Received: 3 February 2020 | Revised: 3 July 2020 | Accepted: 9 July 2020
DOI: 10.1111/jbi.13951

RESEARCH PAPER

Journal of Biogeography WILEY

Montane forest expansion at high elevations drives rapid reduction in non-forest area, despite no change in mean forest elevation

Peter J. Morley[1] | **Daniel N. M. Donoghue**[2] | **Jan-Chang Chen**[3] | **Alistair S. Jump**[1]

[1]Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, UK

[2]Department of Geography, Durham University, Durham, UK

[3]Department of Forestry, National Pingtung University of Science and Technology, Pingtung, Taiwan

Correspondence
Peter J. Morley, Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK.
Email: p.j.morley@stir.ac.uk

Funding information
Deutsches Zentrum für Luft- und Raumfahrt, Grant/Award Number: DEM_FOREST1027; Natural Environment Research Council, Grant/Award Number: NE/L002590/1

Handling Editor: Ole Vetaas

Abstract

Aim: At the elevational limit of forest distribution, montane forests show diverse responses to environmental change with upward shifts, increased tree density and lateral expansion reported. To enable informed analysis of the consequences forest advance will have on montane biodiversity, we quantify changes in the area and elevation of the tree line ecotone and identify how patterns of forest advance are modified by topography and over time.

Location: Central Mountain Range, Taiwan.

Time period: 1963–2016.

Major taxa studied: Montane Forests.

Methods: Changes in the area and elevation of montane forest at the tree line ecotone were quantified using a stratified random sample of aerial photography captured in 1963, 1980, 2001 and 2016. Weighted estimates of habitat area and elevation for each time step were used to quantify the influence of slope aspect and inclination on tree line ecotone change and identify how the rate of habitat change varies over time.

Results: Non-forest area declined by 29% between 1963 and 2016 driven by a 295.0 ha increase in forest area within the study region. Despite no change in mean forest elevation, the mean elevation of establishing forest has increased at a rate of 2.17 m/yr. Changes in forest area and elevation are spatially variable, driven by the complex montane topography. East and south facing slopes show the largest gains in forest area and 0–20° slopes show an increasing rate of forest establishment up to 2016, while slopes facing west or with incline > 46° show negligible change.

Main conclusions: Climate-linked montane forest expansion in the Central Mountain Range in Taiwan is dominated by infilling rather than increases in forest elevation. Forest expansion has significantly reduced non-forest habitat area in this endemic species-rich region. However, considerable terrain-dependent variation in forest advance occurs, offering the potential that non-forest species will continue to persist at high elevations with reduced population size.

KEYWORDS
climate change, densification, forest change, migration, mountain, range edge, Taiwan, tree line

1 | INTRODUCTION

Mountain systems are experiencing higher than average temperature increases (Dirnböck, Essl, & Rabitsch, 2011; IPCC, 2013; Pepin et al., 2015) and high rates of land use change (Haddaway, Styles, & Pullin, 2014; MacDonald et al., 2000). In response to increasing temperatures and land use changes, uphill advances in the position of montane forests have been observed at the elevational limit of forest distribution where montane forest transitions into alpine vegetation (henceforth, referred to as the *tree line ecotone*) (Améztegui, Brotons, & Coll, 2010; Améztegui, Coll, Brotons, & Ninot, 2016; Harsch, Hulme, McGlone, & Duncan, 2009). Changes in the position and structure of tree line ecotones are expected to impact montane biodiversity (Greenwood & Jump, 2014). The relative isolation of mountain environments and high habitat heterogeneity means that disproportionately high numbers of endemic and rare species are found at high elevations (Steinbauer et al., 2016; Vetaas & Grytnes, 2002). Consequently, shifts in the position or structure of the tree line ecotone pose a risk to alpine biodiversity through the extirpation of alpine species and contraction of species ranges as lower distribution limits are pushed towards mountain tops (Jump, Huang, & Chou, 2012).

Shifts in montane forest distribution have primarily been reported as changes in the elevation of the upper ecotone limit. Harsch et al. (2009) reported that 52% of studies published between 1900 and 2008 identified advances in the elevational or latitudinal limit of the tree line. Changes in tree density or growth below the altitudinal limit were not defined as advances in the study by Harsch et al. (2009), yet a growing body of evidence reports substantial increases in tree density or range expansion through across-slope movement of montane forests below the elevational limit in response to environmental change (Bharti, Adhikari, & Rawat, 2012; Feuillet et al., 2020; Greenwood, Chen, Chen, & Jump, 2014; Klasner & Fagre, 2002; Liang, Wang, Eckstein, & Luo, 2011; Mathisen, Mikheeva, Tutubalina, Aune, & Hofgaard, 2014). Changes in the tree line elevation only provide partial information on the response of tree line ecotones to environmental change (Feuillet et al., 2020). Consequently, assessments of change focusing on the assessment of tree line elevation alone potentially provide misleading estimates of forest range shifts and are inadequate to inform how these changes will impact montane biodiversity (Rahbek et al., 2019).

High variability in the response of tree line ecotones to regional warming occurs due to the influence that complex montane topography has on modifying regional climate patterns, resulting in numerous different climate types within close proximity (Rahbek et al., 2019). While temperature has been identified as a primary controlling variable affecting forest position and advance at naturally occurring mountain tree line ecotones (Körner & Paulsen, 2004), topography modifies local climate regimes causing some slopes to experience climatic conditions that may be cooler, drier or more sheltered than neighbouring areas (Malanson et al., 2011; Suggitt et al., 2011). At the local scale, variation in resource availability (e.g. McNown & Sullivan, 2013; Sullivan, Ellison, McNown, Brownlee, & Sveinbjörnsson, 2015), slope morphometry and lithology (Feuillet et al., 2020), radiative stress (Bader, Van Geloof, & Rietkerk, 2007) and drought stress (e.g. Johnson & Smith, 2007; Leuschner & Schulte, 1991; Millar, Westfall, & Delany, 2007) modifies establishment and growth patterns of advancing montane forests. In addition, the structure of a forest stand itself can also act as a feedback mechanism to facilitate or constrain patterns of tree establishment, growth and mortality through increased seed availability, modification of the microclimate and alterations to competitive dynamics (Camarero et al., 2017). Consequently, while regional changes in temperature may exceed thresholds that would be conducive for shifts in the position of the tree line ecotone, controls acting at the local scale can result in tree line ecotones that are structurally diverse and display high heterogeneity in their elevational position and patterns of advance both between and within mountain ranges.

