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

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Abies kawakamii; Alpine forest; Microclimates; Microtopography; Regeneration; Subtropics; Taiwan; Treeline advance

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Abstract

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, if sheltering plays an important role in seedling establishment and if the response varied with seedling age.

Location: The *Abies kawakamii* treelines of the Central Mountain Range, Taiwan, 2800 to 3275 m a.s.l.

Methods: Seedlings were monitored in plots covering a range of treeline structural forms over a period of 2 yrs. Temperatures were recorded at plant-relevant height (5 cm) above ground and depth below ground with data loggers. Microtopographic sheltering (at a 10-m scale) and surrounding vegetation were measured. The influence of the above variables on seedling number and growth was investigated using generalized linear models and linear mixed effect models, respectively.

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

Conclusions: Air and soil temperatures and microtopography 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.

Introduction

Mountain treelines are increasing in elevation in many areas across the globe in response to on-going 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, 2009).

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Microclimate conditions across the treeline ecotone are very different from conditions below the canopy of a developed forest. For advance to occur, seedlings must either be able to tolerate the conditions beyond treeline or exploit microtopographic features providing 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, for example, reducing exposure to excess light and day-time temperature, increasing night-time temperature 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). Topography and the effects of landscape features on the degree of exposure experienced by seedlings can 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 & Smith 1999) and damage to photosynthetic machinery at high temperature. Germino & 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 temperature at high altitudes beyond the canopy cover of the forest (Holtmeier & Broll 1992; Wieser et al. 2010), this could be a mechanism by which treeline is able to advance beyond forest limits by facilitating establishment beyond the canopy.

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

Körner & Paulsen (2004) found the position of treelines on a global scale was 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 uptake of CO_2 through stomata, 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 characterizing patterns of treeline advance at a landscape scale is important for understanding the generalized 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).

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) microtopography 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; and (4) smaller seedlings will be more sensitive to temperature and sheltering than larger seedlings.

Methods

Study site

This work was conducted in the Hehuanshan area of the Central Mountain Range of Taiwan (Fig. 1; 24°08–09′ N, 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 (Liu 1971). At high altitudes these stands

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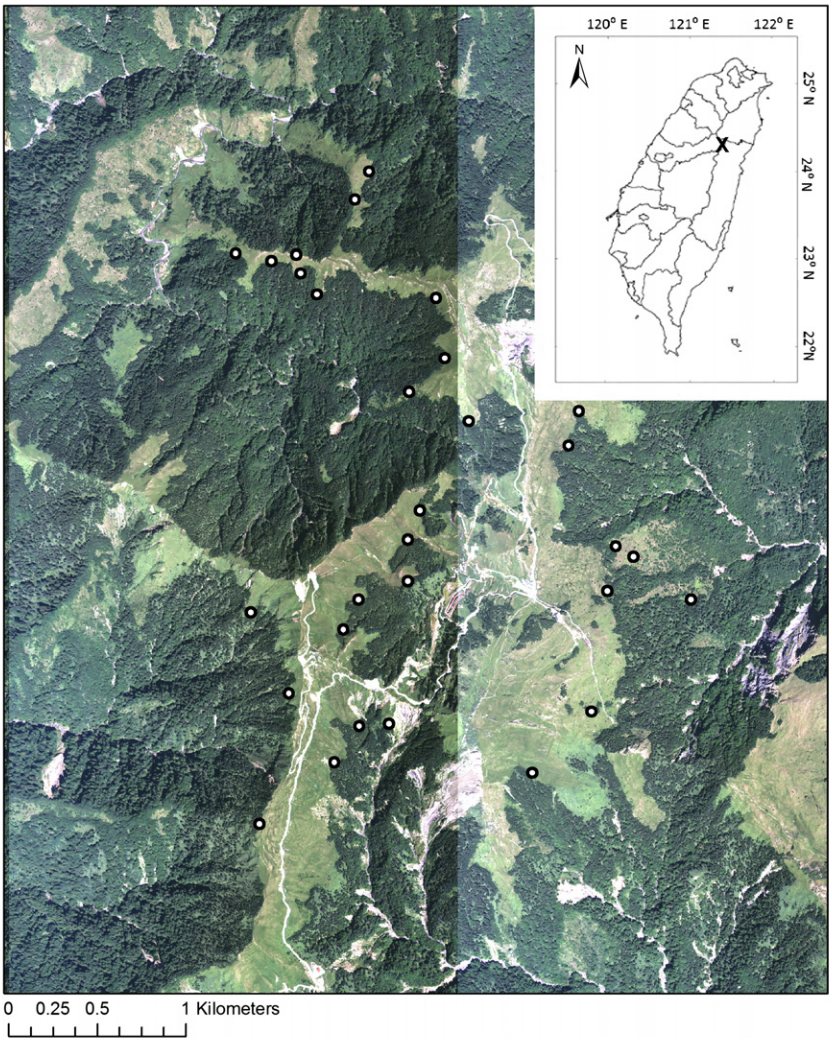

