ORIGINAL ARTICLE

Community change and species richness reductions in rapidly advancing tree lines

Sarah Greenwood[1], Jan-Chang Chen[2], Chaur-Tzuhn Chen[2] and Alistair S. Jump[1,3]

[1]*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, Pingtung 912, Taiwan,* [3]*CREAF (Centre de Recerca Ecològica i Aplicacions Forestals), Cerdanyola del Vallès, Spain*

ABSTRACT

Aim Climate change is causing shifts in the 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, the possible consequences of this for the wider forest community have not been fully considered. In this study, we used epiphytic macro-lichens to investigate the impacts of tree line advance on associated organisms. We hypothesized that the rate of forest advance should influence the species richness and composition of associated communities.

Location The Hehuanshan area, Central Mountain Range, Taiwan (24°08–09′ N, 121°15 − 16′ E).

Methods Lichen communities were sampled on trees occurring at 33 tree line sites displaying varying degrees of advance. Habitat variables were recorded. ANOVA, GLMM, nestedness analysis and indicator species analysis were used to investigate patterns of species richness and community composition and their association with tree line advance and habitat variables.

Results Species richness was lower in tree lines exhibiting rapid advance; reductions were related to tree size (considered here as a proxy for age) and the distance over which advance had occurred. Community composition varied with tree line form and forest position. Only a subset of species found in slowly advancing or stable forest edges occurred in rapidly advancing tree lines.

Main conclusions Differential migration rates between co-occurring species and differences in habitat structure associated with tree line advance can result in community change, but this depends, amongst other factors, on the speed of tree line advance. The importance of advance rate in determining the response suggests that reductions in species richness at tree line could be transitory. However, this will depend on whether advance continues, and on the changes in habitat associated with advance. Given the complexity of tree line behaviour, the findings that we report represent an essential step in understanding community responses to climate change. This understanding is of importance for biodiversity and conservation, especially given the high rate of endemism reported for this and other alpine regions.

Keywords

Abies kawakamii, climate change, GLMM, macro-lichens, response lag, species distributions, Taiwan

*Correspondence: Sarah Greenwood, Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK.
E-mails: sarah.greenwood85@gmail.com; sarah.greenwood@stir.ac.uk

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INTRODUCTION

At high altitudes, low temperatures limit tree occurrence through impacts on growth and survival (Tranquillini, 1979; Körner, 2003). Consequently, ongoing climate warming is driving an upward movement of some altitudinal tree lines; a meta-analysis by Harsch et al. (2009) found evidence of advance at 52% of studied tree line sites. However, the migration and climate response potential of species varies; inter-specific differences in climate response have been found between co-occurring tree line species (Trant & Hermanutz, 2014), and the survival of forest herb species transplanted far beyond their current limits (Van der Veken et al., 2012) 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.

Communities are made up of species with different requirements (Whittaker, 1965) that are expected to respond individualistically to change (Huntley, 1991). This individualism can result in community disassembly as a keystone species advances, both due to migration lag and the altered suitability of newly colonized areas for associated species. Changes in community composition occurred in response to past climate changes (Huntley, 1990), but are also documented in modern times (Klanderud & Totland, 2005; le Roux & McGeoch, 2008). In an investigation of the range shifts of all vascular plants occurring on Marion Island, Antarctica, le Roux & 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 & Totland, 2005).

Tree lines are often spatially complex and a variety of forms have been described that show varying responses to temperature (Harsch & Bader, 2011). Topographic variation can locally modify the rate of tree migration leading to a high degree of spatial variation in tree line advance (Macias-Fauria & Johnson, 2013; Greenwood et al., 2015). Forest structure influences microclimate variables such as moisture, temperature and light availability (Canham & Burbank, 1994) and can thus influence understory species composition. As tree lines advance in response to warming climate with an increase in forest area beyond current limits, and in density below (Mamet & Kershaw, 2012), conditions will, therefore, change for both forest understory and alpine communities (Greenwood & Jump, 2014). Forest understories can be very species rich (Thomas et al., 1999) and forest specialist species are particularly sensitive to changes in forest conditions (Halpern & Spies, 1995).

