variables that produced non-significant relationships were sequentially removed with the model re-run each time a variable was removed. Habitat variables were as follows: Vegetation height (*Y. niitakayamensis*), slope, aspect, altitude, micro-topography, number of trees in plot, number of shrubs in plot, distance to treeline and outlier trees. Microclimate data from the data loggers was used as follows: mean growing season soil/air temperature, maximum growing season soil/air temperature and minimum growing season soil/air temperature, maximum soil/air temperature, minimum soil/air temperature. Seedling growth rates (RGR) were modelled using linear mixed effect models (package lme4 (Bates et al. 2014)). Individual seedling growth rates (mean values for the two growing seasons studied) were included and site was then added as a random effect. Non-significant explanatory variables/fixed effects were sequentially removed as for the seedling number models. F and p values were calculated for each linear mixed effect model through the lmerTest package (Kuznetsova et al. 2014).

Results

Microclimate data

Failure of several of the data loggers during the study period resulted in a dataset with some missing values. However, data were not seriously compromised since failures were spread evenly over sites and air/soil. Some midday air temperature recordings were removed from the final analysis due to unrealistically high temperature values being recorded if poor placement of the mount subjected the data logger to direct sunlight. Comparison of the data from data loggers recording very high midday temperatures and those without allowed us to be confident that the temperature values for 08:00 and 16:00 hrs were reliable.

Average air temperatures over the growing season (defined here as Mar to Oct) varied from 7.7 to 11.8 °C across sites and soil temperatures over this period were in the range 5.8-11.6 °C. Overall, values showed more variation for air temperatures than for soil, especially when considering the difference between day and night time temperatures. There was also less seasonal variation in soil temperatures (Figure 2). Records from a nearby meteorological station show that the years of the study were typical in terms of mean air temperature and data logger values were closely related to the values recorded at the meteorological station over the same time period (Appendix S1 a and b in supporting information).

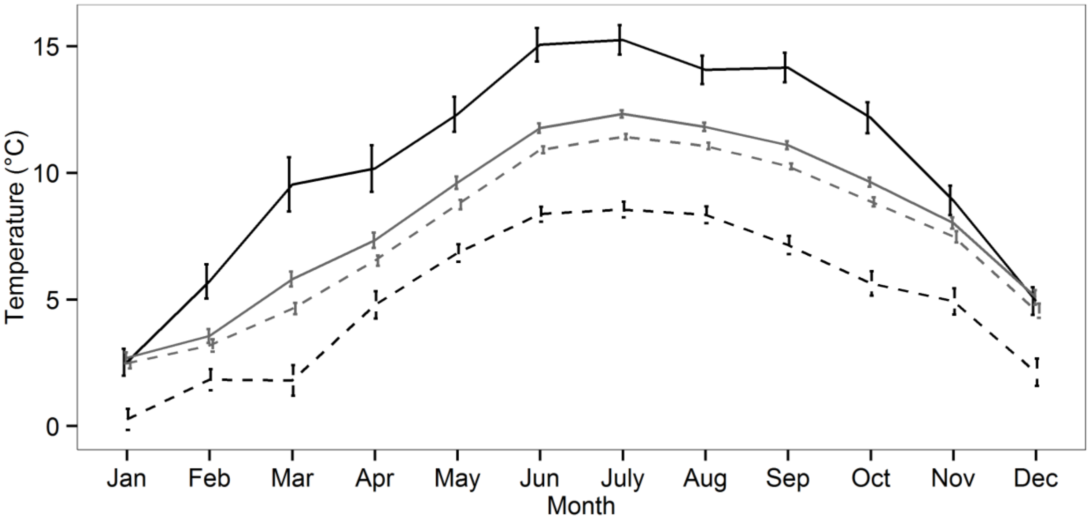

Figure 2: Mean monthly temperatures at treeline on Hehuanshan, Taiwan. Solid black line: mean day-time air temperature, solid grey line: mean day-time soil-temperature, dashed black line: mean night-time air temperature, dashed grey line: mean night-time soil temperature. Temperatures were averaged over sites and times for the whole study period. Night times were 20:00, 00:00, 04:00. Day times were 08:00, 12:00, 16:00. Air temperatures were recorded at a height of 5 cm above ground and soil temperatures at a depth of 5 cm below ground by iButton data loggers. Error bars represent ±1 SE.

Seedling and habitat data

Seedling densities varied throughout the plots from 29 per plot to a minimum of 0. Average number of seedlings per plot was 8.4. Average seedling height at the start of the study was 21 cm. Survival rates of seedlings were high; if seedlings were able to establish and grow for more than one year they generally persisted. Survival was 100% for 16 of the 30 plots and mean survival of the remaining plots was 85%. Similarly, establishment was low during the two year period. Seedling establishment was not uniform between years and shows episodes of high establishment (Figure 3).

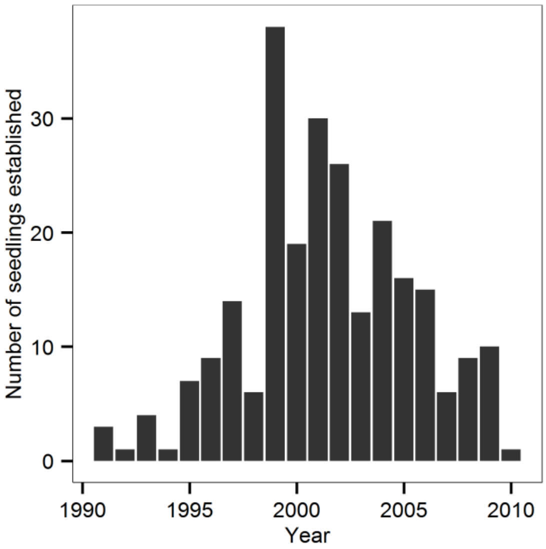

Figure 3: Numbers of seedlings established per year in 30 5 x 5 m plots on Hehuanshan, Taiwan. Seedling age was estimated from bud scar counts.

Smaller mean numbers of seedlings per plot were found at static treelines (mean of 3.2) compared to abrupt (11.8) and diffuse (6.8) (Figure 4), and although overall treeline form had no significant effect on seedling numbers (F = 2.61, p=0.06), there was a significant difference between static and all other treeline forms (p= 0.02). Micro-topographic shelter was higher in abrupt-advancing and lower treelines than in diffuse advancing, infill areas and static treelines, although again ANOVA results suggest no significant effect of form on micro-topographic shelter (F=2.33, p=0.08, df=4) and no significant differences between any forms were indicated by pairwise comparisons. Other habitat variables whose variance was explored by treeline form include mean growing season air and soil temperatures, seedling growth rates and height of *Y.niitakayamensis* (Figure 4) but none of these varied significantly by form according to ANOVA results.

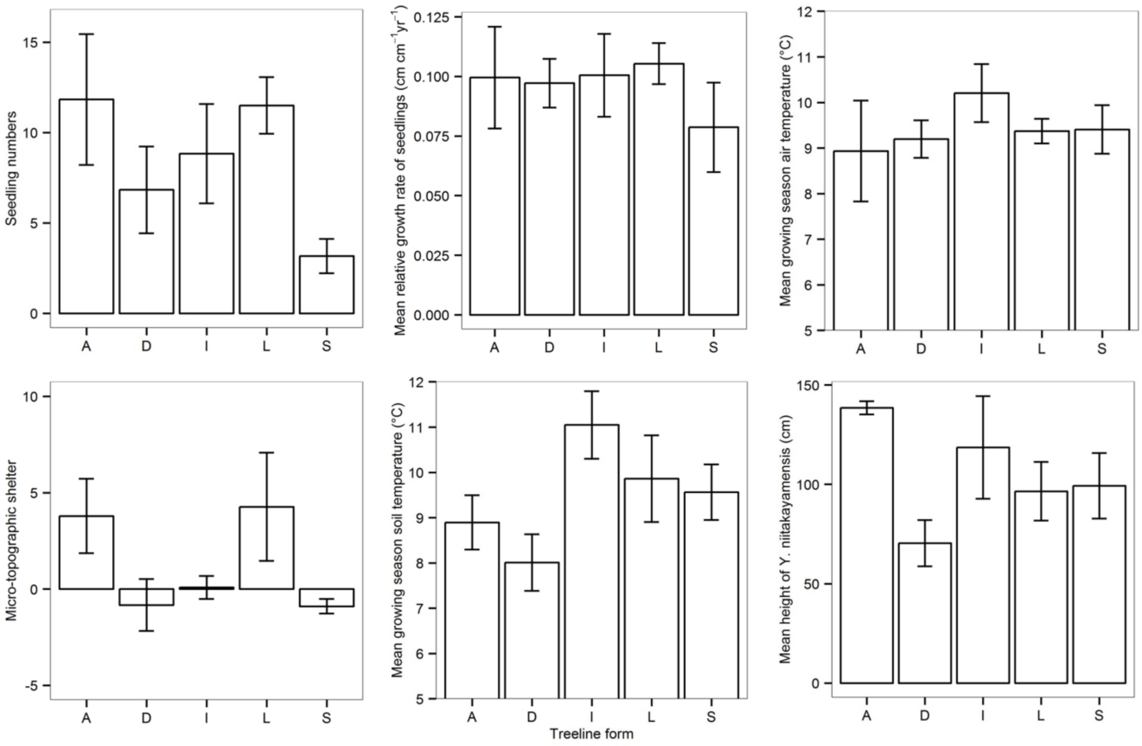

Figure 4: The variation in seedling numbers, growth rates, air and soil temperatures, micro-topographic sheltering and height of surrounding vegetation (*Y.niitakayamensis*) with treeline form on Hehuanshan, Taiwan. Treeline forms are as follows A: abrupt advancing, D: diffuse advancing, I: forest infill, L: lower limit of upper treeline, S: Static, non-advancing treeline, with details of form structure explained in Table 1. Air and soil temperatures were recorded at a height above ground and depth below of 5 cm and micro-topography was determined at a 10 m scale. Temperatures are averaged over all recording times for the growing season (Mar –Oct). Growth was measured annually and rates (RGR: cm cm^{-1} yr^{-1}) were averaged over a two year period (2011-2013). Error bars represent ±1 SE.

The best model for seedling numbers included only growing season mean soil temperature and micro-topographic sheltering (Figure 5). There was no significant interaction effect. Higher seedling numbers were associated with warm soil temperatures and sheltered sites (Table 2). Analysis of only smaller seedlings (=/< 20 cm) shows that they are more sensitive to environmental conditions than larger seedlings. Growing season soil temperatures have a stronger relationship with seedling numbers for this subset of the data (z= 4.747 for smaller only, 2.285 for all seedling), as does micro-topographic shelter (z=3.513 for smaller only, 2.397 for all), and more habitat variables have a significant relationship with the number of small seedlings (Table 3). Analysis of larger seedlings shows few significant relationships with environmental variables; only a close to significant effect of micro-topographic shelter was found (z= 1.726, p=0.08), weaker than that for the whole dataset or for only smaller seedlings (Tables 2 and 3).