Fig. 1. The location of the 30 plots within the study area (white circles) and location of the study area within Taiwan (inset, study area marked with cross).

consist mainly of *Abies kawakamii*, *Tsuga chinensis* and *Pinus taiwanensis*. The area consists of complex topography, with a maximum altitude of 3560 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 of shrubs such as *Juniperis formosana, Rhododendron pseudochrysanthum* and *Rhododendron rubropilosum.*

The treeline in the study area shows considerable variation in its structural form. Aerial photograph analysis and forest inventory work (Greenwood et al. 2014) 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 & Bader 2011).

Microclimate data collection

Thirty study plots of 5 m × 5 m were set up in April 2011; sampling effort was evenly distributed between the five treeline forms (Fig. 1), fieldwork areas were picked randomly within these forms from aerial photographs and plots were then selected randomly when in these areas. At the time of plot selection, two iButton Thermochron DS1921G (Maxim Integrated Products, Inc., San Jose, CA, US) 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 easy identification and

Table 1. Treeline structural forms identified to occur 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 treeline is significantly lower over a small area
Static	Areas of treeline where no advance can be identified and trees at the forest edge are large and old; these edges tend to be abrupt in structure

retrieval. The above-ground height was chosen based on prior measurements of seedlings 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 six times over a 24 h period at intervals of 4 h at: 00:00, 04:00, 08:00, 12:00, 16:00 and 20:00 h (UTC+08:00 h). Sites were visited periodically (five 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 recordings from a nearby meteorological station (Alishan at 23°30′37.42 N, 120°48′18.39 E and 2413 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. Here, we classed trees 50-cm tall or less as seedlings. Plots were searched thoroughly for a period of ca. 1 h in order to standardize 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 during the study period so that survival rates and growth rates could be calculated. Growth rates (RGR: $\text{cm}\cdot\text{cm}^{-1}\cdot\text{yr}^{-1}$) 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 six random points within each plot. In spring 2013, after 2 yrs, data loggers were removed and final recordings made of the seedling numbers, size and condition within each plot.

A measure of sheltering on a small scale (referred to here as microtopographic 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 ca. 10 m from the centre of each plot, in each of the eight cardinal compass directions. 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 elevations as exposed). A mean of all the elevation differences was taken to give one value of microtopographic shelter per site. Elevation differences in the north, northeast and northwest directions were given double weight because prevailing wind direction tends to be from the northwest in this area (Huang 2002).

Statistical analysis

All analyses were performed using R v 0.98.501 (R Foundation for Statistical Computing, Vienna, AT). 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 generalized linear models (GLM), 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 ggplot2 (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 & Ripley 2002) were used to explore the relationships between seedling number and habitat variables. The Poisson distribution was originally used in the models as it is considered suitable for modelling count data (Zeileis et al. 2008), however overdispersion (as suggested by the ratio of residual deviance to residual *df* and tested with the dispersiontest function of the AER package) 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, microtopographic shelter, number of trees in plot, percentage cover of shrubs, distance to treeline and outlier trees. Microclimate data from the data loggers were 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). 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 previous models. *F*- and *P*-values were calculated for each linear mixed effect model through the lmerTest package.

Results

Microclimate data

Failure of several of the data loggers during the study period resulted in a data set 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 h were reliable.

Average air temperatures over the growing season (defined here as March to October) 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 temperature, especially when considering the difference between day and night temperatures. There was also less seasonal variation in soil temperature (Fig. 2). Air and soil temperatures recorded by the data loggers are not significantly correlated, as tested with Spearman correlation ($\rho = 0.39$, $P = 0.08$). 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