The complexity in structure and high spatial variability of advancing tree lines, combined with the uncertainty regarding community level responses to warming, mean that studies investigating community responses to tree line advance are much needed. Epiphytic/corticolous lichens are excellent study organisms with which to study the impacts of tree line advance on the wider forest community: they display high sensitivity to environmental conditions, often have limited colonization and growth rates (Nash, 2008) and are dependent on trees for growth substrate. Many lichens require a long continuity of forest (Rose, 1976), 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). 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 & 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.

Spatially variable changes in tree line position and structure associated with rising temperatures have been observed in the Central Mountain Range of Taiwan (Greenwood et al., 2014, 2015). We sought to determine if tree migration in this area is leading to changes in the lichen community. We hypothesized 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 change would occur due to the restricted colonization speed of some species acting in combination with altered habitat suitability in newly developing forest.

MATERIALS AND METHODS

Study area

The island of Taiwan lies off the south-east 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. There is evidence of recent increases in temperature in the area; Jump et al. (2012) report an increase of around 1 °C over the last c. 50 years, whilst Lin et al. (2015) find evidence of a stronger warming trend in mountainous regions of Taiwan than in lower altitude areas, with predicted increases of 0.6 °C for the period 2015–2039 compared to 1979–2003 mean values, and larger increases of up to 3.2 °C during 2075–2099. Mean annual temperature (1981–2010) recorded by a meteorological station in the Alishan area is 11.2 °C, and mean annual precipitation is 3,932 mm over the same period.

The Hehuanshan region, located in central Taiwan, consists of three main peaks over 3,000 m (Fig. 1). At high altitudes, the dominant tree line species is *Abies kawakamii* (Hayata) T.Ito, an endemic fir that forms almost monospecific stands at the upper limits of its range (*c.* 2800–3500 m). The majority of the high-altitude *A. kawakamii* forest is unmanaged, with no forestry operations occurring in the area. Some logging of this species occurred during Japanese occupation of Taiwan (1895–1945), but this was predominantly at more accessible lower elevations, furthermore the cypress species *Chamaecyparis obtusa* var. *formosana* and *Chamaecyparis formosensis* were preferred for timber (Li *et al.*, 2015). No evidence of recent logging has been observed at any of the tree line sites in this study either from on-ground observation or from the study of aerial photographs dating back to the 1940s (S. Greenwood pers. obs.) Indeed, the dominance of the late successional *A. kawakamii* over pioneers such as *Pinus taiwanensis* suggest that this area is largely undisturbed (Chou *et al.*, 2009). The subalpine grassland above, dominated by the unpalatable *Yushania niitakayamensis* is not used for the grazing of domesticated herbivores or managed in any other way. Populations of native grazing and browsing animals are low at high altitude (Yen *et al.*, 2014; Chiang *et al.*, 2015), and hunting pressure from aboriginal peoples in believed to be unchanged over recent decades (Pei, 1999). Forest fires, whilst representing a potential threat to the species (Chou & Chen, 2006), are not recorded as having occurred in our research area in the last century (Council of Agriculture, Taiwan 2013), and cores collected at tree line sites show no evidence of recent fire (S. Greenwood, unpublished data). The tree line, therefore, represents a range limit that can be considered to be mainly 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 way, with considerable spatial variation (Greenwood *et al.*, 2014, 2015). Following Harsch & Bader (2011) and Greenwood *et al.* (2014), local patterns of tree line advance in the Central Mountain Range of Taiwan can be classified as *abrupt advancing* (tree lines advancing at high density over short distances), *diffuse advancing* (tree lines advancing at low density over longer distances) and *static* (tree lines that are not advancing), and of these, the authors have shown that the diffuse form is advancing most rapidly in the Hehuanshan area (Greenwood *et al.*, 2014).

