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

SARAH GREENWOOD[1], JAN-CHANG CHEN[2], CHAUR-TZUHN CHEN[2] and ALISTAIR S. JUMP[1]

[1]*Tropical Ecology and Conservation Group, Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK* [2]*Department of Forestry, National Pingtung University of Science and Technology, 1 Hseuh Fu Road, Nei Pu Hsiang, Pingtung 912, Taiwan*

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 realized 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.

Keywords: *Abies kawakamii*, aerial photography, alpine habitat, central mountain range, climate change, forest density, fragmentation, Taiwan, topography

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Introduction

Anthropogenic climate change has resulted in unprecedented rates of warming across the globe with temperatures rising by around 0.25 °C per decade in the period 1979–2012 (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; Walther, 2003; Parmesan, 2006; 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 & 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 & Paulsen, 2004). However, an advance is by no means a universal response; many treelines that experience warming temperatures show no change in position (Hättenschwiler & Körner, 1995; Harsch *et al.*, 2009). Environmental variability between sites is high (Lloyd & 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 & 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

Correspondence: S. Greenwood, tel. +44 1786 466550, fax +44 1786 467843, e-mail: sarah.greenwood85@gmail.com

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 subalpine shrubland, in others the transition is smooth (Wiegand *et al.*, 2006) or diffuse (Harsch & 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 & Hik, 2007; Macias-Fauria & 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 & 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 & Boada, 2003; Camarero & Gutiérrez, 2004) and North America (Rochefort *et al.*, 1994; Suarez *et al.*, 1999; Beckage *et al.*, 2008), there is a lack of knowledge on tropical and subtropical treeline advance. Studies of Far East Asia are poorly represented in the scientific literature and the dynamics of high altitude subtropical 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 & 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 & Boada, 2003; Elliott & Baker, 2004; Danby & 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 (Fig. 1). Our aim was to examine the highly spatially variable treeline advance within the region and identify how realized 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.

Materials and methods

Study area

The island of Taiwan straddles the Tropic of Cancer and has more than 200 mountains over 3000 m a.s.l., concentrated within the Central Mountain Range (Guan *et al.*, 2009). The

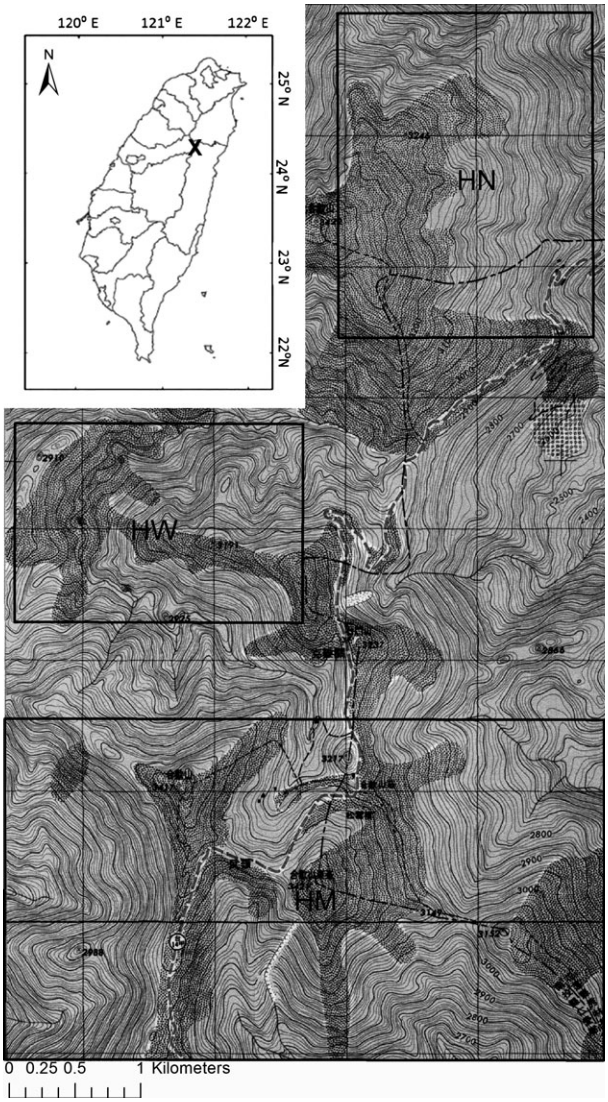

Fig. 1 Location of the study area Hehuanshan (black cross) in the island of Taiwan (inset) and location of the aerial photographs [black outlined boxes (HN: Hehuan North Peak region, HW: Hehuan West Peak region, HM: Hehuan Main Peak region)] within this area on a topographic map (1:25 000 scale).

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 2800–3000 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 Körner (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 & 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 °C for the Alishan area compared with 1934–1970 mean values, while Hsu & Chen (2002) predict rises in temperature over a thirty-year period of between 0.9 and 2.7 °C, compared to 1961–1990 mean values.

Rectification of aerial photograph data

Three sets of repeat aerial photographs were used in these analyses (Figs 1 and 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 as 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 (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, USA).