While numerous studies identify controls on the advance of tree line ecotones, there is a fundamental need for standardized and robust approaches that enable the quantification of change in both the elevation and area of tree line ecotones (Feuillet et al., 2020; Hagedorn, Gavazov, & Alexander, 2019). The best estimates of change and the associated implications typically come from long-term repeat surveys of fixed monitoring sites that are distributed across mountain ranges (e.g. Global Observation Research Initiative in Alpine Environments (GLORIA) which focus on alpine flora; Grabherr, Gottfried, & Pauli, 2000). However, repeat survey data of tree line ecotones are scarce and so the majority of studies are based on incidental historical records and a very limited number of field observations (Gottfried et al., 2012; Steinbauer et al., 2018) which may not provide a reliable picture of change over large areas and at worst may lead to bias in forest range estimates (Fisher, Hurtt, Thomas, & Chambers, 2008). While field observations have steered much of our current understanding of species range shifts and the implications to montane biodiversity, the use of remote sensing data to assess changes in forest distribution is attractive to overcome limitations imposed by poor accessibility to field sites and the lack of historic field data in mountain ranges. Repeat aerial photography data have been used to identify changes in the maximum elevation or tree density of the tree line ecotone (e.g. Feuillet et al., 2020; Greenwood et al., 2014; Klasner & Fagre, 2002; Luo & Dai, 2013; Mathisen et al., 2014; Resler, Fonstad, & Butler, 2004). However, variation in the methods used to analyse aerial photography data alongside a lack of quantitative estimates of uncertainty in the range shifts reported limits the interpretation of the results, and hinders landscape-scale estimation of changes in forest distribution in mountain ecosystems (Morley, Donoghue, Chen, & Jump, 2018).

On average, elevational changes in species range shifts lag behind upward shifts in isotherms in mountain regions (Rumpf et al., 2018). However, the rate of biodiversity change in high-elevation areas seems to be accelerating as the rate of temperature increase accelerates, which will likely lead to tipping points in species loss being met sooner with ongoing climate warming (Steinbauer et al., 2018). Therefore, there is a pressing need to quantify variation in patterns of forest advance over time in order to avoid over- or under-stating the extent of tree line ecotone change and subsequent impacts to montane biodiversity. Here, we assess change in the elevation and area of montane forest at the tree line ecotone using repeat aerial photography data, and quantify the rate of forest advance, identifying how patterns of advance vary according to topography and growth stage.

2 | MATERIALS AND METHODS

2.1 | Study area

This research was conducted in the Central Mountain Range of Taiwan (Figure 1). Despite Taiwan spanning the Tropic of Cancer, high-elevation areas of the Central Mountain Range experience temperate conditions that support conifer-dominated forests at elevations higher than 2,400 m a. s. l. The high-elevation forests of the Central Mountain Range are dominated by four conifer species, primarily *Abies kawakamii* and *Tsuga chinensis* with areas of *Pinus taiwanensis* and *Pinus armandii* establishment. The Mt. Hehuan study area reaches a maximum elevation of 3,560 m a. s. l. with a naturally forming tree line ecotone giving way to grassland that is dominated by the bamboo, *Yushania niitakayamensis*, and has a low density of shrub species, of which *Juniperus* spp. and *Rhododendron* spp. are the most common.

Greenwood et al. (2014), Greenwood, Chen, Chen, and Jump (2015) found that the high-elevation tree line ecotone in Taiwan is predominantly temperature limited, with topography and local sheltering influencing the position, structure and advance of the ecotone through a modification in regional temperature regimes. The importance of local topographic controls in the Central Mountain Range has resulted in a highly reticulate and structurally diverse tree line ecotone. As a consequence, patterns of forest advance within the study area show a high degree of variation over a short distance. Localized reductions in the elevational position of the tree line ecotone are caused by sporadic, naturally occurring small-scale fires and landslides. However, routine anthropogenic disturbance or grazing by either domestic or wild herds is considered of low impact.

2.2 | Aerial photography

Black and white aerial photographs were captured in 1963 (0.3 m pixel size) and 1980 (0.25 m pixel size), colour photographs in 2001 (0.5 m pixel size) and four-band multispectral images in 2016 (0.25 m pixel size). Aerial photographs from 1980, 2001 and 2016 were delivered as orthorectified image products by the Taiwanese National Archive and did not require further geometric corrections (minimum accuracy is 2.5 m). The aerial photographs from 1963 were georeferenced to the images captured in 2016 using a spline transformation in the QGIS Georeferencing plugin (Average number of tie points used was 128, ranging between 78 and 207 between image pairs; the mean error in all image pairs was < 1 pixel).

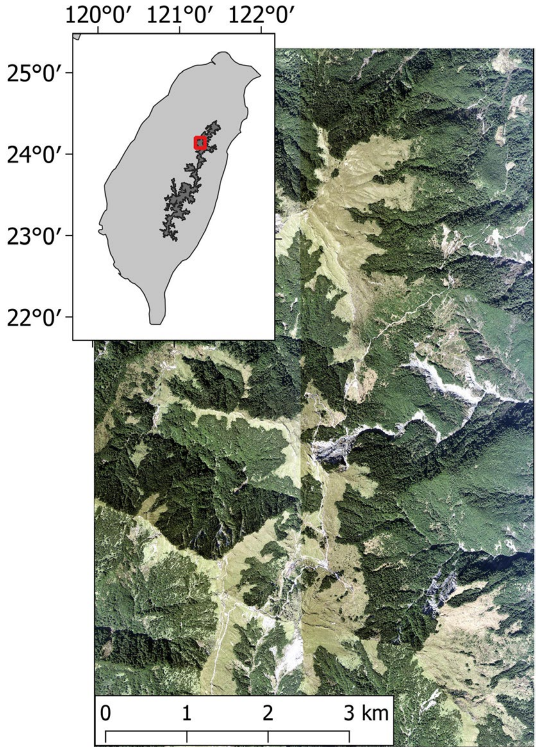

FIGURE 1 Aerial photography from 2016 showing the tree line of high elevation conifer forests in the Mt Hehuan study area of the Central Mountain Range, Taiwan (the area above 2,400 m a. s. l. is shown in black in the inset and the study area marked by the red outline)

2.3 | Change assessment

Probability-based change estimates are a long-established technique for assessing changes in habitat area and condition that have been widely adopted by forest monitoring programmes interested in quantifying change in forest area and forest degradation (Cochran, 1977; Olofsson, Foody, Stehman, & Woodcock, 2013; Pickering et al., 2019). This approach to change assessment uses manual interpretation of remote sensing data at sample plots to estimate the area of each habitat type at each survey date and within a given terrain feature or geographic region of interest (henceforth, stratum) alongside an uncertainty value for the area estimate. Probability-based change estimates are recognized as a reliable method for estimating changes in habitat type or condition enabling changes in habitat to be identified over time with a high degree of confidence (Olofsson et al., 2013; Olofsson, Holden, Bullock, & Woodcock, 2016; Stehman, 2013).