Methods

Thirty-three tree line sites (11 for each tree line form) (Fig. 1) were studied using transects from interior forest to tree line/tree-limit (definitions follow those of Greenwood *et al.*, 2014). Transect length varied between 50 and 140 m depending on the tree line structure (Appendix S1). Pairs of trees were sampled at three or four positions; interior forest (this was generally c 50 m from the defined forest edge, where

canopy structure and tree density became comparatively open and consistent and edge effects could be assumed to be negligible), mid-forest (a forest position halfway between interior forest and the tree line or forest edge), tree line (the forest edge) and tree-limit (the upper limit of tree occurrence, only different from tree line in diffuse advancing forms). One of the trees sampled in each position was of similar diameter at breast height (DBH; 1.3 m) throughout the whole transect, and kept fairly consistent between transects (DBH of *c.* 15–30 cm) so that sampling area was consistent and trees were of comparable ages, as DBH was used as a proxy for tree age. The other sample tree was picked to be representative of that sampling position (interior forest trees were therefore generally larger, edge and tree line trees smaller in girth). Only adult trees and larger saplings were considered, defined as those reaching a height of 1.3 m or above.

Lichen species identity (macro-lichens only) and relative abundance was recorded on basal trunks of trees at each position. Sampling area was a 60 cm wide band around the trunk, centred at breast height. Specimens were collected for identification. Abundance estimates were made using the DAFOR scale, in which species are assigned to an abundance class based on their percentage cover (dominant [>50%], abundant [25–50%], frequent [10–24%], occasional [2–9%] or rare [<2%]) (Sutherland, 1996). Trees were searched carefully for evidence of recent colonization to ensure that no small thalli were missed and search time was made proportional to search area.

Trees were measured for DBH and bark roughness was classified based on an index devised by the authors; bark was given a score between 1 and 4 depending on the roughness, the deepness of cracks and presence of anomalies. A hemispherical photograph was taken from the base of each tree to measure canopy openness. The altitude of each tree was recorded. At the transect level, forest inventory data were collected: all adult trees 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 analyses at the tree level.

Thirty six trees, selected at random, were cored to provide ring data. These covered an altitudinal gradient greater than that of any individual transect. This allowed us to test our assumption that tree size (DBH) could be used as a rough proxy for tree age consistently across the transects; this assumption would be reasonable if we found evidence of a strong relationship between tree size and age (number of rings) that did not vary with altitude, but would be unreasonable if we found significant differences due to altitude. Cores were collected at breast height, stored in paper straws and dried at room temperature. They were then prepared for measurement using standard protocol (Stokes & Smiley, 1968).