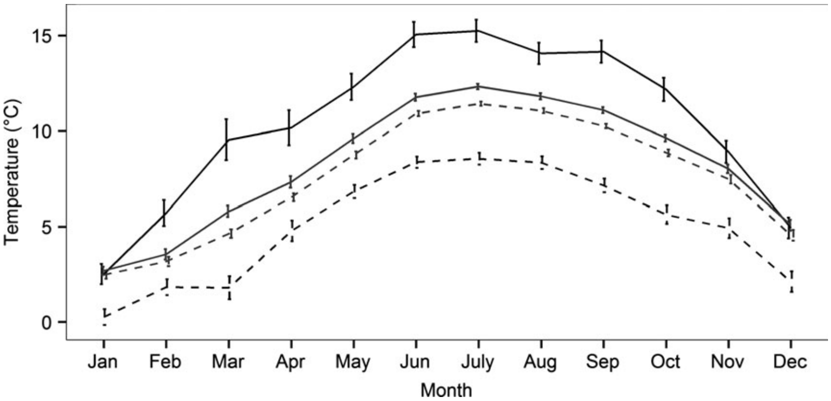

Fig. 2. Mean monthly temperatures at treeline on Hehuanshan, Taiwan. Solid black line: mean daytime air temperature, solid grey line: mean daytime soil temperature, dashed black line: mean nighttime air temperature, dashed grey line: mean nighttime soil temperature. Temperatures were averaged over sites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

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related to the values recorded at the meteorological station over the same time period (Appendix S1a,b).

Seedling and habitat data

Seedling densities varied throughout the plots, from 29 to a minimum of 0; mean number of seedlings per plot was 8.4. Mean 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 1 yr they generally persisted. Survival was 100% for 16 of the 30 plots, and mean survival in the remaining plots was 85%. Similarly, establishment was low during the 2-yr period. Seedling establishment was not uniform between years and shows episodes of high establishment (Fig. 3).

Smaller mean numbers of seedlings per plot were found at static treelines (mean 3.2) compared to abrupt (11.8) and diffuse (6.8) treelines (Fig. 4), and although overall treeline form had no significant effect on seedling number (*df* = 29, *F* = 2.61, *P* = 0.06), there was a significant difference between static and all other treeline forms (*P* = 0.02). Microtopographic shelter was higher in abrupt-advancing and lower treeline than in diffuse advancing, infill areas and static treeline, although again ANOVA results suggest no significant effect of form on microtopographic shelter (*df* = 4, *F* = 2.33, *P* = 0.08) and no significant differences between any forms were indicated in pair-wise comparisons. Changes in mean growing season air and soil temperature, seedling growth rate and height of *Y. niitakayamensis* were also explored with treeline form (Fig. 4), but none of these varied significantly by form according to ANOVA results.

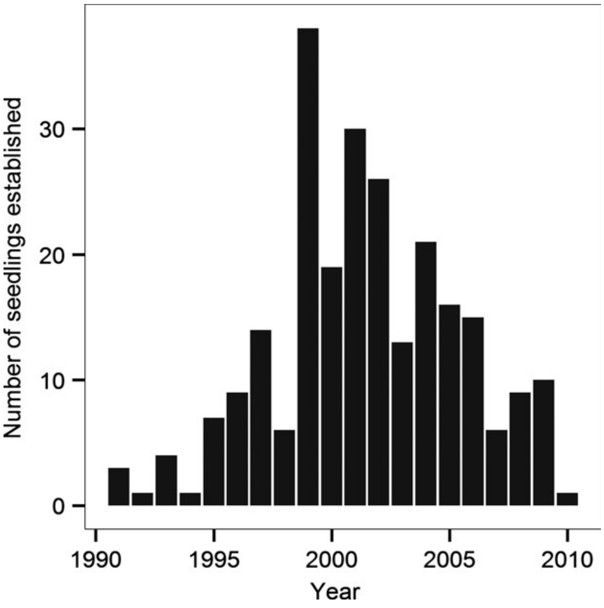

Fig. 3. Number of seedlings established per year in 30 5 m × 5 m plots on Hehuanshan, Taiwan. Seedling age was estimated from bud scar counts.

The best model for seedling numbers included only growing season mean soil temperature and microtopographic sheltering (Fig. 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 number for this subset of the data (*z* = 4.747 for smaller only, 2.285 for all seedling), as does microtopographic 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 no significant relationships with environmental variables; only a close to significant effect of microtopographic shelter was found (*z* = 1.726, *P* = 0.08), much weaker than that for the whole data set or for only smaller seedlings (Tables 2 and 3).

Relative growth rates of seedlings were significantly related only to mean growing season air temperature (*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 temperature or microtopographic sheltering, or between air and soil mean growing season temperatures and microtopographic sheltering.