2.4 | Sample design

A proportional stratified random sampling design was used to assess change in forest distribution at the tree line ecotone. To ensure adequate representation of the entire study area, slope orientation was used as a basis for stratification due to the major influence of topography on the patterns of forest advance in Taiwan's Central Mountain Range (Greenwood et al., 2014, 2015). Stratification was based on 12 categories of slope aspect and incline attributes calculated from a high-resolution TanDEM-X Digital Elevation Model (12 m spatial resolution resampled to 15 m pixel size), using four cardinal compass directions (±45° in either direction) and three inclination classes (0–20°, 21–45° and > 46°). The number of samples taken in each stratum was proportional to the area of the study region occupied by the aspect–incline combination (Table S1.1, Figure S1.1). Following the removal of sample plots that had to be omitted due to a cloud or shadow impairing visual interpretation, a total of 2,785 sample plots were interpreted, equivalent to 1.54% of the total study area.

2.5 | Change attributes

At each of the 2,785 sample locations, a sample plot measuring 15 × 15 m in plan view was created and interpreted manually for each year of change analysis (1963, 1980, 2001 and 2016). Each sample plot was assigned one of four vegetation classes for each year in the change survey (Table 1) enabling change between vegetation classes to be tracked over time (Figure 2). Areas that meet the FAO Global Forest Resources Assessment (2018) criterion of a forest as an area with at least 10% canopy cover and trees greater than 5 m in height are classified here as *forest*. Areas with small trees present within the plot that do not meet the thresholds of a forest as set out by the FAO definition were categorized as *establishing forest*. The scale of the aerial photography (≤0.5 m pixel size) is sufficient to discriminate differences in tree size based on crown size. Areas with partial removal of the forest canopy between time periods are categorized as *disturbed* and treeless areas are categorized here as *non-forest* areas. The distinction between the forest and establishing forest classes is important. Forest resource assessments rarely comment on areas of forest establishment that do not meet the pre-defined criteria for forest cover. However, ecological and biogeographic studies have a much broader interpretation, with the timberline defined as the upper limit of closed forest, the tree line defined broadly as the line connecting the maximum elevation of trees greater than 2 m in height and the species limit by the uppermost trees irrespective of tree height (Körner, 1998). Therefore, in this study we make a separation between mature montane forest (*forest* class) and areas of the tree line ecotone above the continuous forest limit that are undergoing increases in tree size or density (*establishing forest* class). In doing so, we are able to gain a more detailed understanding of the forest–grassland transition that is present at mountain tree lines than a simpler forest/ non-forest vegetation classification.

2.6 | Change estimates

Estimates of vegetation change were calculated in R (R Core Team, 2017) using the *survey* package (*v 3.36;* Lumley, 2018) to determine weighted estimates of the population total, returning estimated total area (ha) and proportional representation of class membership for each stratum and survey period. The *survey* package accounts for the effect of stratification by weighting observations according to the sampling probability. The elevation of each plot was identified from a TanDEM-X Digital Elevation Model and the average elevation of each class calculated for each survey period to quantify the change in class elevation over time. The TanDEM-X Digital Elevation Model has a relative vertical accuracy of 2 m and an absolute vertical accuracy of 10 m. The estimated class area in each survey period was compared over time to identify changes in habitat area. Area estimates were calculated for the whole study area and for each terrain stratum to give the proportion of available area occupied by each vegetation class in each of the four aspect strata and

TABLE 1 Definitions of vegetation classes used here to assess forest change in the Central Mountain Range, Taiwan

Class	Description
Forest	An area of trees that meet FAO (2018) criteria of a forest with at least 10% canopy cover and trees greater than 5 m in height.
Establishing forest	An area of forest establishment, small trees are identifiable in aerial photographs due to their small crown size.
Non-forest	An area that lacks trees.
Disturbed	An area of forest with a reduction in canopy cover but some trees remain.
Omitted	Unable to identify vegetation class due to cloud cover or shadow.

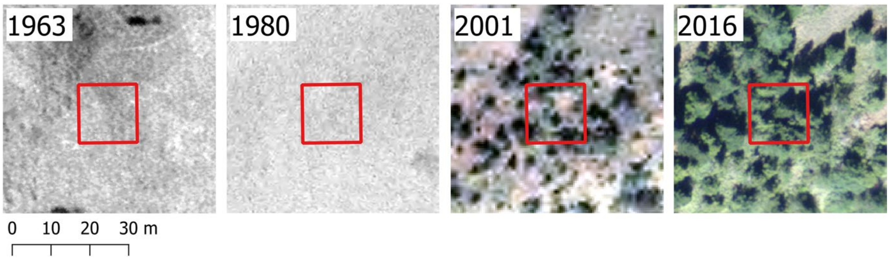

FIGURE 2 Changes in vegetation class over time identified in repeat aerial photographic surveys from the Mt. Hehuan region of the Central Mountain Range, Taiwan. The images show a 15 × 15 m sample plot that is non-forest in 1963 and 1980 and transitions through the establishing forest class and the conversion to the forest class in 2016

TABLE 2 The proportion of changes in vegetation classes between 1963 and 2016 in the Mt. Hehuan region of the Central Mountain Range, Taiwan. Uncertainty is shown as standard error alongside the estimated proportion of change at the upper (97.5%) and lower (2.5%) 95% confidence intervals

Class changes from Non-forest					
1963	2016	Proportion	SE	2.5%	97.5%
Non-Forest	Non-Forest	0.7121	0.0132	0.6863	0.7379
Non-Forest	Establishing	0.2058	0.0117	0.1829	0.2288
Non-Forest	Forest	0.0821	0.0080	0.0663	0.0978
Class changes from Establishing forest					
1963	2016	Proportion	SE	2.5%	97.5%
Establishing	Non-Forest	0.0094	0.0063	−0.0030	0.0218
Establishing	Establishing	0.2125	0.0271	0.1595	0.2656
Establishing	Forest	0.7780	0.0275	0.7241	0.8320
Class changes from Forest					
1963	2016	Proportion	SE	2.5%	97.5%
Forest	Non-Forest	0.0142	0.0021	0.0100	0.0184
Forest	Forest	0.9787	0.0026	0.9735	0.9838
Forest	Disturbed	0.0071	0.0015	0.0041	0.0102

three inclination strata. Variation in the rate of habitat change was investigated for two change classes: recent establishment, defined as a change from non-forest to establishing forest within a change period; and advanced establishment, defined as a change from establishing forest to forest within a single change period. Average rates of advance were calculated as the proportion of available area occupied by a change class divided by the length of the monitoring period (e.g. the proportion of the non-forest area in 1980 that has converted into establishing forest in 2001 divided by 21 years, returns the rate of recent establishment between 1980 and 2001). All uncertainty measures reported are at the 95% confidence intervals unless otherwise stated and area estimates are reported in plan view.