Lichen specimens were identified to species where possible (see Appendix S2). Thin layer chromatography (TLC) was used to aid with the identification of some specimens, and between one and four examples of each species were DNA
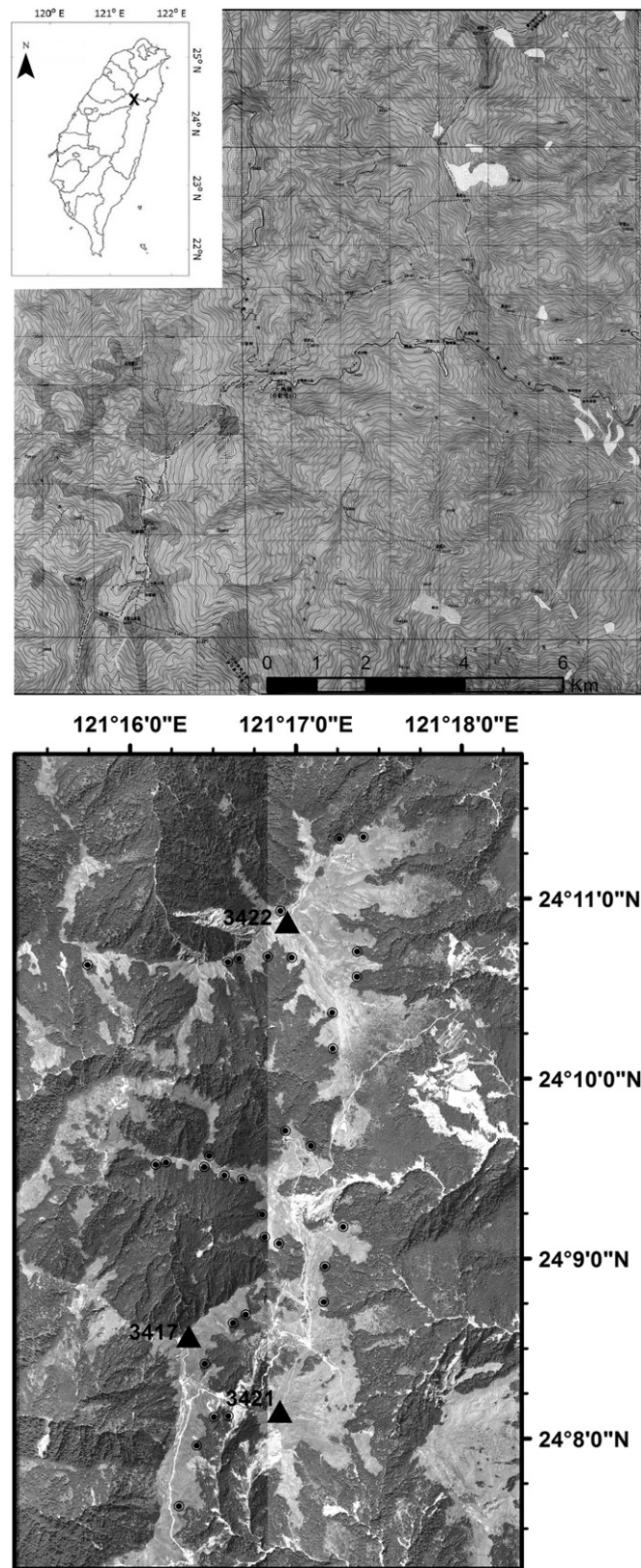
Figure 1 The location of the study area in Taiwan (inset map, marked with a cross), a topographic map of the area surrounding the study sites and an aerial photograph of the tree line study area in 2001, showing the position of each of the 33 transects throughout the Hehuanshan area (enlarged area, transects marked with points). The three main peaks of Hehuanshan are marked with triangular symbols and the altitude in m. a.s.l. is indicated.

barcoded. For more details of this, and for related GenBank accession numbers see Appendix S2.

Statistical analysis

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

All statistical analyses were performed with R 3.0.2 (R Core Team 2013). Plots were constructed in R, using the package 'ggplot2' (Wickham, 2009) and with SigmaPlot (SigmaPlot 12.5). Species accumulation and rarefaction curves were used to estimate the percentage of total species described with our sampling intensity (specpool function in 'vegan' package (Oksanen *et al.*, 2011)). The change in habitat with forest position for each tree line form was explored graphically and tested with ANOVA. Generalized linear models (glm) were used to test for differences 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). Linear models were used to assess the relationship between tree size and age (number of rings), and the influence of altitude was considered as an interaction. A scatterplot was used to visualize this relationship.

The influence of habitat variables on species richness patterns

Generalized 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 with a log link function; a random effect was included to avoid pseudoreplication due to the paired sampling design. Data were checked to ensure all assumptions were met. Original models included all habitat variables (distance, density, canopy openness, altitude, tree size); non-significant variables were sequentially removed as appropriate to improve model fit, with the models re-run each time a variable was removed. In this analysis, data from all tree line forms were pooled and tree line form was not considered as a factor; instead distance from forest interior and tree density were both used as continuous variables. This approach was taken to (1) remove categorical variables from the analysis and (2) explore the importance of distance and density beyond our own classifications of tree line form. Interaction terms were added when relevant, and these were explored visually using 3D plots constructed using values predicted from model coefficients. The variables included in the model 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 these density data to be stratified for each pair of trees sampled; it was split into four sections of interior, forest, tree line 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 & Schielzeth (2013). Variance inflation factors (VIFs) were calculated to check for problems with collinearity in predictor variables ((corvif function) Zuur *et al.*, 2009).