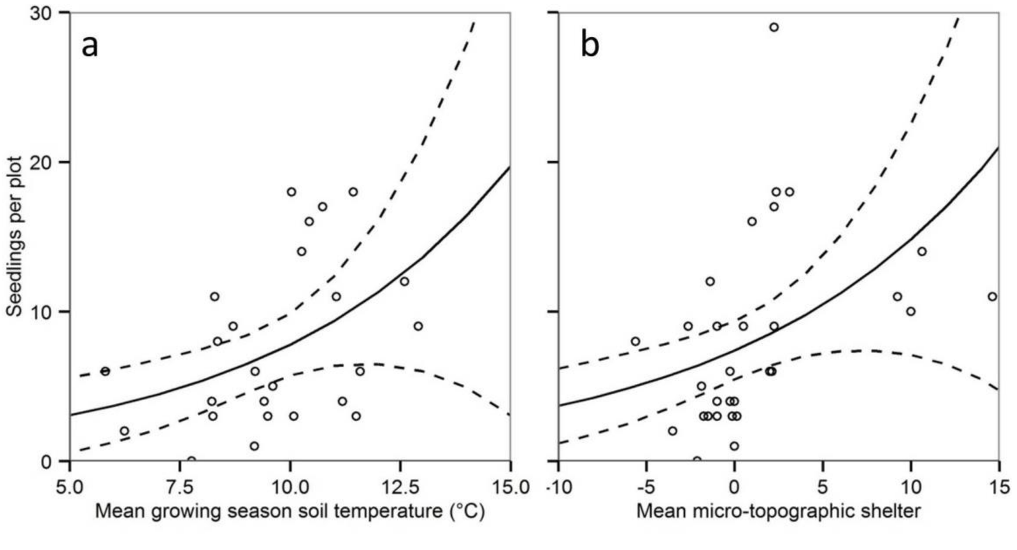

Figure 5: The relationship between (a) mean soil temperature of the growing season, and (b) mean topographic shelter and total numbers of seedlings of all sizes per plot in 5 x 5 m plots at treeline on Hehuanshan, Taiwan. The best fit lines (solid lines) and 95 % CIs (dashed lines) are from a glm (with a negative binomial error distribution and log link) of seedling numbers modelled by only soil temperature (a) and topographic shelter (b) respectively and are included to aid visualization of the effects of each

variable. Soil temperatures were measured by data loggers at 5 cm underground. Mean topographic shelter is calculated by ground measurements at a 10 m scale. See methods for full details. Growing season is defined as the period March to October.

Table 2: The relationships between total seedling numbers and habitat variables on Hehuanshan, Taiwan as modelled by a glm with a negative binomial error distribution and log link function.

Variable	Z value	P value
Growing season soil	2.285	0.02
Micro-topographic shelter	2.397	0.02

Notes: Variables not included in the model due to no significant effect include: growing season air temperature, minimum temperatures of soil and air (both growing season and yearly), mean height of surrounding vegetation (*Y. niitakayamensis*), number of trees in plot and percentage cover of shrubs in plot and distance from treeline and outpost trees.

Table 3: The relationship between seedling numbers and site variables for seedlings up to 20 cm height on Hehuanshan, Taiwan as modelled with a glm with a negative binomial error distribution and log link function.

Variable	Z value	P value
Mean growing season soil temp	4.747	<0.001
Micro- topographic shelter	3.513	<0.001
Mean height of *Y. niitakayamensis*	-2.496	0.01
Minimum year air temp	2.428	0.02
Minimum year soil temp	-2.495	0.01

Relative growth rates of seedlings were significantly related only to mean growing season air temperatures (df = 16, F = 2.3, p = 0.03). Growth rates were higher in sites with warmer growing season air temperatures. No relationship was found with growing season soil temperatures or micro-topographic sheltering or between air and soil mean growing season temperatures and micro-topographic sheltering.

Discussion

Based on assessment of microenvironment at a scale relevant to individual plants, rather than previously published landscape-scale overviews, we identify that microclimate and topographic sheltering influence patterns of establishment above the treeline. Higher seedling numbers are associated with sheltered sites and warm soil temperatures (Table 2). However, regeneration above treeline is not simply mediated by elevated soil temperatures since our results demonstrate that while seedling number is influenced by soil temperature, seedling growth rates are positively related to air temperatures. Furthermore, smaller seedlings were more sensitive to the measured environmental variables than larger seedlings, indicating that early growth is likely to have a significant impact on subsequent survival. These factors operate on a small spatial scale to influence wider landscape patterns through their effects on treeline form and advance.

The importance of soil temperatures identified here is recognised by other authors. Soil temperatures are known to affect many physiological processes in plants such as photosynthesis (Day 1991; Dang and Chen 2013) and growth (Hoch and Körner 2003) with less root growth in colder soils (Smith et al. 2003). Nutrient availability is also affected by soil temperature so warmer soils could lead to increased growth (Rustad et al. 2001; Charru et al. 2014). The relationship between soil temperatures and seedling establishment and growth is complex and warming can potentially have both positive and negative implications since increased soil temperatures can also negatively impact germination in some cold-adapted species (Hoyle et al. 2013).

Körner and Paulsen (2004) provide evidence that soil temperature is a common driver of treeline position on a global scale. They found that tree line position was consistently associated with growing season soil temperatures of between 5.4 and 7.8 ° C at 10 cm depth. This varied consistently depending on latitude; sites located near the equator occurred at lower soil temperatures. The mean soil temperatures found in this study ranged between 5.8 (at lower limit of upper treeline site L5) and 12.9 ° C (at forest infill site I3). The higher temperatures found here could be due to the loggers being placed at a shallower depth of 5 cm, thus allowing for more heat penetration and temperature variability and because the forest infill sites were located slightly below treeline. It is however important to note that whilst a global driver of soil temperature may explain wide scale patterns it does not account for local variability in treeline position, which is likely to be affected by factors such as topography and substrate (Resler et al. 2005) as well as temperature.

Seedlings respond positively to micro-topographic sheltering on Hehuanshan (Tables 2 and 3) since higher seedling numbers were found in more sheltered sites. This result agrees with a larger scale study of patterns of adult trees in the same region (Greenwood et al, 2014) and also with other studies of establishment patterns and treeline dynamics (Holtmeier and Broll 2007; Holtmeier and Broll 2012; Resler et al. 2005).

We did not find a relationship between micro-topographic sheltering and any measure of air or soil temperature. This suggests that the importance of micro-topography for seedlings is related to some factor other than temperature. Wind speed, soil formation, soil moisture retention and winter-time snow cover are all mediated by micro-topography (Holtmeier and Broll 1992) and influence seedling establishment patterns. Wind exposure is known to play a role in the formation of dwarfed krummholz structures at treelines (Tranquillini 1979; Korner 2003; Gamache and Payette 2004) and these structures themselves can facilitate the growth and survival of seedlings by protecting them from excessive wind speeds (Batlorri et al. 2009). Soil moisture has been associated with topography and the presence of boulders (Resler 2006) and these features are known to provide shelter and increase establishment success (Resler et al. 2005), while snow cover is related to topographic depressions and can have an important protective effect on seedlings (Drescher and Thomas 2013).

The finding of a positive relationship between growth rate and air temperature is unsurprising, given that temperatures are generally low and limiting at altitudinal treeline (Körner 1998). This finding suggests that warming temperatures in the area are likely to lead to increased success of *A. kawakamii*, with further advance likely. Other authors have found evidence of increased growth due to warmer temperatures at treeline, for both seedlings (Piper et al. 2013), and adult trees (Charru et al. 2014).

We did not find any relationship between total seedling numbers and *Y. niitakayamensis* height or the presence of shrubs and trees (Table 2). Smaller seedlings were negatively associated with *Y. niitakayamensis* height, with smaller numbers of seedlings occurring where the bamboo was very high (Table 3). We thus found no evidence of facilitative interactions at treeline, although such interactions are commonly reported (Llambi et al. 2013; Batlorri et al 2009; Germino et al. 2002). In our study site *Y. niitakayamensis* grows in extremely dense swathes, where it has the potential to block light to seedlings growing below; this could explain the result of a negative relationship of smaller seedlings with *Y. niitakayamensis* height. The dominance of *Y. niitakayamensis* could also explain why the presence of trees and shrubs has little facilitative impact, as the bamboo is already reducing exposure to excessive sunlight and wind. In this respect our study system differs from most alpine environments where plant cover tends to be low to the ground and sparse, and shrubs and outpost trees are perhaps more important modifiers of the environment.

Here we found that smaller seedlings had a stronger relationship with shelter and microclimate and with the surrounding vegetation, suggesting that smaller seedlings are more sensitive to environmental conditions and have a more restricted niche than older seedlings. This size-related difference is also suggested by the high survival rates in this study; we found that seedlings that made it past the first year of establishment were less likely to die beyond this time. However the experimental design might influence the results here; data loggers were placed at 5 cm above and below-ground, the height determined by the size of recently established seedlings. The mean height of seedlings recorded in the plots was higher (21 cm) than the placement of the data loggers, so many seedlings likely experienced conditions slightly different from those monitored by the data loggers. The high surrounding vegetation could moderate this effect however, as it is unlikely that seedlings or saplings growing at 50 cm (the height limit used here) or less were growing above the boundary layer.

The positive relationships found between seedling numbers and warm soil temperatures, and between growth rates and air temperatures indicate that establishment is likely to continue to respond to warming climate, further advance of treeline is thus expected. However the importance of micro-topography presents a potential limitation to advance, and offers explanation for the complex pattern of the upper treeline throughout the Central Mountain Range of Taiwan. Remote sensing analyses have demonstrated the importance of shelter for treeline form and advance on a large scale (Greenwood et al, 2014), here we have identified the microsite-scale processes that influence these regional patterns: seedlings will establish more successfully, and treeline will thus advance further in sites that offer some degree of topographic shelter.

Conclusions

While soil temperatures have been correlated with treeline position globally, few studies have directly investigated the impacts of soil temperatures on seedlings at the treeline. Our results, based on direct measurement of soil and air temperature at a scale relevant to individual plants in previously understudied subtropical mountains is particularly valuable in this respect since it enables us to make a direct link between the pattern observed at the landscape scale (Greenwood et al., 2014) and the microsite scale factors responsible for such spatial variation. Future research assessing the importance of micro-topographic variation at the landscape scale should make it possible to better understand how environmental drivers, such as soil nutrients, snow pack, moisture and litter accumulation, co-vary with soil temperature and micro-topography, to enable a mechanistic understanding of the driving variables responsible for treeline advance in this ecosystem. Furthermore, the topographic limitation of treeline advance found here has implications for the conservation of alpine species threatened by the invasion of trees into alpine habitats. If trees are only able to migrate successfully into areas that are sheltered then alpine species might be expected to persist in more exposed sites, potentially requiring us to revise estimates of alpine plant extinction due to upslope migration of trees into alpine areas.

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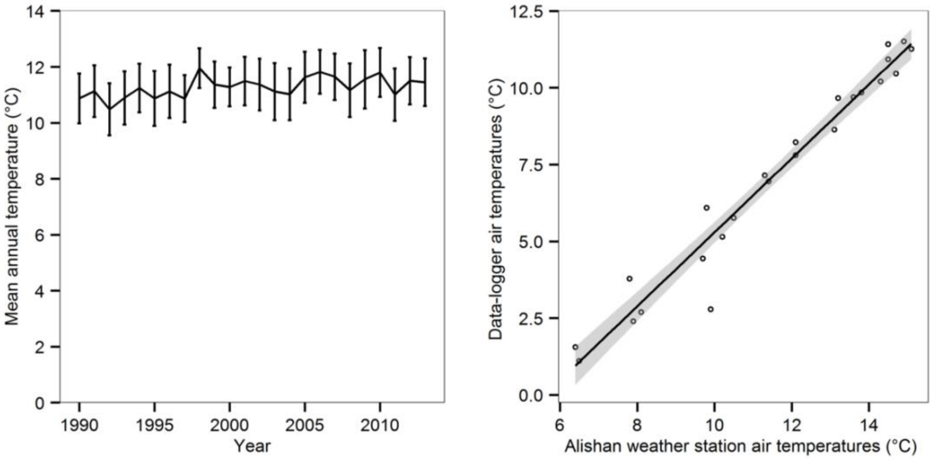
Appendix S1



App. S1a (left) and b (right hand image). S1a shows the variation in mean annual temperature from 1990-2013 with ± 1 SE. Examination of the last three years (the period of study) shows that the study years were typical. S1 b shows the linear relationship between data logger and meteorological station air temperature recordings. Data are monthly means over the study period. $R^2 = 0.96$, p=0.001.