3 | RESULTS

3.1 | Landscape-scale change estimates

In the Mt. Hehuan region, *c.* 20.6% ± 2.3% of the non-forest area in 1963 was establishing forest in 2016 with a further 8.2% ± 1.5% of the non-forest area in 1963 identified as forest by 2016 (Table 2). Forest disturbance in the Mt. Hehuan region is rare, 1.4% ± 0.4% of the forest area in 1963 became non-forest by 2016 while a further 0.7% ± 0.3% experienced a reduction in canopy cover between 1963 and 2016 (Table 2). There was no evidence indicating anthropogenic causes for forest advance or loss in the Mt. Hehaun region. In areas of forest loss, complete removal of substrate was visible in the aerial photography suggesting that forest loss is primarily caused by landslide events with no direct evidence in the aerial photography to suggest fire or forest management caused a loss in forest area. Between 1963 and 2016, forest advance in the Mt. Hehuan study area has led to an estimated net increase in forest area of 295.0 ha and an estimated net decrease in the non-forest area of 332.6 ha (Figure 3a, table S1.2).

Despite the increase in forest area, the mean elevation of the forest class has not changed over time (elevation in 1963 was 2,917 m ± 9 m and in 2016 was 2,914 m ± 9 m; Figure 3b). However, the mean elevation of establishing forest has increased, rising 115 m in elevation from 2,887 m a.s.l. ± 26 m in 1963 to 3,002 m a.s.l. ± 21 m in 2016. While there has been a change in the elevation of establishing forest, the increase in the area occupied by establishing forest is modest with an increase of just 20.1 ha between 1963 and 2016 (Figure 3, table S1.2). There has been continued tree growth within areas of establishing forest throughout the study period resulting in 77.8% ± 5.4% of the area occupied by establishing

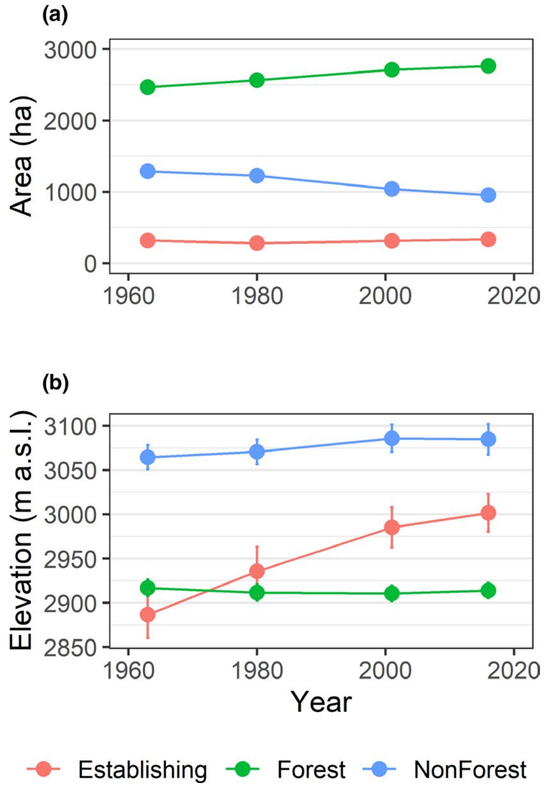

FIGURE 3 Temporal changes in the area occupied (a) and mean elevation (b) of each of the three vegetation classes (montane forest, establishing forest and non-forest) in the Mt. Hehuan area of the Central Mountain Range, Taiwan. Uncertainty of the estimates is shown at the 95% confidence intervals

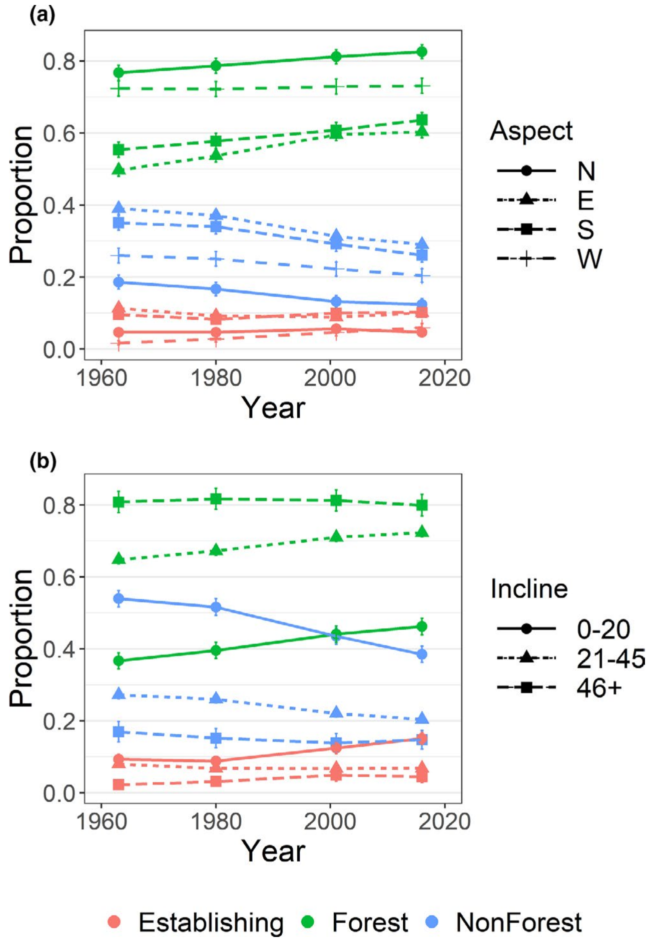

FIGURE 4 Temporal changes in the proportion of aspect (a) and incline (b) terrain strata occupied by each vegetation class (forest, establishing forest and non-forest) in the Mt. Hehuan area of the Central Mountain Range, Taiwan. Uncertainty of the estimates is shown at the 95% confidence interval

forest in 1963 transitioning to forest by 2016 (Table 2). Failed forest establishment is rare in Mt. Hehuan, just 0.9% ± 1.2% of the area of establishing forest in 1963 returned to non-forest by 2016. However, 21.3% ± 5.3% of the area of establishing forest in 1963 remained within the establishing forest class in 2016, indicating a limitation on tree growth in some areas (Table 2).