Community change in advancing tree lines

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 & Ulrich, 2011). Nestednodf calculated 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. The species data were 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 data set shows a higher degree of nesting than a random distribution created by null modelling.

The Bray–Curtis dissimilarity index was used to calculate the difference in community composition between each forest position/tree line form combination. A Mantel test tested the correlation of the Bray–Curtis dissimilarity with habitat variation and the adonis function of 'vegan' was used to test for significant differences in community composition with tree line advance form and sampling position. The function mulitpatt from the 'Indicspecies' package (De Caceres & Legendre, 2009) was used to explore the association of species with tree line form/forest position groupings.

RESULTS

Species richness patterns

All specimens found in the sample plots were identified to species level, excluding *Cladonia* spp which were treated collectively. Sixty two species were found in total, 29 of which occurred at the tree-limit, 55 at tree line, 54 at mid-forest and 48 in interior forest (considering all transects and tree line forms together). Species accumulation curves and rarefaction estimates suggest that the sampling may not have fully described all the species likely to be present (Table 1). However, although the estimated total numbers of species in each forest position are higher, the overall pattern is the same; total species numbers are lower at tree-limit and interior forest and highest overall at tree line.
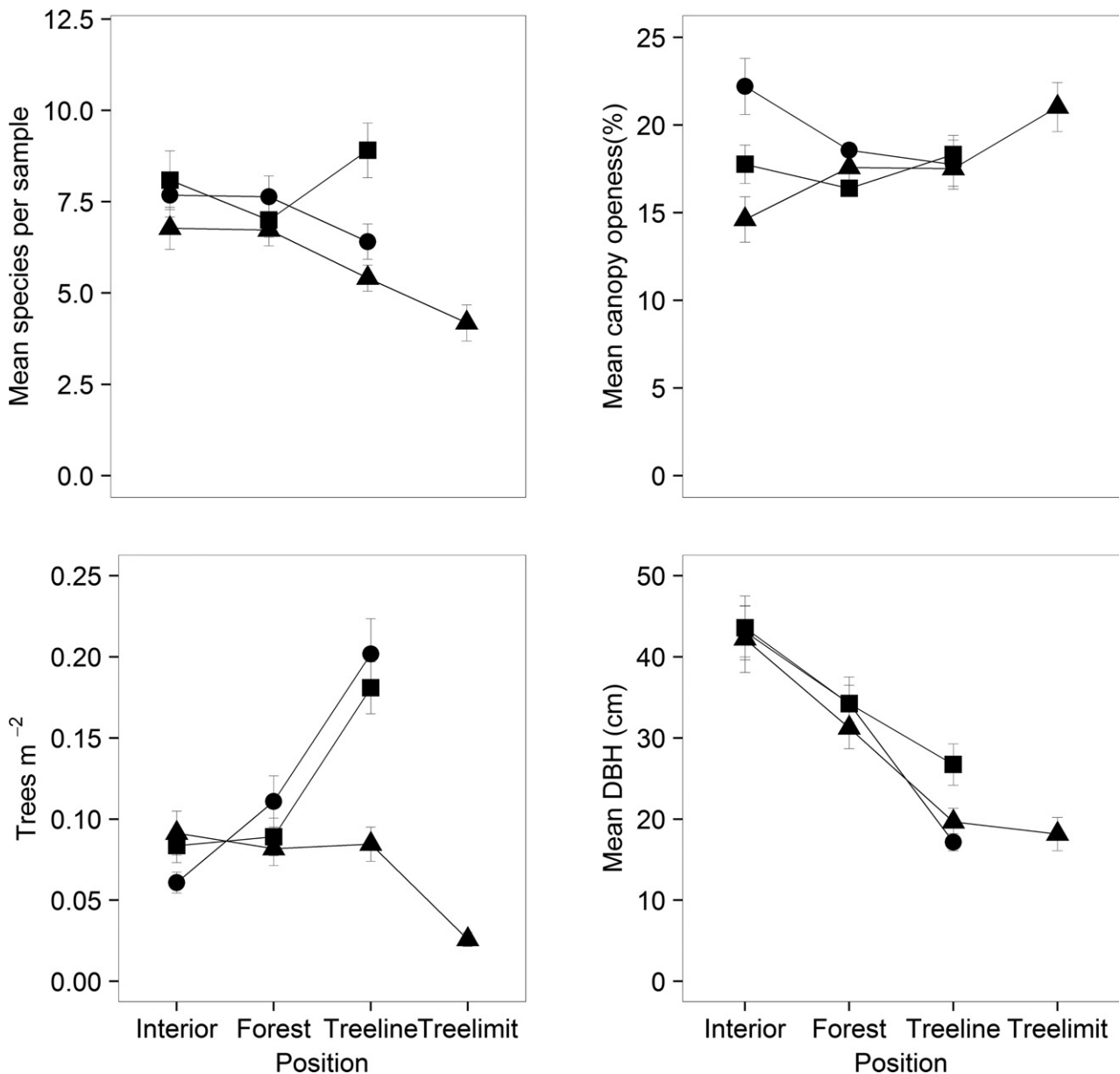
Variation in species richness and habitat variables with tree position and tree line form