Chapter 6

How fast is too fast? Rapid forest change leads to community disassembly and reduced diversity in advancing forests

Title: How fast is too fast? Rapid forest change leads to community disassembly and reduced diversity in advancing forests.

Running title: Community impacts of treeline advance

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Key words: *Abies kawakamii*, alpine forest, climate change, epiphytes, GLMM, nestedness, NMDS, species richness, Taiwan

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Abstract

Climate change is causing shifts in the geographical range of species worldwide. In high altitude areas forests are often observed to be shifting their upper limits to higher altitudes in response to warming temperatures. Although this phenomenon is well described in the literature, the possible consequences of this for the wider forest community have not been fully considered. Studies of community wide responses to climate change often find a degree of community disassembly due to differential migration rates and niche variation of previously co-occurring species. In this study we focus on epiphytic macro-lichens to investigate the possible impacts of treeline advance on associated organisms. We find that species richness is lower in treelines that are advancing rapidly. Community composition is associated with tree size and forest density such that only a subset of species occurring in slowly advancing or stable forest edges is found in rapidly advancing treelines. Our results indicate that differential migration rates between co-occurring species and changes in habitat structure associated with advance are resulting in community disassembly but that this process is strongly dependent on the speed of tree migration. Alpine areas are often rich in endemic species that may be threatened with extinction as treelines rise and habitat fragments. More widespread impacts will be experienced in lowland boreal regions where treeline advance is expected to be rapid and over very large areas. Given the complexity of treeline behaviour the findings that we report represent an essential step in unravelling the complexities of community responses to climate change.

Introduction

At high altitudes, low temperatures limit tree occurrence through impacts on growth and survival (Tranquillini, 1979; Körner, 2003; Körner and Paulsen, 2004). Consequently, ongoing climate warming is driving an upward movement of altitudinal treelines worldwide (Harsch et al. 2009). However, the migration potential of species varies and the survival of forest herb species transplanted far beyond their current limits (Van der Veken et al. 2012) strongly suggests an effect of migration limitation on distribution. Where trees are able to migrate quickly over large distances many species of the forest community may not be able to track these changes, leading to substantial modification of the species composition of communities at the leading edge of a species distribution.

Since communities are made up of species with different requirements (Whittaker, 1965), they are unlikely to respond as a unit but rather individualistically (Huntley, 1991), resulting in community disassembly as a keystone species advances, both due to migration lag and altered suitability of newly colonised areas for the growth and survival of associated species. Such radical changes in community composition occurred in response to past climate changes (Huntley, 1990; Edwards et al. 2005; MacDonald et al. 2008) but also in modern times (le Roux and McGeoch 2008; Klanderud and Totland, 2005). In an investigation of the range shifts of all vascular plants occurring on Marion Island, Antarctica, le Roux and McGeoch (2008) found that as species shifted upslope, patterns of species richness and community composition were affected, and that communities did not respond as a unit to warming climate. Inter-specific interactions can affect climate response and species interactions may change with warming: dominant species can influence the response of rarer species to warming (le Roux et al. 2012) and warming has the potential to change patterns of dominance and thus community composition (Klanderud and Totland, 2005).

Treelines are often spatially complex and a variety of forms have been described depending on their response to rising temperatures (Harsch and Bader, 2011). For any given tree species, topographical variation can locally modify the rate of migration leading to a high degree of spatial variation in treeline advance (Danby and Hik 2007; Macias-Fauria and Johnson 2013). Forest structure influences microclimate variables such as moisture, temperature and light availability (Canham and Burbank, 1994; Kammer et al., 2009) and can thus influence understory species composition (Chen et al. 1999). As treelines expand in response to warming climate with an increase in forest area beyond current limits (Beckage et al. 2008), and in density below (Mamet and Kershaw 2012), conditions will, therefore, change for both forest understory species and for alpine communities. Forest understories can be very species rich (Thomas et al. 1999) and forest specialist species are particularly sensitive to changes in forest conditions (Halpern and Spies 1995). However, expansion of forests into alpine grasslands will reduce alpine habitat area (Moen et al. 2004) potentially leading to increased competition and displacement of alpine plants (Halloy and Mark, 2003).

The complexity of treeline advance in terms of its form and geographic variability combined with the high levels of uncertainty regarding community level responses to warming climate mean that studies investigating community wide responses to climate warming during tree migrations are much needed. Epiphytic/Corticolous lichens are ideal study organisms with which to study the impacts of treeline advance on the wider forest community; they display high sensitivity to environmental conditions, often have limited colonisation and growth rates (Nash, 2008) and are dependent on trees for growth substrate. Many lichens require a long continuity of forest (Rose, 1976; Selva, 1994), damp shaded conditions and the rough, fissured bark of older trees (Holien, 1996) and thus are likely to be particularly affected by changes in forest range and structure. The sensitivity of lichens to forest conditions has led to their widespread use as indicators of ecological continuity (Rose, 1976; Whittet and Ellis, 2013). Forest structure has been found to be more important than climate for epiphyte communities (Moning et al. 2009) whilst evidence suggests that historical forest conditions have more impact on epiphyte diversity than current (Ellis and Coppins, 2009) and that epiphytic lichens are slow to respond to habitat changes. It is probable that they will respond to changing climate in a way that differs to the response of trees, so although they are intimately linked with trees their fate in the face of changing climate may be different.

Given the highly spatially variable changes in forest distribution linked to rising temperatures in the Central Mountain Range of Taiwan (Greenwood et al. 2014), we sought to determine if rapid tree migration is leading to disassembly of the lichen community. We hypothesised that we should find lower species richness at advancing forest edges and that this reduction should be greatest where forest advance was most rapid. We predicted that community disassembly would occur due to the restricted colonisation speed of some species acting in combination with altered habitat suitability in newly developing forest.

Material and methods

Study area

The island of Taiwan lies off the southeast coast of China and is traversed by the Tropic of Cancer. Although much of the island experiences a subtropical climate with warm humid conditions and seasonal typhoons, at high altitudes conditions range between temperate and alpine. The Hehuanshan Mountain Range, located in central Taiwan, consists of three main peaks over 3,000 m (Figure 1). At high altitudes the dominant treeline species is *Abies kawakamii*, a species of endemic fir that forms almost monospecific stands at the upper limits of its range (c. 2,800-3,000 m). The majority of the high altitude *A. kawakamii* forest is unmanaged. Similarly, the subalpine grassland above is not used for the grazing of domesticated herbivores or managed in any other way. The treeline, therefore, represents a range limit that is governed by natural species dynamics without significant local anthropogenic influence.

The *A. kawakamii* forest is advancing upward in altitude on Hehuanshan in a complex and topographically mediated with considerable spatial variation; treelines are advancing in some areas whilst remaining static in others (Greenwood et al. 2014). Following Harsch and Bader (2011) and Greenwood et al. (2014), local patterns of treeline advance in the Central Mountain Range can be classified as *abrupt advancing* (treelines advancing at high density over short distances), *diffuse advancing* (treelines advancing at low density over long distances) and *static* (treelines that are not advancing), and of these the authors have shown that the diffuse form shows the greatest upslope advance in the Hehuanshan area (Greenwood et al. 2014).

Transect structure

Thirty three treeline sites (11 for each advance form) (Figure 1) were studied during Nov/Dec 2011 and March/April 2012. Transects were conducted from interior forest to treeline in static and abrupt forms or to tree-limit at diffuse advancing forms. Transect length varied between 50 and 140 m depending on the degree of advance at that site (Table 1). Sites were selected through stratified random sampling using aerial photographs in order to cover the three major treeline advance forms. Transects were walked from treeline/limit to interior forest (the decision on when that was reached was based on tree density and size and canopy features but was consistent throughout the study (distance was generally c. 50 m from the defined forest edge)). Along each transect pairs of trees were sampled at 3 or 4 points as follows; interior forest, mid-forest (a forest position halfway between the start of the transect in interior forest and the treeline or forest edge), treeline (the forest edge) and tree-limit (the upper limit of tree occurrence, only different from treeline in diffuse advancing forms). One of the trees sampled in each transect section was of similar diameter at breast height (DBH) throughout the whole transect, and kept fairly consistent between transects (DBH = c.15-30 cm) so that sampling area was consistent and trees were of comparable ages (although trees at treeline are likely to be slightly younger than similar sized interior trees). The other sample tree was be picked to be representative of that portion of the transect (interior forest trees were therefore generally larger, edge and treeline trees smaller in girth).

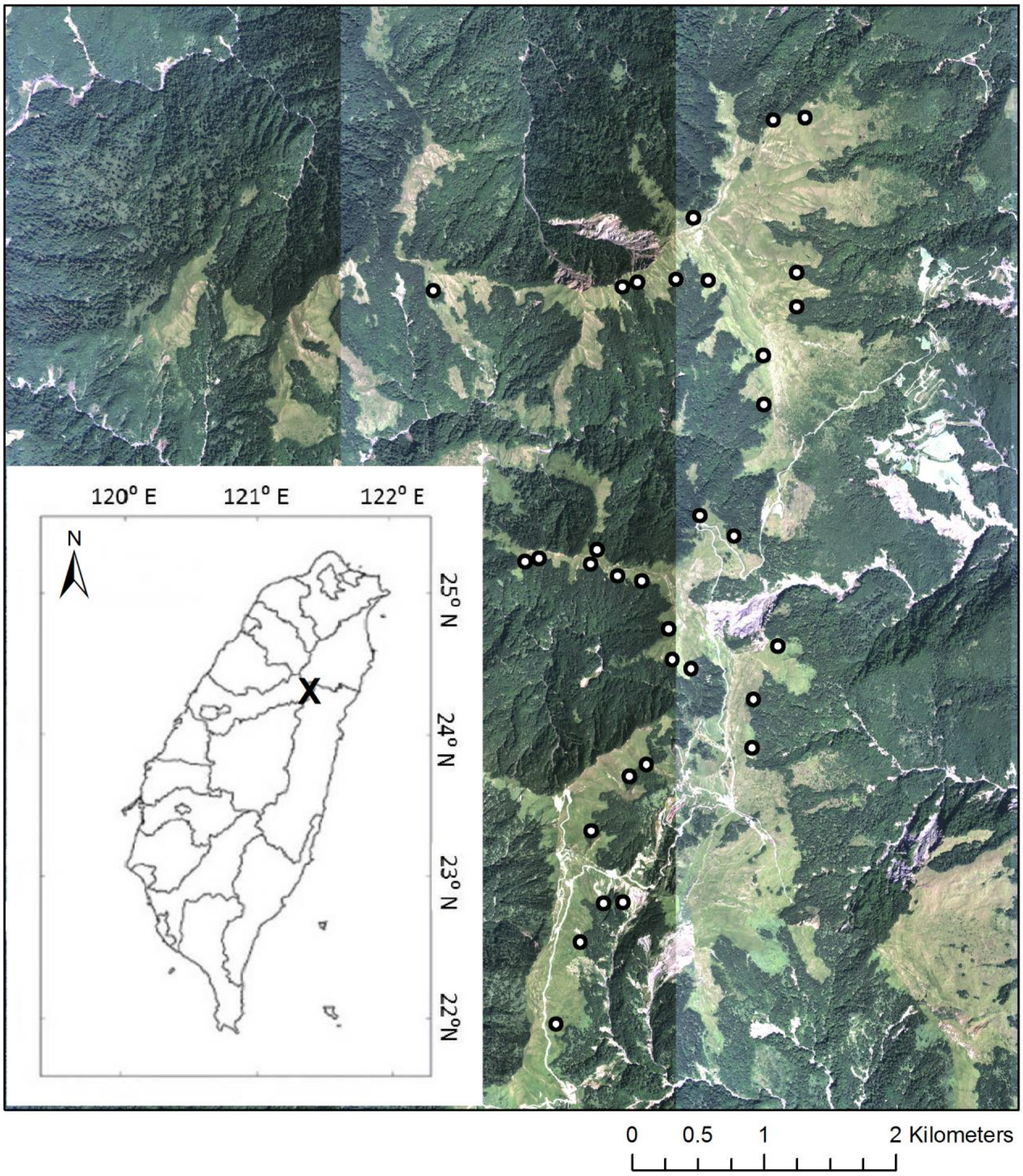

Figure 1: The location of the study area in Taiwan (inset map, marked with a cross) and the position of each of the 33 transects throughout the Hehuanshan Range (enlarged area, white points)

Table 1: Explanation of treeline forms/structures used in the sampling design on Hehuanshan, Taiwan. The number of transects for each form, mean transect length and number of sampling points.