3.2 | Variation in forest change

While the proportion of forest on west-facing slopes has remained stable, the three remaining aspect classes all show an increase in forest area with east- and south-facing aspects showing the largest change in forest area between 1963 and 2016 (increase in the proportion of area occupied by forest of 10.7% and 8.3%, respectively, Figure 4a). Similarly, the proportion of area occupied by forest has remained constant on slopes > 46°, but has increased on slopes of 0–45° between 1963 and 2016 (Figure 4b). Despite similar changes in the proportion of area occupied by forest on slopes of 0–20° and 21–45° incline, the gain in forest area over the study period is greater on slopes with 21–45° incline (221 ha) rather than slopes with 0–20° incline (76 ha). This discrepancy occurs because the 21–45° stratum occupies a larger proportion of the Mt. Hehuan study area (Figure S1.1). While there have been large changes in forest area between 1963 and 2016, the proportion of area occupied by establishing forest has remained stable in a majority of aspect and inclination strata. Two of the terrain strata considered here show increases in the proportion of area occupied by the establshing forest class, with establishing forest area increasing by 4.3% on west-facing slopes and by 3.0% on slopes with 0–20° between 1963 and 2016 (Figure 4).

The rate of recent establishment (a change from non-forest to establishing forest within a single change period) peaked across the study area between 1980 and 2001 and remained stable between 2001 and 2016 (Figure 5a). Only north-facing aspects and slopes >46° deviate from this landscape pattern of recent establishment rates, with slopes facing north or >46° showing a sharp peak in recent establishment between 1980 and 2001 followed by a decline in the rate of advance between 2001 and 2016 (Figure 5c and e). While at a landscape scale, the rate of recent establishment stabilizes after the 1980–2001 change period, the rate of change for advanced establishment, defined as the conversion between establishing forest and forest within a single change period, peaks between 1980 and 2001 in Mt. Hehuan (Figure 5b). There is also greater variation between terrain strata for the advanced establishment with east- and west-facing aspects and slopes <46° mirroring the landscape-scale pattern while north- and south-facing aspects and slopes >46° show a deviation from this trend (Figure 5d and f). The rate of advanced establishment on north- and south-facing slopes stabilizes after 2001 with south-facing slopes showing a small increase in the rate of advanced establishment between 2001 and 2016 (Figure 5d). Slopes > 46° show an inverse relationship to the landscape-scale pattern of advanced establishment with a strong decline in the rate of change between 1980 and 2001 and higher rates of advanced establishment during the 1963–1980 change period and the 2001–2016 change period (Figure 5f).

4 | DISCUSSION

Repeat aerial photographic survey data reveal that forest advance has led to a loss of 29% of the non-forest area present in 1963 in the Mt. Hehuan region of the Central Mountain Range, Taiwan (Table 2). While there has been an increase in forest area of 295.0 ha between 1963 and 2016 in the Mt. Hehuan study area, the mean elevation of the forest class has not changed over the study period. The