Habitat varied across transects from interior forest to tree line/limit and the nature of variation depended on tree line form (Fig. 2). Mean tree density increased from interior for-

Table 1 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 of R.

Position	Number of trees	Species numbers	Chao estimate	Jackknife estimate	Bootstrap estimate
Tree-limit	22	29	34 ± 4.2	39 ± 4.7	34 ± 3
Tree line	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

est to tree line in abrupt advancing and static tree line forms, but decreased in this direction in diffuse advancing tree line forms. Tree density varied significantly with position in abrupt (df = 64, 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 tree line in all tree line 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 form, with significant variation dependent on form only in diffuse advancing tree lines where it

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

increased from interior forest to tree-limit (df = 86, $F = 11.07$, $P = 0.001$). Mean species per tree was highest at static tree lines and lowest at diffuse tree-limits. Species richness varied significantly with forest position in diffuse tree lines, with a decrease 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, $F = 0.68$, $P = 0.414$).

We found evidence of a strong relationship between tree age and size ($R^2 = 0.86$, $P < 0.001$), and no effect of altitude (see Appendix S3). This supports our assumption that tree size can be used as a rough proxy for tree age.

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, with species richness positively associated with tree size and negatively with distance from the forest interior. A GLMM including distance, tree size and an interaction of these two variables gave significant values for tree size and the interaction term (Table 2; Fig. 3). Visual inspection of the interaction of tree size and distance shows that species richness varies with tree size more at longer distances from the forest interior, where large trees are predicted to host large numbers of species, but small ones are not. The estimated variance explained by the model including the fixed effects (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.

Community change in advancing tree lines

The Bray–Curtis dissimilarity indices showed that interior and mid-forest positions were similar between forms (values of 0.14–0.26), but tree line positions varied slightly more depending on form (0.20–0.35). The two communities that

Table 2 The relationship between lichen species richness and habitat variables along transects running from forest interior to tree line/limit on Hehuanshan as modelled by a GLMM (function glmer of lme4 package in R) with Poisson error 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 & Schielzeth (2013) were 13 and 30% respectively.

Fixed effect	Z value	P value
Distance from interior	−1.7	0.088
Tree size (DBH)	2.18	0.001
Distance: Tree size interaction	2.54	0.011