Treeline Form	Description	No. of transects	No. of sampling locations along transects	Mean transect length
Abrupt advancing	Treelines with an abrupt edge and evidence of advance. A dense band of young at the edge of the forest.	11	3: Interior forest, mid forest, treeline	50
Diffuse advancing	Treelines that show evidence of advance, occurring in a diffuse manner; regeneration over a long distance at low density. Young trees scattered upslope at low density beyond the treeline, forming the tree limit at their upper limits.	11	4: Interior forest, mid forest, treeline, tree limit	100
Static advancing	Treelines that show no evidence of recent advance. Mature trees occur at the edge of the forest and the treeline is abrupt in nature.	11	3: Interior forest, mid forest, treeline	50

Epiphyte sampling

Lichen species identity (macrolichens only) and relative abundance was recorded on basal trunks of trees occurring at each sampling position. The sampling area was a 60 cm wide band around the trunk, centred at breast height (1.3 m (DBH)). Specimens were collected for later species identification. Abundance estimates were made using the DAFOR scale (Sutherland, 1996). Trees were searched carefully for evidence of recent colonisation to ensure that no small thalli were missed and search time was made proportional to search area to keep effort constant over all trees sampled.

Habitat variables

Trees were measured for DBH, bark roughness was classified based on a bark roughness index devised by the authors (for details see Appendix A) and a hemispherical photograph was taken from the base of each tree to enable measurement of canopy openness. The altitude of each tree was recorded. At the transect level, forest inventory data were collected: all trees occurring within transects were measured for DBH and relative positions recorded. This transect level inventory data was later split to allow for forest density data to be applied in analysis at the tree level.

Species identification

Specimens collected in the field were identified to species level, using morphology and relevant publications for Taiwan and the wider region of East Asia (Appendix B). Where a species level ID was not possible, specimens were either identified to genus level or assigned a morphotype classification. Thin layer chromatography (TLC) was used to aid with the identification of some specimens, following the methods of Orange, James and White (2010). Solvent G was used on a glass plate and plates were sprayed with sulphuric acid and water and observed under UV light as well as natural light.

Between one and four examples of each species were also DNA barcoded. Methods of extraction, amplification and purification followed those described by Kelly *et al*. (2011). Purified PCR product was sequenced in forward and reverse directions via a commercial service (Macrogen Europe). Contigs were edited and assembled using BioEdit software (Hall, 2013). Most specimens were successfully barcoded and at least one example of each species yielded useable sequence data except for three species of *Usnea,* one *Heterodermia,* one *Cetrelia,* one *Lobariella* and one *Hypotrachyna* for which specimens either yielded low concentration DNA after extraction or failed to yield useable sequence data (Appendix C, Table A1). These un-barcoded species were all rare in the sample sites, both in terms of occurring in small number of sites and being at very low abundance in the occurring sampling areas. BLASTN searches in GenBank (www.ncbi.nlm.nih.gov/genbank/) were used for initial sequence identity and top hits were recorded for comparison with the morphological species identification. In most cases this revealed a close match between sequence ID and morphological ID and where these did not agree specimens were reclassified as appropriate. Voucher specimens of the species identified in this study are stored in the herbarium of The Royal Botanic Garden Edinburgh and associated sequence data are stored in GenBank, for accession numbers see Appendix C (Table A1).

Statistical analysis

The variation in species richness and habitat variables with tree position and treeline form

All statistical analyses were performed with R studio (R core team 2013). Plots were also constructed in R, using the package ggplot2 (Wickham, 2009). Species accumulation and rarefaction curves were used to estimate the percentage of total species described with our sampling intensity. Chao, Jack-knife and Bootstrap methods (available using the specpool function of the vegan package (Oksanen et al. 2011)) were used and compared. The way in which measured habitat variables change with forest position in each of the treeline forms was explored graphically and tested with ANOVA. Generalised linear models (glm) were used to test the significance of changes in mean species richness per tree; two glms with a quasipoisson error distribution, one including tree position, and one not, were compared with ANOVA (package lmerTest (Kuznetsova et al. 2014).

The influence of habitat variables on species richness patterns

General linear mixed effects models ((GLMM) glmer function of lme4 package (Bates *et al*. 2014)) were used to explore the relationships between mean species richness per tree and habitat variables. A poisson error distribution (Zeileis et al. 2008) was used in the models with a log link function; a random effect was included to avoid psuedoreplication due to the paired sampling design. Original models included all habitat variables; non-significant variables were sequentially removed as appropriate to improve model fit, with the models re-run each time a variable was removed and AIC values compared. In this analysis data from all treeline forms was pooled and treeline form was not considered as a factor, instead distance from forest interior and tree density were both used as continuous variables. The original model included the following predictor variables: Species numbers ~ distance from interior forest + tree density + DBH+ canopy openness+ altitude+ aspect+ bark roughness + (1|plot/tree), family=poisson. These variables are all expressed at the tree level; all data were collected at this level with the exception of tree density, collected at transect level. Detailed recording allowed for this density data to be stratified for each pair of trees sampled; it was split into 4 sections of interior, forest, treeline and tree limit and applied as appropriate. The variance explained by the best model was estimated through the calculation of marginal and conditional R^2 values following the methods of Nakagawa and Shielzeth (2013). Variance inflation factors (VIFs) were calculated to check for problems with collinearity in predictor variables ((corvif function) Zuur et al. 2009).

Community disassembly/nestedness of advancing treelines

To determine whether sites with lower species richness were a subset of those with higher species richness rather than containing predominantly novel species, we used the functions nestednodf and oecosimu from the vegan package (Almeida-Neto *et al*. 2008, Almeida-Neto and Ulrich 2011). Nestednodf was used to calculate nestedness and then this was compared with a null model using oecosimu. Nestednodf output gives a statistic for nestedness of rows (sites), where 0 indicates no nesting and 100 indicates perfect nesting. Simulation method r1 was used with 1000 simulations to create a null model. This method maintains the total species per site found in the dataset and fills presences using species frequencies as probabilities (the likelihood of a species being used to fill a cell depends on its overall frequency in the original dataset). A null model is thus produced and the species data is tested for nestedness against this random distribution, the alternative hypothesis was that the statistic is greater than simulated values so a significant p value indicates that the dataset shows a higher degree of nesting than a random distribution created by null modelling.

Community composition patterns, dissimilarity and indicator species

Non-Metric Multi-Dimensional Scaling (NMDS) using vegan and MASS packages (function metaMDS with default settings) was used to explore community composition patterns and their relationship with habitat variables, forest position and treeline advance form. Bray Curtis dissimilarity index was used to calculate the difference in community composition between each forest position/treeline form combination and visualized using NMDS. Function envfit in vegan was used to fit environmental variables to the ordination, with R^2 and p values indicating goodness of fit and significance. A mantel test was used separately to test the correlation of Bray Curtis dissimilarity with habitat variation and the adonis function of vegan was used to test for significant differences in community composition with treeline expansion form and sampling position. The function mulitpatt from the Indicspecies package (De Caceres and Legendre, 2009) was used to explore the association of species with treeline form/forest position groupings.

Results

Species richness patterns

All specimens found in the sample plots were identified to species level, excluding *Cladonia* spp which are treated collectively. A total of 62 species were found over the whole study area (Appendix C, Table A1), a total of 29 of which occurred at the tree-limit, 55 at treeline, 54 at mid forest and 48 in interior forest (considering all transects per treeline form together). Mean species per tree was highest in static treelines and lowest in diffuse tree-limits (Figure 2). Species accumulation curves and rarefaction estimates suggest that the sampling may not have fully described all the species likely to be present (Table 2). However, although the estimated total numbers of species in each forest position are higher, the overall pattern is the same; species numbers are lower at tree limit and interior forest and highest overall at treeline.

Table 2: Total species numbers found in each sampling position along transects running from forest interior to tree limit on Hehuanshan, Taiwan and the total number predicted by various rarefaction methods (±1SE) from the function specpool in the vegan package

Position	**n**	**Species numbers**	**Chao estimate**	**Jack-knife estimate**	**Bootstrap estimate**
Tree limit	22	29	34±4.2	39±4.7	34±3
Treeline	66	55	63±6	66±3.3	60±2
Mid forest	66	54	58±3.3	63±3	59±2
Interior	66	48	51±2.8	54±2.8	51±1.8

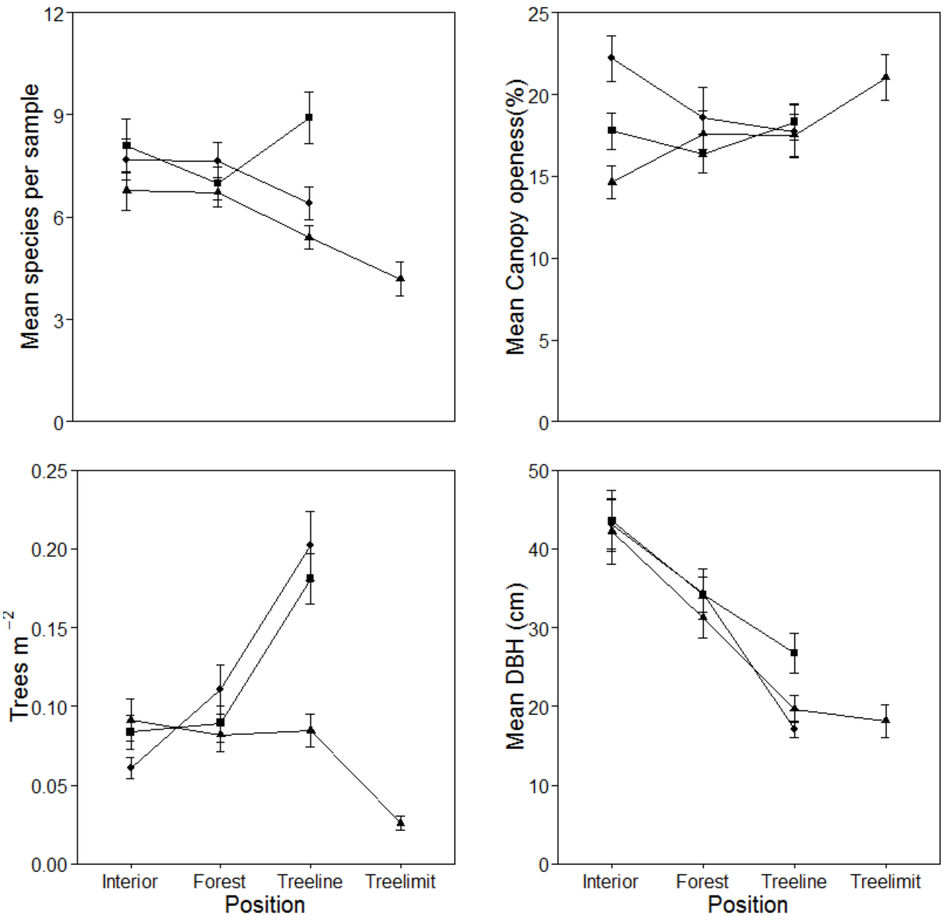

Figure 2: Variation in species richness (top left) and 3 main habitat variables (canopy openness, tree density and DBH) along transects running from interior forest to treeline/limit in 3 treeline form on Hehuanshan, Taiwan. Circles represent abrupt advancing forests, triangles diffuse advancing and squares static, non-advancing treelines. Mean values are shown ±1 SE.