Discussion

Based on assessment of microenvironment at a scale relevant to individual plants, rather than previously published landscape-scale overviews, we found 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 temperature. Furthermore, smaller seedlings were more sensitive to the measured environmental variables than larger seedlings, indicating that early growth may 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 recognized by other authors. Soil temperature is known to affect many physiological processes in plants, such as

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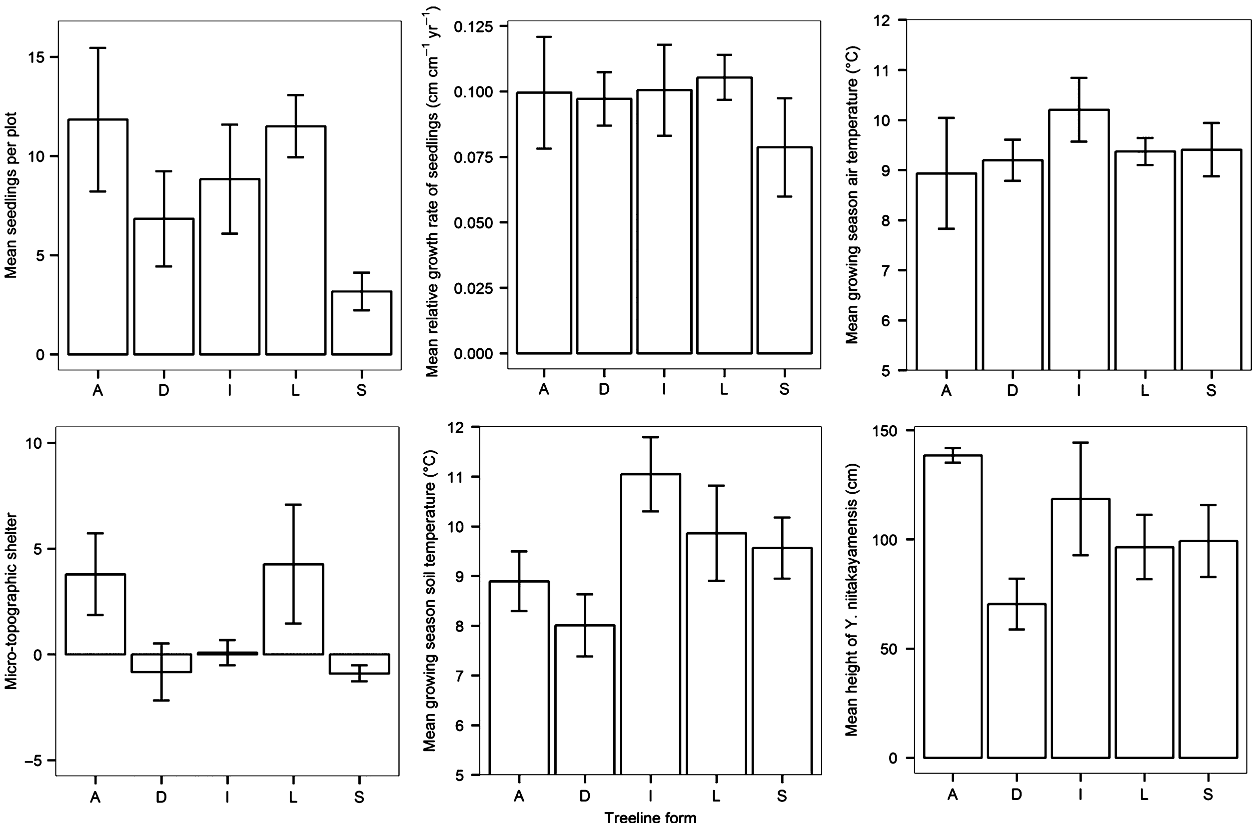

Fig. 4. The variation in mean seedling number, growth rate, air and soil temperatures, microtopographic sheltering and height of surrounding vegetation (*Y. niitakayamensis*) with treeline form on Hehuanshan, Taiwan. Treeline forms are as follows A: abrupt advancing, D: diffuse advancing, I: forest infill, L: lower limit of upper treeline, S: Static, non-advancing treeline, details of form structure are explained in Table 1. Air and soil temperatures were recorded at a height above the ground and depth below of 5 cm and microtopographic shelter was determined at a 10-m scale. Temperatures are averaged over all recording times for the growing season (March–October). Growth was measured annually and rates (RGR: cm·cm^{-1}·yr^{-1}) were averaged over a 2-yr period (2011–2013). Error bars represent ±1 SE.

photosynthesis (Day et al. 1991; Dang & Chen 2013) and growth (Hoch & 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 temperature and seedling establishment and growth is complex and warming can potentially have both positive and negative implications since increased soil temperature can also negatively impact germination in some cold-adapted species (Hoyle et al. 2013).

Körner & Paulsen (2004) provide evidence that soil temperature is a common driver of treeline position on a global scale. They found that treeline 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 °C (at lower limit of upper treeline site L5) and 12.9 °C (at forest infill site I3). The higher temperature 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. However, it is important to note that whilst a global driver of soil temperature may explain widespread 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.