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

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

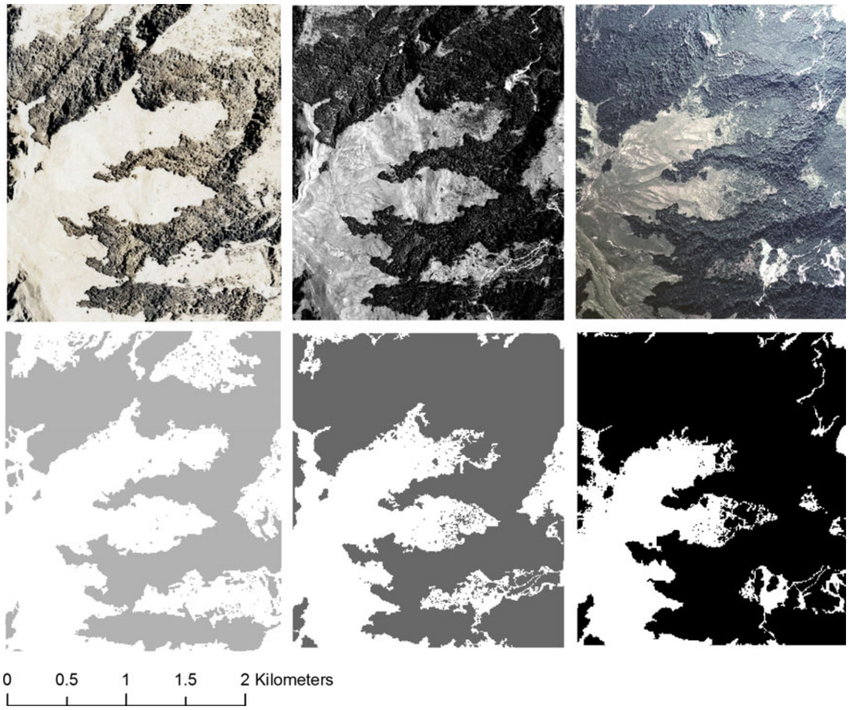

Fig. 2 Forest and grassland extent in the Hehuan North Peak region of the Central Mountain Range of Taiwan. Upper panels show aerial photographs and lower panels the raster layer of forest cover for each photograph respectively. Images from left to right are from 1948, 1964 and 2001.

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.

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 × 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 × 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.

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:

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

where:

S_{ij} = Topographic shelter index

W_k = weight in cardinal compass direction (k)

d_k = distance in cardinal compass direction (k)

$\mathrm{STD}\, d'_k)$ = 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 × 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 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 (Fig. 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.

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).

Kolmonogrov–Smirnov tests show that the frequency of slope (D = 0.15 (North Peak Region) and 0.06 (West Peak Region), P < 2.2e-16 for both image sets) and aspect (D = 0.23 for North Peak and 0.07 for West Peak, P < 2.2e-16 for both) values of new establishment is independent of the available habitat area. Trees reached higher mean elevation at south west and south aspects (Fig. 4).

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^{-1}) 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^{-1} 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). Shelter is

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

Region	Mean distance 48–60 s (m)	Mean distance 60 s–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

Table 4 Temporal changes in treeline position based on comparing within image point locations from aerial photographs of the Central Mountain Range

Region	Mean distance 1960 s (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

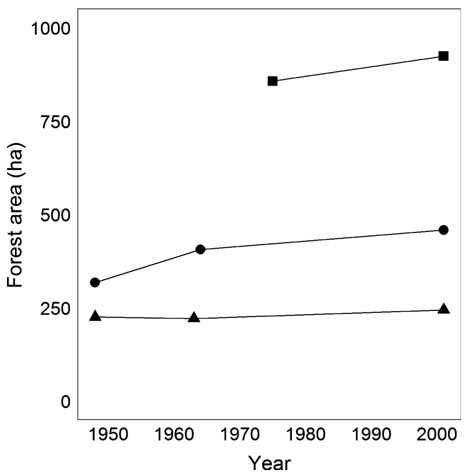

Fig. 3 Temporal changes in forest area in three regions of the Central Mountain Range of Taiwan: North Peak (circles), West Peak (triangles) and Main Peak regions (squares).

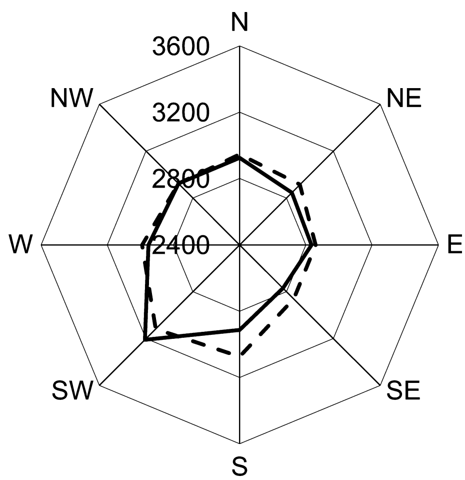

Fig. 4 Mean elevation (in metres) of newly established *Abies kawakamii* trees above treeline at each aspect for two regions of the Central Mountain Range of Taiwan. Hehuan North Peak is represented by a solid line, Hehuan West Peak with a dashed line.

significantly higher in diffuse treelines and lower in static treelines (Fig. 5).