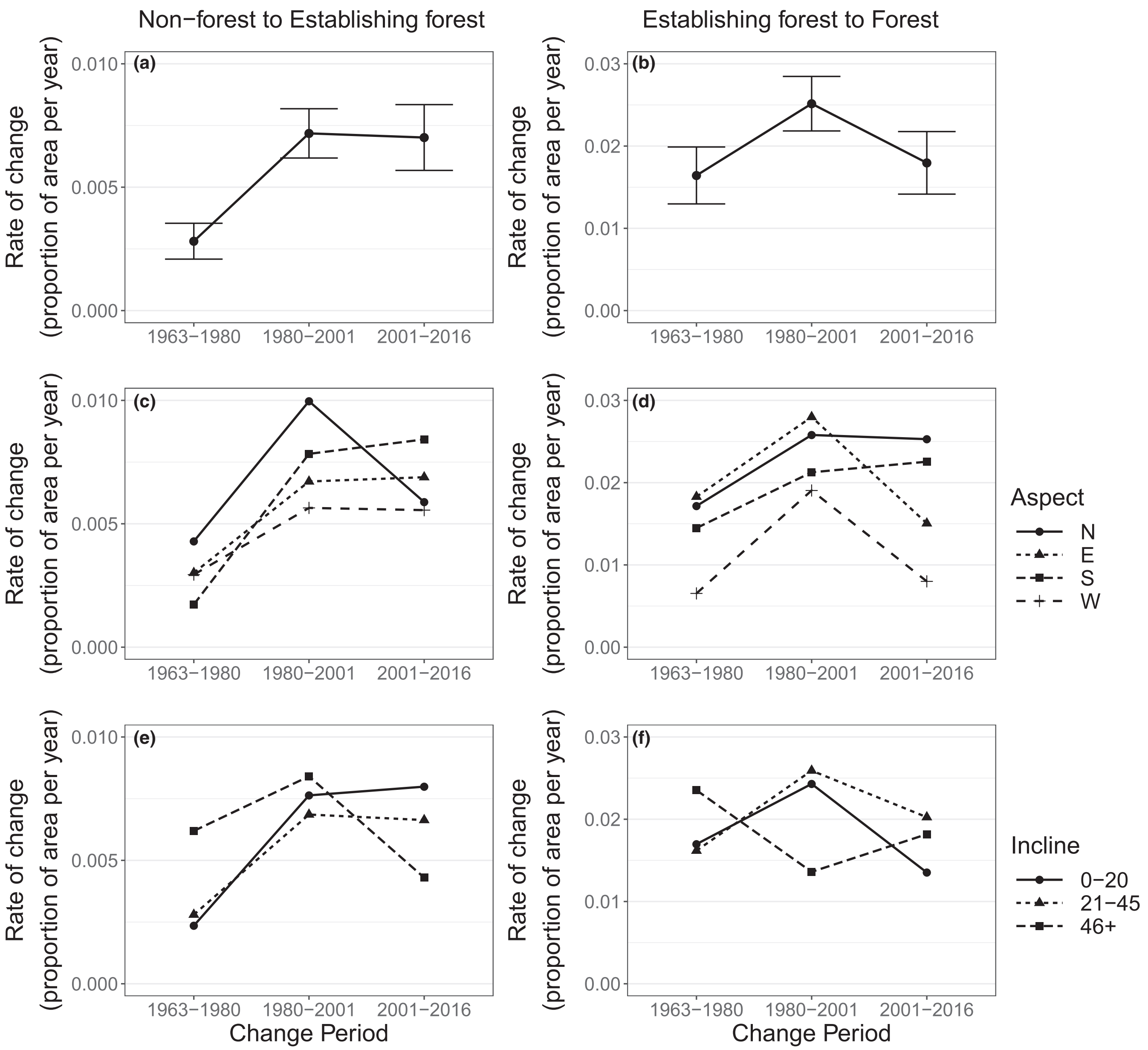

FIGURE 5 Temporal variation in the rate of forest advance in the Mt. Hehuan study area (Taiwan). The rate of recent forest establishment, defined as the change from non-forest to establishing forest within a single change period (1963–1980, 1980–2001 and 2001–2016) is shown for the study area as a whole (a), by aspect (c) and by incline (e). The rate of advanced establishment, defined as the change from establishing forest to forest within a change period is shown for the study area as a whole (b), by aspect (d) and by incline (f). Uncertainty in the estimates in panels a and b is shown at the 95% confidence intervals

substantial increase in forest area, yet stasis in mean forest elevation reported here, (Figure 3) has also been observed globally including in the Khibiny Mountains, Russia (Mathisen et al., 2014), the Tibetan Plateau (Liang et al., 2011), Glacier National Park, USA (Klasner & Fagre, 2002), the Sudetes mountains, Czech Republic (Treml & Chuman, 2015) and the Pyrenees, France (Feuillet et al., 2020). In Taiwan, our findings are consistent with patterns of forest advance previously identified in field assessments by Greenwood et al. (2014) who identified that forest advance in Taiwan's Central Mountain Range predominantly displays infilling below the upper tree line with only modest changes in maximum elevation (27–33 m gain in maximum elevation).

The process of infilling occurs because localized depressions in elevation of the ecotone enable tree recruitment to occur both from below and across slope from the edges of these depressions (Treml & Chuman, 2015). The montane forests of the Central Mountain Range have a highly reticulate tree line owing to strong topographic and micro-climatic controls on tree line position and seedling establishment (Greenwood et al., 2014, 2015). The reticulated nature of the tree line means that the forest has reached its maximum potential elevation in many areas, as determined by mountain ridge tops. As a result, it is not possible for the forest to shift further upslope but the localized depressions of the tree line ecotone experience substantial increases in forest area resulting in an increase in the mean elevation at which new establishment occurs. Therefore, the nature of the tree line ecotone has enabled a 115 m uphill advance in the position of establishing forest between 1963 and 2016 (equivalent to 2.17 m/yr; Figure 3b) despite no increase in elevation of the forest class.

Jump et al. (2012) report a rise in temperatures in the Central Mountain Range of 1.05°C up until 2009 compared to the 1934–1970 mean. Given the estimated temperature lapse rate for Taiwan calculated by Guan, Hsu, Wey, and Tsao (2009) of 0.5°C 100 m^{-1}, we could expect an increase in mean forest elevation to be around 200 m between 1934 and 2009 (equivalent to 2.67 m/yr) if elevational change in forest cover was keeping pace with rises in isotherm position. With an estimated increase in elevation of 2.17 m/yr, the estimated uphill advance of establishing forest lags behind the temperature increase at a rate of 0.5 m/yr. This lag likely occurs due to the substantial influence of microclimate and local sheltering on seedling establishment and growth in the Central Mountain Range that restrict the speed of elevational shifts of the montane forest (Greenwood et al., 2015). If the establishing forest class had not been considered separately, the 0.5 m/yr lag identified would have been identified as more extreme, substantially altering our interpretation of the impact of climate change on the tree line ecotone. Feuillet et al. (2020) highlight that some studies have concluded an absence of environmental change impacts due to a lack of change in tree line elevation, yet densification below the tree line and increases in the elevation of establishment in localized depressions here (Figure 3) and elsewhere are occurring despite a lack of change in tree line position (Klasner & Fagre, 2002; Liang et al., 2011; Mathisen et al., 2014; Treml & Chuman, 2015). Consequently, it is increasingly important that multiple responses of the tree line ecotone are considered to ensure studies avoid potentially erroneous conclusions of the impact of environmental change on high-altitude ecosystems.

The increases in forest area and mean elevation of establishing forest reported for the study area as a whole mask important variation in patterns of forest advance within the region. East- and south-facing aspects show larger increases in forest area between 1963 and 2016 than west- and north-facing slopes (Figure 4a). Similarly, forest advance between 1963 and 2016 is greatest on slopes with inclinations between 0 and 45°, with the greatest decline in non-forest area occuring on 0 and 20° slopes (Figure 4b). This substantial decline in non-forest area is driven by a 6% increase in the area of 0–20° slopes that are occupied by establishing forest. Greenwood et al. (2014, 2015) show that seedling establishment in the Central Mountain Range, Taiwan, is strongly controlled by topography, with higher recruitment associated with east-facing or shallow slopes and more sheltered areas. Furthermore, as temperature thresholds are passed at a given elevation, a larger area of habitat is likely to be affected by environmental change when the slope inclination is shallow (Jump, Mátyás, & Peñuelas, 2009). Therefore, in combination with an increased probability of forest establishment on shallow and concave slopes (Feuillet et al., 2020; Greenwood et al., 2014, 2015), environmental changes lead to higher rates of forest establishment and rapid declines in grassland area once shallow slopes become favourable for seedling establishment.