Our results suggest that seedlings respond positively to microtopographic 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 (Resler et al. 2005; Holtmeier & Broll 2007, 2012).

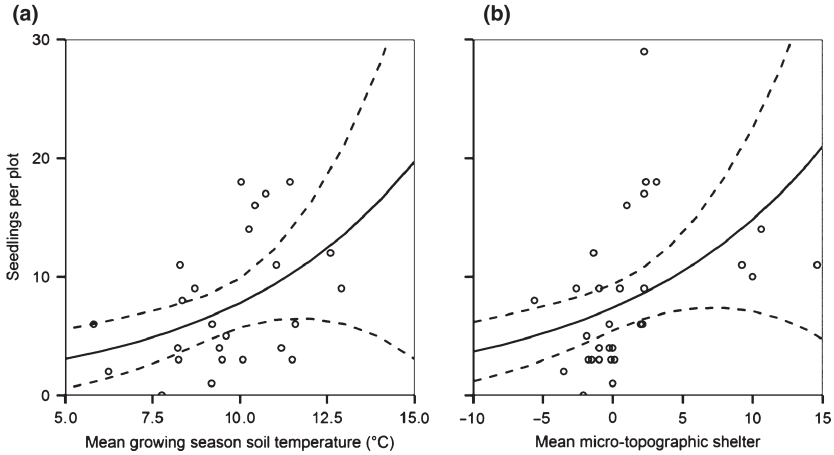

Fig. 5. The relationship between (**a**) mean soil temperature of the growing season, and (**b**) mean microtopographic shelter and total number of seedlings of all sizes per plot in 5 m × 5 m plots at treeline on Hehuanshan, Taiwan. The best fit lines (solid lines) and 95% CI (dashed lines) are from a GLM (with a negative binomial error distribution and log link) of seedling number modelled by only soil temperature (**a**) and microtopographic shelter (**b**), respectively, and are included to aid visualization of the effects of each variable. Soil temperatures were measured with data loggers 5 cm under the ground. Microtopographic shelter is calculated from 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 relationship between seedling number and habitat variables on Hehuanshan, Taiwan, as modelled by a GLM with a negative binomial error distribution and a log link function.

Variable	*Z*-Value	*P*-Value
Mean Growing Season Soil Temperature	2.285	0.02
Microtopographic Shelter	2.397	0.02

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 annual), 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 number and habitat variables for seedlings up to 20-cm tall on Hehuanshan, Taiwan, as modelled by a GLM with a negative binomial error distribution and a log link function.

Variable	*Z*-Value	*P*-Value
Mean Growing Season Soil Temperature	4.747	<0.001
Microtopographic Shelter	3.513	<0.001
Mean Height of *Y. niitakayamensis*	−2.496	0.01
Minimum Annual Air Temperature	2.428	0.02
Minimum Annual Soil Temperature	−2.495	0.01

We did not find a relationship between microtopographic sheltering and any measure of air or soil temperature, indicating that the importance of microtopography for seedlings is related to some factor other than temperature. Wind speed, soil formation, soil moisture retention and winter snow cover are all mediated by microtopography (Holtmeier & Broll 1992) and influence seedling establishment patterns. Wind exposure is known to play a role in the formation of krummholz structures at treelines (Tranquillini 1979; Körner 2003; Gamache & Payette 2004), and these structures themselves can facilitate the growth and survival of seedlings by protecting them from excessive wind speeds (Batllori 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 & Thomas 2013). Seeds may also be more likely to accumulate in topographic depressions.

Our 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 fewer seedlings occurring where the bamboo was very tall (Table 3). We thus found no evidence of facilitative interactions at treeline, although such interactions are commonly reported (Germino et al. 2002; Batllori et al. 2009; Llambí et al. 2013). In our study site *Y. nii-*

takayamensis grows in extremely dense swathes, where it has the potential to out-compete seedlings for light and other resources; this could explain the 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 excess 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. However, the experimental design might influence the results here; data loggers were placed at 5 cm above and below the 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 to 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 a warming climate, and further advance of treeline is thus expected. However, the importance of microtopography presents a potential limitation to advance, and offers an 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), and 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 under-studied subtropical mountains, are particularly valuable in this respect since they enable 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 microtopographic 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 microtopography, to enable a mechanistic understanding of the driving variables responsible for treeline advance in this and similar ecosystems. 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 up-slope migration of trees into alpine areas.

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Supporting Information

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

Appendix S1. (a) Variation in mean annual temperature from 1990–2013 ± 1 SE. (b) Linear relationship between data logger and meteorological station air temperature recordings.