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.
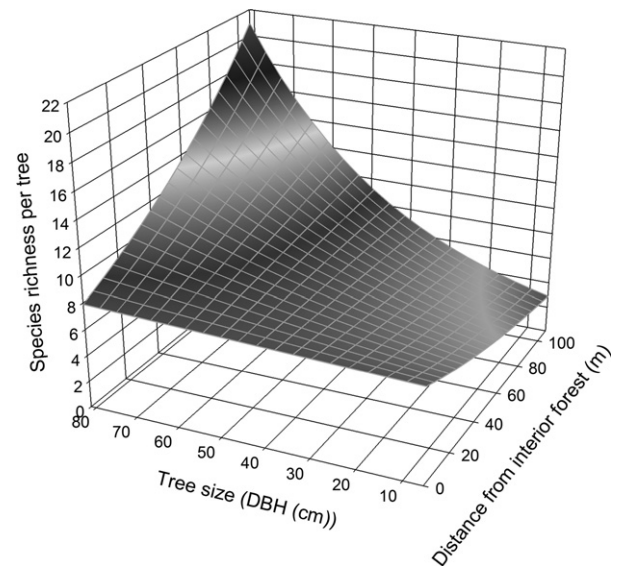
Figure 3 The interaction between tree size (dbh in cm) and distance from forest interior (m) on lichen species richness per tree based on values predicted from generalized linear mixed model including tree size, distance from interior forest and an interaction term between tree size and distance, with a Poisson error distribution of residuals and log link function.

were most different were abrupt interior and diffuse tree-limit (0.57). Mantel test of correlation (using Pearson's product-moment correlation) between dissimilarity and all numeric habitat variables showed a correlation of dissimilarity with habitat variation ($r = 0.7$, $P = 0.001$). Tree line form had a strong and significant effect on variation in community composition according to Adonis results ($F = 61.8$, $R^2 = 0.4$, $P = 0.01$), and there was a weak, but significant effect of sampling position ($F = 7.0$, $R^2 = 0.1$, $P = 0.01$). There is evidence of nesting occurring in the species data set (nodf (rows) = 72.4, $P = 0.003$). Species-poor sites, such as tree-limit in diffuse advancing tree lines are a subset of species-rich, interior forest sites.

Several species such as *Fuscopannaria ahlneri* and *Coccocarpia parmicola* were found to be associated with static tree line positions. *Hypotrachyna sinuosa* is an indicator of closed and diffuse tree line and diffuse tree-limit positions, whereas *Hypogymnia flavida* and *Myelochroa irrugans* are associated with tree line and 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 tree line/limit and similarly *Nephromopsis morrisonicola* was associated with all forest positions in abrupt advancing and static forms, but not with diffuse form tree line and tree-limit positions.

DISCUSSION

We investigated the changes in forest habitat and lichen communities across stable and advancing tree lines, and

found a change in forest habitat occurring from interior forest to tree-limit in rapidly advancing diffuse-form tree lines, accompanied by a decrease in lichen species richness and change in community composition that was not found in static and abrupt advancing tree lines. Tree size and distance from interior forest were the two main factors driving lichen species richness patterns. Tree size was used as a proxy for tree age, and its importance here is likely strongly related to the time available for colonization, with a substantial lag evident between tree and subsequent lichen colonization.

The interaction between tree size and distance from interior forest was also found to be important for species richness. Close to interior forest, species richness varies only a little with tree size, but at long distances from the forest interior this changes, with the model predicting high species richness on large trees far from the forest interior. This result illustrates the importance of the time-lag and that a significant time period may elapse between tree and subsequent lichen colonization. It suggests that, given time, advancing tree lines could provide suitable habitat for species-rich lichen communities. In fact, the highest numbers of species are predicted by the model on very large trees at the tree-limit, suggesting that colonization time is of key importance, and that the more open conditions present at tree-limit sites might be suitable for many lichen species if old, large trees are present. Our assumption of tree size and age being consistent across our sampling locations was supported through the analysis of tree cores, thus allowing us to use tree size as a proxy for age, and, therefore, time.

Our results suggest that rapid tree line 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 tree line (Greenwood et al., 2014), has, at least in the short term, negative consequences for the lichen community because certain species are not able to respond effectively to, or tolerate changes in, forest position and habitat when tree line advance is happening quickly. However, the higher species richness of abrupt advancing tree lines indicates that lichen communities can respond effectively to slower tree line advance rates with less associated changes in forest structure.