The rate of recent establishment (conversion from non-forest to establishing forest within a change period) has remained stable after an initial increase during the 1980–2001 change period, with only north-facing aspects and slopes with inclinations > 46° showing a decline in the rate of recent establishment between 2001 and 2016. However, the rate of advanced establishment (conversion from establishment to forest within a change period) peaked between 1980 and 2001 at the landscape scale, with north- and south-facing slopes showing a stable rate of establishment after 2001 rather than declining. Differences between the rates of change between these two change classes (recent vs advanced establishment) might be explained by differences in the factors that limit seedling establishment and subsequent growth. While the initial establishment and colonization of new areas in both recent and advanced establishment scenarios are likely to be triggered by a release from a temperature limitation, in order for colonized areas to be converted into forest, the newly colonized areas must also have favourable conditions for rapid growth. The relative importance of any individual control or set of controls on tree recruitment and subsequent growth vary over the life cycle of an individual tree (Greenwood et al., 2015). Consequently, areas that undergo establishment but do not continue to grow sufficiently to be classified as forest may exist in areas where a threshold for establishment has been surpassed, but the necessary conditions for subsequent growth are not met. This pattern of growth restriction occurs in 21.3% ± 5.3% of the areas identified as establishing in 1963, where the trees failed to grow sufficiently to move into the forest class by 2016 (Table 2). There is no evidence to suggest that the areas of slow growth exhibit a stunted growth form such as the krummholz tree lines commonly found in other areas (Greenwood et al., 2014). Understanding the mechanisms that lead to variable rates of establishment and growth should be a priority for new research. The rates of change reported here do not match the accelerating rate of temperature change reported (Jump et al., 2012), and so detailed time series data regarding range shift lags and the interactions with biotic and abiotic factors controlling tree establishment and growth is required to enable improved forecasts of forest growth and range expansion at the tree line ecotone.

The ability to identify heterogeneous patterns in the location, structure and rate of ecotone advance, as shown here, is vital to enable the discrimination of areas that are likely to experience rapid changes in habitat structure from those where stasis might be expected under future climate scenarios (Hagedorn et al., 2019). Forest advance is expected to impact biodiversity of the alpine zone, yet local variability in shifts in the tree line ecotone will modify landscape-scale impacts (Greenwood & Jump, 2014). Forest advance in Mt. Hehuan has reduced the available area of non-forest habitats by 29% and caused a 20–32 m increase in the mean elevation of remaining non-forest habitats through range contraction (Figure 3; elevation gain increases to 32 m when landslide events are excluded). This reduction in habitat area is a particular problem for alpine flora given the typically high rates of endemism and accelerating rate of warming-induced species richness increase in alpine areas (Jump et al., 2012; Steinbauer et al., 2018). Jump et al. (2012) show that the elevation of mountain plant species distribution has increased, on average, by 3.6 m/yr in Taiwan during the last century, indicating that some forb and shrub species are advancing uphill more rapidly than the montane forest. Furthermore, variation in the rate of forest advance caused by slope morphology and substrate (Figures 4–6; Feuillet et al., 2020; Greenwood et al., 2014, 2015) may enable alpine flora to persist despite tree line shifts and infilling occurring in other areas (Bruun & Moen, 2003). Therefore, it is likely that the presence of refugia in areas of slow change or growth limitation will play an increasingly vital role in the maintenance of alpine biodiversity in mountain systems as forest advance continues. However, even where such refugial areas occur, contraction in population size of alpine species is likely due to a reduction in the non-forest areas, risking population loss and diminishing but not removing their risk of local extinction.

The quantification of forest advance and its variability in mountain regions is vital to improve our understanding of tree line ecotone response to environmental change and the mechanisms that drive the observed variation in response. Such knowledge is of fundamental importance to enable the impacts of tree line ecotone change on montane ecosystem function and biodiversity to be quantified. While the need for standardized methods to quantify variation in ecotone response is recognized, little progress has been made (Feuillet et al., 2020; Malanson et al., 2011). Here, we demonstrate an important methodological application of change assessment using probability-based sampling of repeat aerial photography to enable a precise and unbiased quantification of montane forest range shifts. Aerial photography data with 0.25–0.5 m pixel size (typical of many aerial surveys) are of sufficiently high quality to identify tree recruitment at the tree line ecotone and have been used to enable research in areas where historical field datasets are lacking (e.g. Feuillet et al., 2020; Greenwood et al., 2014; Mathisen et al., 2014). As such, aerial photography offers an important resource to study contemporary changes in tree recruitment and forest range shifts that complements existing field-based assessment of change and may enhance assessments of longer-term historical patterns that use dendroecology techniques (e.g. Camarero & Gutiérrez, 2004; Liang et al., 2011). Despite locally excellent data availability, repeat aerial photography is not available in many mountain ranges of the world. However, rapid advances in the spatial resolution of satellite-borne Earth observation data (0.3–0.6 m pixel size) offer significant opportunities to progress towards standardized methods for assessment of forest change and understanding tree line ecotone dynamics (Bader & Ruijten, 2008; Bolton, Coops, Hermosilla, Wulder, & White, 2018; Carlson et al., 2017; Weiss, Malanson, & Walsh, 2015). Integrating the methods that we demonstrate here with rapidly improving Earth observation data for the mountain regions of the world provides a significant opportunity to understand the drivers of mountain forest change, and will enable a robust assessment of the impacts forest advance on biodiversity and ecosystem function from local to global scales.

5 | CONCLUSIONS

Producing precise and unbiased estimates of forest range shifts in mountain systems is of critical importance to enable an informed analysis of the consequences of forest advance for biodiversity and ecosystem services. The integration of repeat aerial photography analysed with a change-sample assessment enables precise and unbiased estimates of forest change that could not be achieved in any other way. In Taiwan's Central Mountain Range, this approach reveals a complex pattern of tree line advance in which rates of forest advance vary according to topography and over time. At the landscape scale, the non-forest area in the Mt. Hehuan region has declined by 29% over the period 1963 to 2016. However, while there has been a substantial increase in forest area, there has not been a change in the mean elevation of the forest class between 1963 and 2016. In contrast, the mean elevation of the establishing forest class has increased at a rate of 2.1 m/yr lagging 0.5 m/yr behind the estimated change in isotherm position. The results reported here highlight the critical importance of considering changes in both elevation and area of montane forest habitat at the tree line ecotone in order to fully capture species response to environmental change. In doing so, we identify that east- and south-facing slopes alongside shallow slopes have experienced the largest declines in non-forest habitat, and 0–20° slopes are at high risk of ongoing loss in habitat area due to an increase in the area of forest establishment. The precise quantification of changes in montane forest elevation and area shown here improves our understanding of the drivers of variation in forest response to environmental change enabling regional-scale assessment of tree line change and facilitating prediction of future forest range shifts and the impacts of forest range shifts on biodiversity and ecosystem function in mountain systems.

ACKNOWLEDGEMENTS

This work was funded by the Natural Environment Research Council, UK, [NERC IAPETUS DTP, grant number NE/L002590/1]. TanDEM-X data were provided by the DLR Science Team [grant number DEM_FOREST1027].