Variation in habitat variables with tree position and form

The measured habitat variables varied throughout transects from interior forest to treeline/limit but the nature of variation depended on treeline form (Figure 2). For example mean tree density increased from interior forest to treeline in abrupt advancing and static treeline forms but decreased in this direction in the diffuse advancing treeline form. Tree density varied significantly with form in abrupt (df=56, F=54.28, p<0.001) and diffuse advancing forms (df=86, F=45.57, p<0.001), but not in static (df=64, F=0.13, p=0.716). Tree size (DBH) decreased significantly from interior forest to treeline in all treeline forms (abrupt advancing, df=64, F=46.78, p<0.001; diffuse advancing, df=86, F=45.13, p<0.001; static, df=64, F=15.99, p<0.001) and canopy openness was variable within position and treeline advance form, with significant variation dependent on form only in diffuse advancing treelines where canopy openness increased from interior forest to tree-limit (df=86, F=11.07, p=0.001). Mean species number per tree varied significantly with forest position in diffuse treelines, with species richness decreasing from interior forest to tree limit (df= 86, F=18.30, p<0.001) but not in abrupt (df=64, F= 2.66, p=0.107) or static (df=64, F= 0.68, p=0.414).

The influence of habitat on species richness patterns

Tree size and distance from forest interior were the two main factors related to species richness of lichens. A GLMM including distance and tree size gave z values of -2.64 and 2.17 and p values of 0.008 and 0.03 for distance and tree size respectively. However model results also indicated a significant interaction effect. When an interaction term (distance and tree size) was included then the effect of distance alone was no longer significant (Table 3). The estimated variance explained by the full model including the interaction term (conditional R^2) was 30 %; the variance explained by a model including only random effects (marginal R^2) was 13 %. Correlation of fixed effects show that the two explanatory variables are correlated (0.5). However, VIF values of <2 (1.3) suggest that collinearity of the fixed effects is not a major problem in this model.

Table 3: The relationship between lichen species richness and habitat variables along transects running from forest interior to treeline/limit on Hehuanshan as modelled by a GLMM (function glmer of lme4 package in R) with Poisson distribution of residuals and log link function. Tree position is nested within transect as a random effect to account for the paired sampling design. Marginal and conditional R^2 values, calculated according to Nakagawa and Shielzeth (2013) were 13 and 30% respectively.

Fixed effect	Z value	P value
Distance from interior	-2.64	0.088
Tree size (DBH)	2.17	0.001
Distance: Tree size interaction	2.54	0.011

Notes: This table shows the model with the best combination of factors, other variables that were originally included as fixed effects but removed sequentially due to non-significant p values included: bark roughness, altitude, canopy openness and forest density.

Similarity of the lichen community between sampling locations

Bray Curtis dissimilarity indices (Appendix D, Table A2) show that in general interior and mid forest positions are very similar regardless of advance form, treeline positions vary slightly more depending on advance form and treeline positions of all forms are quite different from interior and mid forest positions. The two communities that are most different are abrupt interior and tree limit. Mantel test of correlation (using Pearson’s moment correlation) between dissimilarity and all numeric habitat variables show a correlation of dissimilarity with habitat variation (r=0.7, p=0.001). Treeline form has a strong and significant effect on variation in community composition according to adonis results (F=61.8, R^2= 0.4, p=0.010), and there is a weak but significant effect of sampling position (F=7.0, R^2=0.1, p=0.010). There is evidence of nesting occurring in the species dataset (nodf (rows) = 72.4, p = 0.003). Species poor sites, such as tree limit and diffuse advancing treeline are a subset of species rich, interior forest sites.

Community composition patterns

NMDS of all treeline sites (Appendix E, Figure A1) shows a high degree of similarity of sites in terms of their lichen community, and little separation based on treeline advance form. Three main habitat variables were found to be associated with the two axes of variation but with low explanatory power: DBH (R^2= 0.1, p= 0.050, NMDS1= -0.73, NMDS2=0.69), altitude (R^2=0.12, p=0.025, NMDS1=-0.72, NMDS2=-0.69) and bark roughness (R^2=0.1, p=0.070, NMDS1=-0.96, NMDS2=0.27). Treeline form was also found to have a small impact on community variation along the NMDS axes (R^2=0.1, p=0.008).

A comparison of separate NMDS plots for both diffuse and static form treeline transects shows some variation in community composition between forest positions in both static and diffuse treeline forms (Appendix E, Figures A2 and A3). However there is more overall spread in the diffuse form sites, and much more separation of treeline/limit and forest/interior sampling locations. Forest position has a significant effect in both static (R^2= 0.1, p=0.002) and diffuse advancing (R^2= 0.3, p=0.001) treeline structures. In the diffuse advancing NMDS forest density (R^2 = 0.5, p=<0.001), bark roughness (R^2=0.2, p=<0.001) and DBH (R^2=0.3, p=<0.001) are all acting on community variation mainly along NMDS axis 1 and canopy (R^2=0.2, p=0.002) and altitude (R^2= 0.1, p=0.008) are acting along both axes 1 and 2 (Figure 4). In the static NMDS, DBH (R^2=0.2, p=0.001) and bark roughness (R^2=0.2, p=0.006) are the only significant habitat drivers of community composition, and these are both acting along NMDS axes 1 and 2. For all three NMDS analyses presented here, a convergent solution was not reached after 1000 attempts. However, results of multiple runs were generally consistent. Stress values were fairly high (all above 0.2 (see plots for details)), so plots should be interpreted with care (Clark, 1993).

Indicator species analysis

Several species such as *Fuscopannaria ahlneri* and *Coccocarpia parmicola* were found to be associated with static treelines (Appendix F, Table A3). *Hypotrachyna sinuosa* is an indicator of closed and diffuse treeline and diffuse tree limit whereas *Hypogymnia flavida* and *Myelochroa irrugans* are associated with treeline/tree limit in all forms. *Sphaerophorus taiwanesis* and *Cladonia* spp. were suggested as indicators of interior forests for all forms. *Lobaria retigera* and *Nephromopsis laureri* were associated with all positions in static forms but not closed or diffuse treeline/limit and similarly *Nephromopsis morrissonicola* was associated with all forest positions in abrupt advancing and static forms but not with diffuse form treeline and tree limit positions.

Discussion

Habitat characteristics vary with forest position and treeline form (Figure 2). In diffuse advancing treelines, tree size and density decrease from interior forest to tree limit and there is variation in species composition dependent on form. Accompanying this change in these rapidly advancing diffuse treelines, there is a decrease in species richness of lichens that is not found in static and abrupt advancing treelines. Results of the GLMM (Table 3) indicate that lichen species richness is related to tree size and distance from interior forest. The significance of the interaction term and the effect of its inclusion in the model show that the importance of distance is somewhat dependent on tree size; at small distances from interior forest tree size has little influence on species richness but at long distances from forest interior the effect of tree size becomes more important. These results demonstrate that rapid treeline advance (an estimated advance of c. 0.3 m yr^{-1} in altitudinal metres for diffuse advancing compared with c. 0.09 m yr^{-1} in the abrupt form treeline (Greenwood et al. 2014)), and the associated change in forest structure has negative consequences for the lichen community because the community is not able to effectively respond to, or tolerate changes in forest position and habitat when treeline advance is happening quickly. However, the higher species richness of abrupt advancing treelines indicates that lichen communities are able to respond effectively to slower treeline advance rates with less associated changes in forest structure. Nestedness analysis suggests that the species richness at diffuse advancing edges is lower because only a subset of those species found in areas with higher richness are colonising diffuse advancing edges. Furthermore, NMDS and dissimilarity indices show that community composition varies more with forest position in diffuse advancing treelines.

Lichens are known to be slow to respond to changes in forest structure and habitat (Ellis and Coppins, 2007; Johansson et al. 2013), and to have limited establishment rates (Nash, 2008; Sillett, 2000). Consequently, the reduction in species richness and change in composition that we detect is likely to result from the differential migration and colonisation rates of lichens and trees acting together with changes in forest conditions at diffuse advancing treelines. In the more rapidly advancing treelines, conditions are not favourable for many species of lichen found in stable and slow advancing treelines. The observed reduction in forest specialists with more rapid treeline advance is likely to be applicable to the wider forest understory community because these plants are also known to have lower migrational capacity than that of trees (Roberts, 1989; Matlack, 1994).

The changes in habitat that occur when treelines advance rapidly in a diffuse form are key in shaping the lichen community; habitat factors that are most strongly associated with changes in community composition along the two NMDS axes in all three NMDS plots are DBH and bark roughness (Appendix E); these two factors are correlated as DBH and bark roughness will both increase as trees age. Similar factors are, therefore, driving species richness and community composition (Table 3 and Appendix E). When diffuse and static sites are compared (Appendix E, Figures A2 and A3) we can see that high values of DBH and bark roughness tend to be associated with interior and forest communities for both forms and that diffuse treeline/limit communities are associated with high values of altitude and canopy openness.

Tree size is an important determinate of lichen species richness (Friedel et al. 2006; Kiraly *et al*. 2013). This is due to a longer continuity of habitat allowing for more establishment and growth (Gustafsson *et al*. 1995), and a larger area of available habitat and increased habitat complexity due to deeper cracks and fissures on older bark (Friedel *et al*. 2006). Forest structure is also important for lichens (Moning *et al*. 2009) and factors such as canopy openness (Li *et al*. 2013) and the amount of dead wood (Caruso et al. 2008) have been found to be associated with lichen species richness. Higher richness is often found in old growth, primary forests (Kuusinen and Siitonen 1998) and changes such as thinning due to forest management often have negative impacts (Sillett *et al*. 2000; Nascimbene *et al*. 2013). The changes in forest structure and treeline position reported by Greenwood et al. (2014) and summarised in this study are leading to different forest conditions at rapidly advancing forest edges when compared with those advancing more slowly with consequent impacts on the ecology of these new forests.