Subsamples from the Hehuan North and West Peak areas show a large variation in the degree of advance based on treeline form (Fig. 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 ($F = 17.77$, $P = 0.00075$).

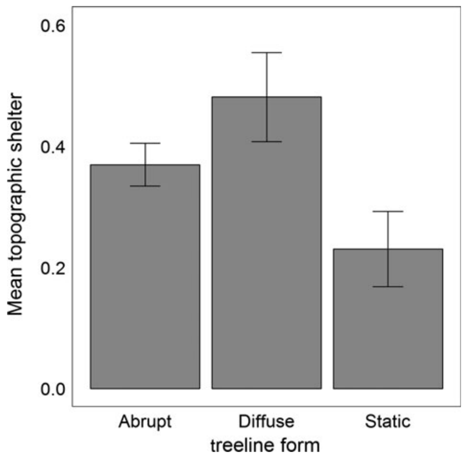

Fig. 5 Topographic sheltering score associated with principal treeline structures in the Central Mountain Range. A higher topographic sheltering score is associated with more sheltered areas.

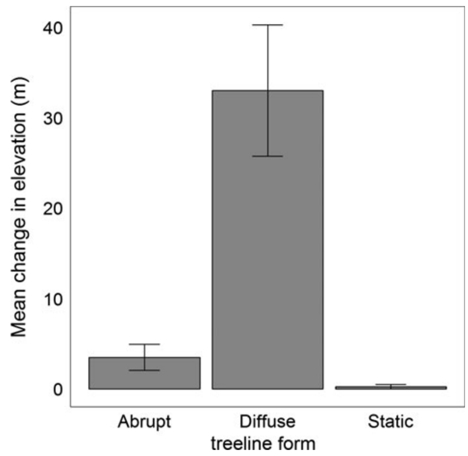

Fig. 6 Mean change in elevation of the treeline in the Central Mountain Range between years 1963/4 and 2001 for the principal treeline structures identified within the area.

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^{-1} can be observed between 1975 and 2001 (Fig. 7 and Figure S5). 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.

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 & 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. Moen *et al*., 2004; Kullman, 2007). However, it is important to recognize 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 Fig. 6). Guan *et al.* (2009) calculated altitudinal temperature lapse rates for Taiwan to be 0.5 °C 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; while some treelines are highly responsive to warming (Devi *et al*., 2008), others show a marked lag behind isotherm movement (Szeicz & Macdonald, 1995). Disparities between isotherm movement and treeline position highlight the complex interaction of ecological and physical factors that are responsible for realized 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

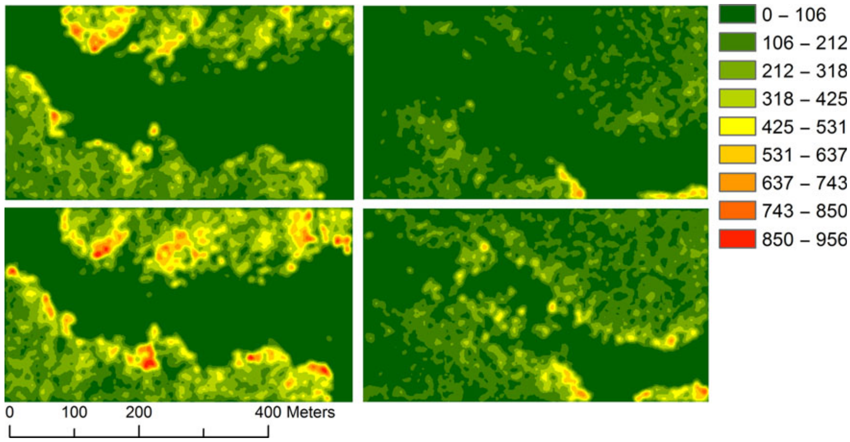

Fig. 7 Changes in tree density from 1964 to 2001 from locations immediately below the treeline of the Central Mountain Range. Images are in pairs; top two images are from 1964, bottom two are the same subsamples from 2001. Density values are shown in trees per ha, rounded to the nearest tree.

and dispersal (Dullinger *et al.*, 2004), establishment limitations such as poor soil conditions (Lloyd *et al.*, 2002) and competition from alpine species (Holtmeier & 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 & Kershaw, 2013).

Topography (aspect, slope, sheltering) influences treeline behaviour in Taiwan (Figs 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. While 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 recognized (Butler *et al.*, 2003; Danby & 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 (Macias-Fauria & 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 & 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 & Smith, 1999) but, to date, little work has been conducted in the subtropics where the driving mechanisms may differ.

In this study, changes in treeline position led to large increases in forest area (Fig. 3) and also in forest density (Fig. 7). 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 & 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 & 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 & Shiyatov, 2003) while in Arizona, diversity has been reduced by a decrease in open areas (Moore & 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 & Moen, 2003). The topographic influence on advance, found here and in other studies (Kullman & Oberg, 2009; Macias-Fauria & 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 & Hik, 2007; Kullman & 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 subtropics 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 biodiverse 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

Additional Supporting Information may be found in the online version of this article:

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.