Species richness at diffuse advancing edges is lower, and community composition is different, because only a subset of those species found in areas with higher richness have colonized in the time period since tree line advance. It is important to consider the fact that this may be a transitory response; the slower migration and colonization of lichens compared to trees, and the fact that corticolous lichens cannot occur in an area until after trees have colonized means that lichen species richness is likely to increase over time, with most of the species present in stable tree lines eventually colonizing advancing tree lines. This will, however, depend on forest structure and habitat, which varies with tree line form. If diffuse tree line forms continue to advance rapidly at low density then longer term changes in the lichen community are possible. Future research of lichen community composition combined with direct measurements of tree age

through intensive tree core sampling could provide further details into the nature and length of the time-lag between tree and lichen colonization.

Lichens are known to be slow to respond to changes in forest structure and habitat (Ellis & Coppins, 2007), to have limited establishment rates (Nash, 2008) and thus to rely on large tress that provide both a longer continuity of habitat, and increased habitat complexity (Friedel et al., 2006). The reduction in species richness and change in composition that we detect is likely to result from the differential migration and colonization rates of lichens and trees acting together with changes in forest conditions at diffuse advancing tree lines. 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 & Siitonen, 1998), and changes such as thinning due to forest management often have negative impacts (Nascimbene et al., 2013). In the more rapidly advancing tree lines, conditions may be, at least temporarily, unfavourable for many species of lichen found in stable and slow advancing tree lines. The observed reduction in forest specialists with more rapid tree line advance is likely to be applicable to the wider forest understorey community because these plants are also known to have lower migrational capacity than that of trees (Roberts, 1989).

In this study, the use of lichens was most appropriate as the understorey flora is depauperate in the area. However, it would be interesting to see if the patterns observed here are comparable to that of the ground flora of bryophytes and vascular plants in other areas where tree line advance is occurring. Although macro-lichens proved useful for this study, there are limitations associated with their application; access was restricted to the lower trunks, whereas greater species richness is found in the upper canopy. Furthermore, lichen identification is difficult and time consuming, and there is a possibility of missing very small thalli and thus underestimating species richness, although this risk did not vary systematically in this investigation. The nature of their relationship with trees, and the fact that the lichens investigated here cannot occur in an area until after trees have colonized also makes the determination of the relative importance of habitat change more complex.

Lichens are, however, important aspects of the forest community in their own right: they provide habitat for invertebrates, nesting material for birds (Galun, 1988; Gunnarsson et al., 2004) and play a role in nutrient cycling (Knops et al., 1996). They also tend to be composed of highly diverse communities and so make a large contribution to local biodiversity. Here, we found that certain species were associated with specific forest position and tree line forms and were excluded from others. Squamulose and large foliose growth forms tend to be associated with interior forest or static tree lines 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). The species *Lobaria retigera* was found frequently in our samples and was shown to be indicative of several forest positions, excluding advancing tree lines 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 & 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 and wind speeds are likely higher, temperatures more variable and desiccation more likely.

Our data suggest that the rate and form of tree line 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 at tree-limit 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, then, even if lichen migration is slower than that of trees, the full complement of species typical of established forest may eventually colonize the newly forested areas. 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 suggest that where advance occurs over a very wide area, such as advance of woody species into arctic tundra sites (Lescop-Sinclair & Payette, 1995), then the reduction in co-occurring species richness found here could be a sustained response. Future research that considers wider aspects of the community such as forest understorey vascular plants or forest dwelling invertebrates would be useful in order to better understand community wide, long-term responses to tree line advance. Increased understanding of these processes is crucial from a conservation perspective, and will improve predictions of regional biodiversity change in response to changing climate.

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SUPPORTING INFORMATION

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

Appendix S1 Explanation of tree line advance structures

Appendix S2 Literature used for lichen species identification, methods of barcoding and lichen species list and accession numbers

Appendix S3 Tree size age correlation and altitude effects.

BIOSKETCH

Sarah Greenwood is a post-doctoral researcher at the University of Stirling. Her work focuses on the response of forest ecosystems to global change. She undertook this work as part of her doctoral studies at the University of Stirling, UK and The National Pingtung University of Science and Technology, Taiwan.

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