Here we found that certain species were associated with specific forest position and treeline forms and were excluded from others. Squamulose and large foliose growth forms tend to be associated with interior forest or static treelines as do lichens with a cyanobacterial photobiont. Growth form and photobiont are often identified as traits important in determining species distribution of lichens (Rose, 1976; Kuusinen, 1996). The species *Lobaria retigera* was found frequently in our samples and was shown to be indicative of several forest positions, excluding advancing treelines and tree limits. This species is considered an indicator of old growth conditions in British Columbia where it shows a high sensitivity to edge effects such as heat stress and desiccation (Stevenson and Coxson, 2008), similar responses could explain its absence from advancing edges in this study. The forest at newly advancing edges is not yet established enough to support species such as this and the lower density of trees means light intensity is likely higher, temperatures more variable and desiccation more likely.

Our data demonstrate that the rate and form of treeline advance affects whether or not co-occurring species are able to track changes; when advance occurs quickly over a long distance there is a reduction in species richness because some species are not able to establish quickly in, or tolerate conditions in the new forest. However, we find high species richness in abrupt advancing edges where the upslope migration has occurred more slowly and is associated with less change in forest structure. This lag in species richness in rapidly advancing forest is, therefore, likely to be maintained as long as rapid migration continues. If tree migration is halted, due to changing environmental conditions or a lack of habitat availability for tree establishment, even if lichen migration is slower than that of trees, the full complement of species typical of established forest will eventually colonise the newly forested areas. However, migration of species due to increasing global temperature is not limited to montane areas but is expected to occur over much larger areas in the lowlands where temperature changes less for any given distance (Jump et al. 2009). The findings we report here indicate that where advance occurs over a very wide area, such as advance of woody species into arctic tundra sites (Lescop-Sinclair and Payette 1995; Lloyd et al. 2003; Lloyd and Fastie, 2003) then the reduction in co-occurring species richness found here could be a sustained response.

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Appendices

Appendix A

Bark roughness index

1: Smooth bark; no fissures or cracks.

2: Fairly smooth; some cracks and fissures but none of significance (all c.1- 2 mm deep or less)

3: Rough; fissures and cracks deep (2 -5 mm), some anomalies.

4: Very rough; fissures and cracks very deep (>5 mm), anomalies common.

Appendix B

Literature used for species identification

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Appendix C

Table A1: Lichen species list and accession numbers for GenBank and RBGE Herbarium.

Species name	***In GenBank***	***In RBGE***	***Accession number***
Allocetraria madreporiformis	*2*	*0*	S4 32 CIS1 C6 32 CIS2
Anzia formosana	*2*	*2*	C8 32 HYPB3 S4 31 HYPB5
Bryoria bicolor	*1*	*1*	S5 11 BB2
Cetrelia braunsiana	-	-	-
Cetrelia cetraoides	*1*	*1*	S9 11 PAP1
Cetrelia chicitae	*1*	*1*	S5 31 PEX1
Cetrelia japonica	*1*	*1*	C1 21 PSA3
Cetrelia olivetorum	*1*	*1*	S3 22 PAU1
Cetrelia pseudolivetorum	*2*	*2*	D4 32 PT2 C10 32 PT3
Cladonia spp.	-	-	-
Coccocarpia erythoxyli	*1*	*1*	S9 22 COP2
Coccocarpia palmicola	*1*	*1*	S5 21 COE3
Everniastrum cirrhatum	*2*	*2*	D11 42 EVC1 D3 22 EVC2
Fuscopannaria ahlneri	*2*	*2*	S6 11 PNSP4 S8 11 PNSP2
Fuscopannaria leucostica	*2*	*2*	S10 31 GR1 S3 32 GR4
Heterodermia boryi	*2*	*2*	D3 42 HL2 S2 11 HL3
Heterodermia casarettiana	*2*	*2*	D3 32 HS1 C3 22 HO1
Heterodermia isidiophora	*2*	*2*	S5 12 HI3 S4 11 HI2
Heterodermia japonica	*2*	*2*	C6 21 HJ2 S4 22 HJ3
Heterodermia microphylla	-	-	-
Heterodermia subascendens	*2*	*0*	D3 32 HS1 S10 22 HS2
Hypogymnia flavida	*2*	*2*	C6 12 HYF3 S11 12 HYF2

Hypogymnia hengduanensis	*1*	*1*	C9 12 HYH4
Hypogymnia pseudoenteromorpha	*1*	*3*	C11 11 HYPE1 S5 31 HYPE2 C4 12 HYPE3
Hypogymnia stricta	*1*	*0*	S6 22 HYS3
Hypogymnia subarticulata	*1*	*1*	S3 11 HYS2
Hypogymnia taiwanalpina	*1*	*0*	D3 32 HYT1
Hypogymnia vittata	*1*	*1*	D4 21 HYT2
Hypotrachyna majoris	-	-	-
Hypotrachyna sinuosa	*1*	*1*	D7 12 HYSi1
Leptogium burnetiae	*1*	*1*	D6 32 LEPB3
Leptogium pseudofurfaraceum	*2*	*2*	S10 31 LEPA4 S5 21 LEPA3
Lobaria quercizans	*1*	*1*	D3 41 LD2
Lobaria retigera	*1*	*1*	D6 31 LI1
Lobariella wrightii	-	-	
Menegazzia anteforata	*2*	*1*	D4 12 MAN1 S8 11 MAN2
Menegazzia primaria	*1*	*1*	C5 12 MPS3
Menegazzia pseudocyphellata	*1*	*1*	D5 11 MPS2
Menegazzia terebrata	*2*	*2*	D1 11 MPR1 S11 21 MPS1
Myelochroa irrugans	*2*	*2*	C5 12 MYI1 S1 11 MYI5
Nephroma helveticum	*1*	*1*	S9 11 PPR1
Nephromopsis laureri	*2*	*2*	S7 32 N/P1 S5 21 N/P2
Nephromopsis morrisonicola	*1*	*1*	S6 12 NM4
Parmelia adaugescens	*2*	*2*	S9 11 PAAD3 D3 12 PAAD5
Parmelinopsis afrorevoluta	*2*	*2*	D3 22 CTX1 S1 12 CTX4
Parmeliela parvula	*2*	*2*	S11 31 GR2 S4 32 GR3
Peltigera polydactyla	*2*	*2*	D8 42 PHO3 S3 31 PPR3
Phaophyscia hirtuosa	*1*	*0*	D4 PYPE1

Phsyconia muscigena	*1*	*0*	C1 21 HDS1
Pseudocyphellaria desfontainii	*1*	*1*	D11 41 PDE1
Sphaerophorus taiwanensis	*1*	*1*	C1 31 ST4
Sticta filicina	*1*	*1*	C8 32 SF2
Sticta nylanderiana	*1*	*1*	S10 32 SPL4
Sticta wrightii	*2*	*0*	D2 31 SPR2 D3 31 SPL3
Sulcaria sulcata	*1*	*1*	S9 12 BB1
Usnea articulata	-	-	-
Usnea diffracta	-	-	-
Usnea himalayana	-	-	-
Usnea longissima	*1*	*1*	D11 11 UL4
Usnea malmei	*2*	*2*	S3 11 UN3 D11 22 UN4
Usnea pycnoclada	-	-	-
Usnea trichoideodes	*2*	*2*	S2 11 UL1 S711 UL2

Appendix D

Table A2: Bray Curtis dissimilarity indices for all forest position/ treeline form combinations of lichen community data collected along transects on a treeline ecotone on Hehuanshan, Taiwan.

	Tree limit	**Abrupt Treeline**	**Diffuse Treeline**	**Static Treeline**	**Abrupt Forest**	**Diffuse Forest**	**Static Forest**	**Abrupt Interior**	**Diffuse Interior**
Abrupt Treeline	0.28								
Diffuse Treeline	0.29	0.2							
Static Treeline	0.35	0.23	0.27						
Abrupt Forest	0.39	0.2	0.22	0.27					
Diffuse Forest	0.35	0.23	0.16	0.2	0.2				
Static Forest	0.42	0.34	0.29	0.31	0.26	0.22			
Abrupt Interior	0.57	0.39	0.38	0.38	0.26	0.26	0.26		
Diffuse Interior	0.45	0.32	0.24	0.33	0.2	0.24	0.24	0.26	
Static Interior	0.44	0.32	0.24	0.27	0.22	0.14	0.24	0.2	0.16

Appendix E

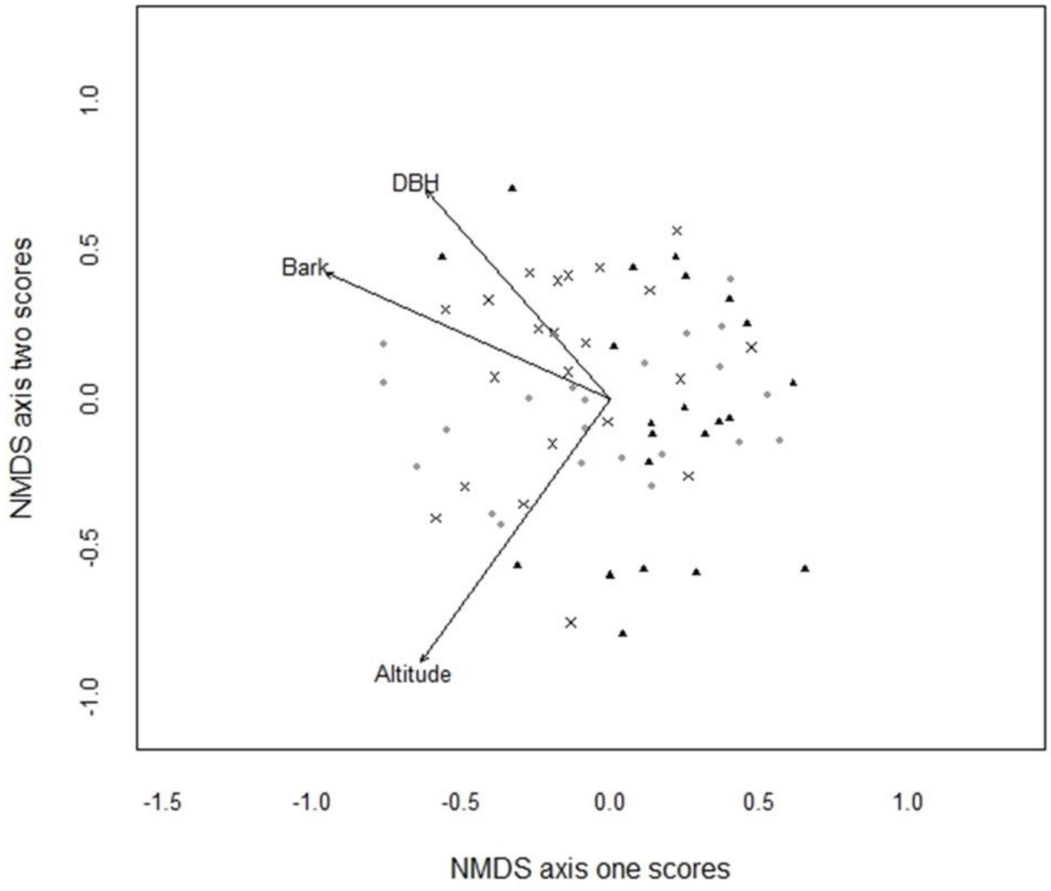

Figure A1: Community variation in an NMDS analysis of treeline sample sites of epiphytes on Hehuanshan, Taiwan. Treeline forms are shown by symbols as follows: abrupt advancing: grey circles, diffuse advancing: black triangles and static treeline forms: black crosses. The main habitat factors associated with community variation are shown. Stress value is 0.28.

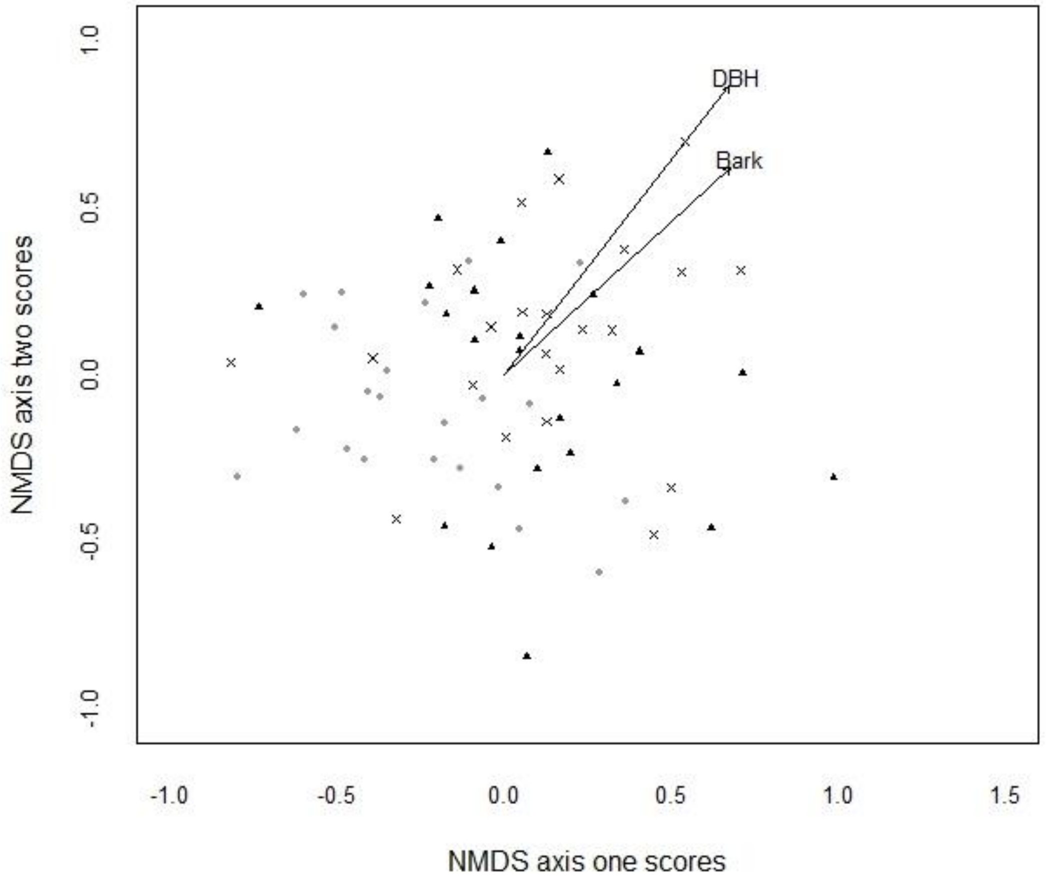

Figure A2: Community variation in static treeline form transects in an NMDS analysis of epiphyte communities on Hehuanshan, Taiwan. Forest position is shown by symbols as follows: treeline: larger grey circle, forest: black triangle, interior: grey cross. Main habitat factors associated with community variation are shown. Stress value is 0.27.

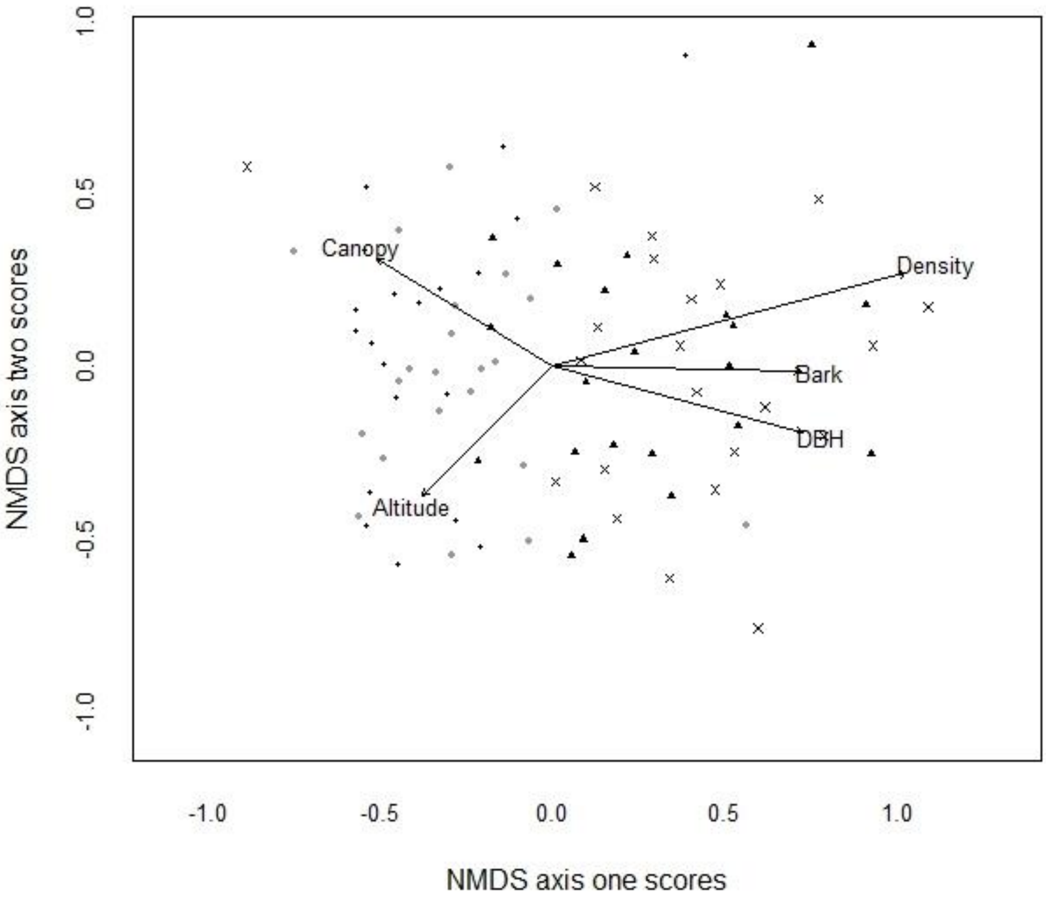

Figure A3: Community variation in diffuse treeline form transects in an NMDS analysis of epiphyte communities on Hehuanshan, Taiwan. Forest position is shown by symbols as follows: tree-limit: small grey circle, treeline: larger grey circle, forest: black triangle, interior: grey cross. Main habitat factors associated with community variation are shown. Stress value is 0.24.

Appendix F

Table A3: Indicator species and their associated habitats. Relevant traits that may affect habitat preferences are also shown. For certain species/trait combinations no data were available, these are shown as a dash (–) in the table.

Species name	**Associated forest position/**	**Reproduction**	**Growth form**	**Sorediate/isidiate**	**Photobiont**	**Ascospore size**	**Reference**
Fuscopannaria ahlneri	Static treeline	Apothecia common	Squamulose	-	Cyanobacteria (Nostoc)	-	-
Cococarpia palmicola	Static treeline	Apothecia infrequent	Small foliose	Isidiate	Cyanobacteria (Scytonema)	7-14 x 3-5 µm	Nash et al.2001
Hypotrachyna sinuosa	Expanding treelines	-	Foliose	Sorediate	Green algae (iCoccomyxa).	-	Kurokawa and Lai 2001
Hypogymnia flavida	Treeline/limit	-	Foliose	Neither	Green algae (chlorococcoid)	-	McCune 2009
Sphaerophorus taiwanesis	Interior Forest	-	Coralloid/shrubby	Neither	Green algae	-	-
Cladonia spp.	Interior Forest	-	Squamulose	-	Green algae (Asterochloris)	-	Wang et al. 2011
Myelochroa irrugans	Treeline/limit	Apothecia	Foliose	Neither	Green algae (Trebouxia)	7-10 x 11-16 µm	Kurokawa and Lai 2001
Lobaria retigera	All except expanding treelines/limit	Apothecia infrequent	Large foliose	Isidiate	Cyanobacteria	30-40 x 5-7 µm	Ren et al. 2012
Nephromopsis laureri	All except expanding treelines/limit	Apothecia infrequent	Foliose	Sorediate	Green algae	6-12 x2.5-6 µm	Thell et al. 2005
Nephromopsis morrisonicola	All except diffuse expanding treelines/limit	Apothecia	Large foliose	Isidiate	Green algae	6-12 x2.5-6 µm	Thell et al. 2005

Chapter 7

General Discussion and Synthesis

The impacts of climate variation on high altitude forests in Taiwan have been investigated here at a number of spatial scales, allowing for a good understanding to be gained of treeline patterns and process in the Central Mountain Range. This research sought to characterise the recent changes in the treeline forests, to investigate the mechanisms behind the observed change, and to explore the possible consequences of advance for the wider community.

The analysis of aerial photographs allowed for changes in treeline position to be characterised and for topographic drivers of change to be identified at a large spatial scale (Chapter 3). The mechanisms behind the observed shift were explored through an investigation of two key processes associated with advance: tree growth climate relationships and their variation over time and with altitude (Chapter 4), and regeneration patterns in relation to topography and microclimate conditions (Chapter 5). This provided mechanistic, detailed information at a much smaller scale of inquiry. The consequences of the observed changes in treeline position, structure and forest density for the wider community were explored through an investigation of epiphytic lichen communities across static and advancing treeline ecotones, representing an intermediate study scale, with sampling over a fairly large area and consideration of community level responses (Chapter 6). This use of mixed spatial scale was appropriate as it allowed for landscape scale patterns to be identified but for more useful information on process to be gained at a smaller scale, more relevant to individual trees and localised areas.

Treeline is advancing in a complex and topographically mediated way in the Central Mountain Range of Taiwan, with a variety of structural forms present at treeline (Chapter 3). Tree growth has increased in recent years (Chapter 4), seedling distribution patterns are driven by soil microclimate conditions and topography (Chapter 5) and treeline advance has the potential to change community composition of associated species, although this depends on the rate of advance (Chapter 6).

Characterising treeline advance

There is widespread evidence of altitudinal treeline advance occurring globally (Kullman, 2002; Peñuelas and Boada, 2003; Beckage *et al*., 2008; Devi *et al.*, 2008; Harsch *et al.*, 2009; Kharuk *et al*., 2009), but the nature of the response is variable, with high heterogeneity on global (Harsch *et al.*, 2009), local and regional (Danby and Hik 2007; Macias-Fauria and Johnson 2013; Hofgaard *et al.*, 2013) scales. The degree of advance reported varies, some studies report rapid advances; e.g. of a more than 100 m gain in treeline altitude in the Swedish Scandes over the last century (Kullman, 2002) and up to 60 m altitude gain in the Russian Urals over the same time period (Devi et al. 2008), whilst others report very little (Sziecz and MacDonald, 1995), or no change in treeline position (Hättenschwiler and Körner, 1995; Cullen *et al.*, 2001) and there may be a considerable time lag between a change in climate and a response at treeline (Lloyd, 2005; Rannow, 2013).

Treeline studies provide vital information on the factors responsible for range limits (Korner, 1998), and provide early indications of climate response (Smith *et al.*, 2009). Temperature is thought to be the main determinant of treeline position on a broad scale (Tranquillini, 1979; Korner, 1998; Jobbágy and Jackson, 2000; Korner and Paulsen, 2004), although the exact nature of the physiological limitation imposed by low temperature is still debated (Korner, 1998; Hoch and Korner, 2003; Wieser and Tausz, 2007; Bansal and Germino, 2008). Studies of global treeline position (e.g. Korner and Paulsen, 2004) have allowed for greater understanding of the drivers of treeline advance. However, the detail provided by regional examples is vital. Although the relative importance of drivers will vary with scale (Holtmeier and Broll, 2005), the information gained from regional level studies needs to be applied on a global scale before a full understanding can be gained of treeline position and advance (Holtmeier and Broll, 2007; Smith *et al*., 2009).

Treeline advance in the Central Mountain Range of Taiwan is spatially variable and related to topography and treeline form (Chapter 3). Other authors have found evidence of topographic limitations to advance (Resler *et al.*, 2005; Resler, 2006; Butler *et al.*, 2003; Kullman and Oberg, 2009; Macias-Fauria and Johnson, 2013), and of a link between treeline structural form and climate response (Harsch *et al*., 2009). Regional variations in treeline position and advance rate have been associated with; land use (Peñuelas and Boada, 2003; Norman and Taylor, 2005), soil conditions (Holtmeier and Broll, 1992) and vegetation above treeline (Cullen *et al*., 2001; Dullinger *et al*., 2003) as well as climatic conditions (Peñuelas and Boada, 2003; Kullman, 2007; Shiyatov *et al*., 2007; Beckage *et al*., 2008; Kharuk *et al*,. 2009). An understanding of the drivers of variation at a regional scale is of importance as it allows for wide scale patterns to be discerned, and for areas where future advance is likely to be identified.

Understanding treeline advance

In order to better understand treeline advance, and to predict the nature of the response of treelines to changes in climate it is necessary to consider some of the mechanisms behind the process of treeline advance. In many cases where treelines are not responding through an advance, other changes such as increased growth, or changes in growth form have been observed (Villalba and Veblen, 1997; Lescop-Sinclair and Payette, 1995; Kharuk *et al.*, 2009, 2010) and these growth related changes often occur alongside an advance (Devi *et al.* 2008). Increases in forest density (Lescop-Sinclair and Payette, 1995; Sziecz and MacDonald, 1995; Camarero and Gutiérrez, 2004; Liang *et al.*, 2010) through increased regeneration within alpine forest areas is also common and regeneration beyond the treeline, and the successful progression of seedlings to adults is the key process by which treelines advance (Smith *et al*., 2009). Increased understanding of these key processes of tree growth and regeneration allows for more accurate prediction of treeline advance.

Tree growth and climate

Recent increases in tree growth at treeline are reported in response to warming (Bunn *et al*., 2005; Salzer *et al*. 2009; King *et al*., 2013; Chapter 4) and although changes in growth do not lead to an advance, (Holtmeier and Broll, 2007) advance is more likely to occur when climate becomes more favourable for growth. An understanding of the growth climate relationship therefore gives crucial insight into the limitations imposed by temperature at treeline. Tree growth is often temperature limited at high altitude (Mäkinen *et al.*, 2002; Zang *et al*., 2010; Yu *et al*., 2013), although local variations in soil conditions and precipitation levels may mean that moisture availability is also important (Graumlich, 1993; Takahashi *et al*., 2003; Wang *et al.*, 2004).

Changes in tree growth have implications for species conservation (Büntgen *et al*., 2013), range limits (Beckage *et al.*, 2008), climate proxy records (D'Arrigo *et al.*, 2008) and ecosystem carbon budgets (Saxe *et al.*, 2001). The increased growth rates found on Yushan, combined with the changes in treeline position, forest area and density as recorded on Hehuanshan suggest that the carbon stocking potential of high altitude forest in Taiwan has increased recently. This is a phenomenon that has been reported in several areas (e.g. Wang *et al*., 2013), although the relationship between carbon sequestration, climate and treeline advance is complicated (Hu *et al*., 2010) and much regional variation has been described (Gang *et al*., 2013).

Combining dendroecological work with the analysis of repeat aerial photographs on a wide spatial scale could provide useful information, and, if combined with allometric data would allow for accurate estimations of carbon stocking and changes to carbon stocking potential with warming. It is necessary to consider changes to soil properties associated with changes in tree cover (Kammer *et al*., 2009; Greenwood and Jump, 2014) as well as increased forest area and tree growth. Soil conditions and respiration rates are of vital importance in determining ecosystem carbon budgets, as has been shown in studies of Arctic treeline expansion (Wilmking *et al.*, 2006; Hartley *et al*., 2012). However, soil conditions at alpine treelines are likely to differ from Arctic sites (Michaelson *et al*., 1996), so the consequences of advance will be different (Steltzer, 2004; Kammer *et al*., 2009) and research needs to be conducted on the impacts of alpine treeline advance on soil properties and carbon storage. This is a key research direction for the future, given its potential to impact carbon dynamics and feedback to future warming.

Seedling establishment beyond the treeline

The establishment and survival of seedlings beyond treeline is vital for treeline advance but this life stage is understudied compared to that of adult trees at treeline (Smith *et al.,* 2009). Although some level of regeneration is common above treeline without leading to advance (Lloyd, 2005), it is a prerequisite of advance that seedlings are able to establish and grow to adult trees beyond the current limits of closed forest. Mortality of very young seedlings is often high (Batllori *et al*., 2009), making them useful indicators of the physiological limitations imposed by altitude/low temperatures at treeline (Smith *et al*., 2009).

Microclimate conditions are known to be important in allowing seedlings to establish beyond treeline; studies have found facilitative effects, with seedling survival associated with the presence of adult trees and other vegetation (Germino *et al*., 2002; Batllori *et al*., 2009). The presence of rocks and boulders (Smith *et al*., 2003, Holtmeier and Broll, 2003), and topographic features (Resler *et al*., 2005; Resler, 2006) that provide shelter often lead to higher establishment and topographic aspect can affect establishment patterns (Germino *et al.,* 2002). In the Central Mountain Range, areas offering small-scale topographic shelter were associated with higher numbers of seedlings than more exposed sites and soil microclimate conditions were associated with higher seedling numbers (Chapter 5). Soil temperature is known to be important for nutrient availability, photosynthesis, assimilation and growth (Day *et al.*, 1991; De Lucia *et al*., 1991, 1992; Hoch and Korner, 2003; Dang and Chen, 2013) and global treeline position has been associated with a small range of soil temperatures (Korner and Paulsen, 2004).

Further investigation of soil properties and of seed rain and how it is affected by topography would allow for the drivers of establishment to be better described, as would experimental work transplanting seedlings to variety of sites and using open top chambers to manipulate temperature.

The consequences of treeline advance for the wider community

Holtmeier and Broll (2007) identify that treeline advance has the potential to influence community dynamics and composition. However, to date there have been few direct studies of the impacts of treeline advance on the wider forest or alpine community.

Communities do not respond as units to change, but instead species respond individualistically (Huntley, 1991), thus leading to new combinations of species occurring together after a change in conditions (Huntley, 1990; Edwards *et al*., 2005; MacDonald *et al*., 2008; le Roux and McGeoch, 2008; Klanderud and Totland, 2005). Trees have the ability to modify their environments, affecting soil conditions (Kammer *et al*., 2009), light levels (Canham and Burbank, 1994) and microclimates, and thus will impose pressures on associated species (Halpern and Spies, 1995; Chen *et al.*, 1999). It is therefore likely that treeline advance will lead to changes in the associated community, with potential losses of species (Greenwood and Jump, 2014); this is of particular concern given the high endemicity of alpine areas (Jump *et al.,* 2012).

The few direct studies of the community impacts of treeline advance have generally found a reduction in alpine grassland, with associated reductions in species richness when trees invade alpine habitats (Halloy and Mark, 2003; Moiseev and Shiyatov, 2003; Moen *et al*., 2004; Moore and Huffman, 2004), although the relationship between tree cover and species richness at treeline sites is not always clear (Camarero *et al.,* 2006; Pardo *et al*., 2013). Small scale variation and microsite properties may be more important than tree cover (Camarero *et al.*, 2006), some plants may be adapted to a higher level of forest cover than is found currently (Hofgaard and Wookey, 2002) and the structure of advancing forest may mean that conditions do not change drastically for some time in invaded sites (Kullman, 2010). Given the complexity of community level responses on a landscape scale further research is necessary.

Throughout the Central Mountain Range of Taiwan treeline advance is spatially heterogeneous and structurally complex (Chapter 3), so it was likely that the impacts on community composition would be spatially variable. Epiphytic lichen species richness was lower in treelines that were advancing rapidly and only a subset of the community occurring at stable sites was found at advancing treelines, but this was associated with changes in habitat structure that were only occurring in certain areas (Chapter 6). These results indicate that differential migration rates between co-occurring species results in community disassembly, dependent on the speed of treeline advance.

Future studies that include both above and below ground interactions would be extremely useful; for example to investigate how patterns of mychorrizal fungi and other components of the soil community vary across treelines and how these are impacted by advance. Jump *et al.* (2012) found that many alpine plant species were shifting their ranges upwards in the Central Mountain Range of Taiwan; further research into patterns of shifts in alpine grassland and nival species, and how these changes compare to treeline advance would be useful in order to determine the overall decrease in area of alpine grassland, alpine and nival habitats. The consequences of advance are likely to be higher in Arctic areas, where advance can proceed over longer distances than in alpine sites (Lescop-Sinclair and Payette, 1995; Lloyd *et al*., 2003; Lloyd and Fastie, 2003), so studies considering community impacts on tundra would be useful, although see Chapin *et al.* (1995) and Walker *et al.* (2006) for thorough investigation of community responses to warming, although not treeline advance in Arctic tundra.

Conclusion

This work has investigated the response of high altitude forests in the Central Mountain Range of Taiwan to environmental variation. It has sought to characterise the change in treeline position (Chapter 3), to begin to understand the mechanisms driving it (Chapters 4 and 5), and to consider possible impacts of treeline advance (Chapters 2 and 6), thus providing a vital first step towards understanding treeline advance patterns and process in the area, and improving understanding and predictive ability on a global scale.

Here we have contributed to the global discussion on treeline advance and drivers of change by providing detailed information on the advance of treelines in a subtropical region; this work represents one of the most in depth studies of subtropical treelines to date. Due to the high heterogeneity in the response and structure of treelines (Harsch *et al*., 2009;Wiegand *et al.,* 2006), regional studies such as this are required to allow for global scale patterns to be identified and understood, particularly given the dearth of knowledge of subtropical and tropical alpine areas.

The importance of topography (Resler *et al.*, 2005, 2006), treeline structure (Harsch *et al*., 2009) and sheltering (Huang, 2002) for advance has been confirmed, and much needed process based information on tree growth and establishment patterns at subtropical treelines has been provided. Tree growth at treeline has been shown to be increasing in response to warming and establishment beyond treeline has been found to be associated with warm soil conditions, suggesting that future advance is likely if warming continues. Community impacts have been considered, and we have determined that treeline has the potential to influence community dynamics, this is a vital consideration given the wide scale nature of treeline advance but one that has not received adequate attention until now.

An essential first step in understanding the patterns, causes and consequences of treeline advance in the Central Mountain Range of Taiwan has been provided, substantially increasing our ability to predict global treeline responses and subsequent impacts on ecosystem structure and function over the coming years. By providing information from a new region in an understudied part of the world, and through unique efforts to explore the drivers and impacts of advance, this research makes a valuable contribution to global treeline research.

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