DATA ACCESSIBILITY

The data interpreted by the authors and used for area calculations and change estimates are available through DataSTORRE: the University of Stirling's Online Repository for Research Data https://datastorre.stir.ac.uk/. The authors are unable to release the original aerial photography or TanDEM-X data used in this study due to licence agreements that restrict the distribution of the data. Aerial Photographs used in this study are subject to access and usage restrictions on the authors. Please contact J-C. Chen (zzzjohn@mail.npust.edu.tw) and A.S. Jump (a.s.jump@stir.ac.uk) to discuss access in the first instance.

ORCID

Peter J. Morley https://orcid.org/0000-0002-7503-2520
Daniel N. M. Donoghue https://orcid.org/0000-0002-9931-9083
Alistair S. Jump https://orcid.org/0000-0002-2167-6451

REFERENCES

Améztegui, A., Brotons, L., & Coll, L. (2010). Land-use changes as major drivers of mountain pine (Pinus uncinata Ram.) expansion in the Pyrenees. *Global Ecology and Biogeography*, *19*(5), 632–641. https://doi.org/10.1111/j.1466-8238.2010.00550.x

Améztegui, A., Coll, L., Brotons, L., & Ninot, J. M. (2016). Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. *Global Ecology and Biogeography*, *25*(3), 263–273. https://doi.org/10.1111/geb.12407

Bader, M. Y., & Ruijten, J. J. A. (2008). A topography-based model of forest cover at the alpine tree line in the tropical Andes. *Journal of Biogeography*, *35*(4), 711–723. https://doi.org/10.1111/j.1365-2699.2007.01818.x

Bader, M. Y., Van Geloof, I., & Rietkerk, M. (2007). High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecology*, *191*(1), 33–45. https://doi.org/10.1007/s11258-006-9212-6

Bharti, R. R., Adhikari, B. S., & Rawat, G. S. (2012). Assessing vegetation changes in timberline ecotone of Nanda Devi National Park, Uttarakhand. *International Journal of Applied Earth Observation and Geoinformation*, *18*(1), 472–479. https://doi.org/10.1016/j.jag.2011.09.018

Bolton, D. K., Coops, N. C., Hermosilla, T., Wulder, M. A., & White, J. C. (2018). Evidence of vegetation greening at alpine treeline ecotones: Three decades of Landsat spectral trends informed by lidar-derived vertical structure. *Environmental Research Letters*, *13*(8), 084022. https://doi.org/10.1088/1748-9326/aad5d2

Bruun, H. H., & Moen, J. (2003). Nested communities of alpine plants on isolated mountains: Relative importance of colonization and extinction. *Journal of Biogeography*, *30*(2), 297–303. https://doi.org/10.1046/j.1365-2699.2003.00806.x

Camarero, J. J., & Gutiérrez, E. (2004). Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the spanish pyrenees. *Climatic Change*, *63*(1/2), 181–200. https://doi.org/10.1023/B:CLIM.0000018507.71343.46

Camarero, J. J., Linares, J. C., García-Cervigón, A. I., Batllori, E., Martínez, I., & Gutiérrez, E. (2017). Back to the future: the responses of alpine treelines to climate warming are constrained by the current ecotone structure. *Ecosystems*, *20*(4), 683–700. https://doi.org/10.1007/s10021-016-0046-3

Carlson, B. Z., Corona, M. C., Dentant, C., Bonet, R., Thuiller, W., & Choler, P. (2017). Observed long-term greening of alpine vegetation—a case study in the French Alps. *Environmental Research Letters*, *12*(11), 114006. https://doi.org/10.1088/1748-9326/aa84bd

Cochran, W. G. (1977). *Sampling techniques*, 3rd ed. New Yoirk: John Wiley & Sons.

Dirnböck, T., Essl, F., & Rabitsch, W. (2011). Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, *17*(2), 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

FAO (2018). *Global Forest Resources Assessment 2020* (p. 2018). Rome: Food and Agriculture Organization of the United Nations.

Feuillet, T., Birre, D., Milian, J., Godard, V., Clauzel, C., & Serrano-Notivoli, R. (2020). Spatial dynamics of alpine tree lines under global warming: What explains the mismatch between tree densification and elevational upward shifts at the tree line ecotone? *Journal of Biogeography*, *47*(5), 1056–1068. https://doi.org/10.1111/jbi.13779

Fisher, J. I., Hurtt, G. C., Thomas, R. Q., & Chambers, J. Q. (2008). Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecology Letters*, *11*(6), 554–563. https://doi.org/10.1111/j.1461-0248.2008.01169.x

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., … Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, *2*(2), 111–115. https://doi.org/10.1038/nclimate1329

Grabherr, G., Gottfried, M., & Pauli, H. (2000). GLORIA: A global observation research initiative in alpine environments. *Mountain Research and Development*, *20*(2), 190–191. https://doi.org/10.1659/0276-4741(2000)020[0190:GAGORI]2.0.CO;2

Greenwood, S., Chen, J.-C., Chen, C.-T., & Jump, A. S. (2014). Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. *Global Change Biology*, *20*(12), 3756–3766. https://doi.org/10.1111/gcb.12710

Greenwood, S., Chen, J. C., Chen, C. T., & Jump, A. S. (2015). Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline. *Journal of Vegetation Science*, *26*(4), 711–721. https://doi.org/10.1111/jvs.12269

Greenwood, S., & Jump, A. S. (2014). Consequences of treeline shifts for the diversity and function of high altitude ecosystems. *Arctic, Antarctic, and Alpine Research*, *46*(4), 829–840. https://doi.org/10.1657/1938-4246-46.4.829

Guan, B. T., Hsu, H. W., Wey, T. H., & Tsao, L. S. (2009). Modeling monthly mean temperatures for the mountain regions of Taiwan by generalized additive models. *Agricultural and Forest Meteorology*, *149*(2), 281–290. https://doi.org/10.1016/j.agrformet.2008.08.010

Haddaway, N. R., Styles, D., & Pullin, A. S. (2014). Evidence on the environmental impacts of farm land abandonment in high altitude/mountain regions: A systematic map. *Environmental Evidence*, *3*(1), 1–7. https://doi.org/10.1186/2047-2382-3-17

Hagedorn, F., Gavazov, K., & Alexander, J. M. (2019). Above- and below-ground linkages shape responses of mountain vegetation to climate change. *Science*, *365*(6458), 1119–1123. https://doi.org/10.1126/science.aax4737

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, *12*(10), 1040–1049. https://doi.org/10.1111/j.1461-0248.2009.01355.x

IPCC. (2013). Climate Change 2013 The Physical Science Basis Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (T. F. Stocker, D. Qin, G.-K. Plattner, M. M. B. Tignor, S. K. Allen, J. Boschung, … P. M. Midgley, Eds.). Cambridge, UK and New York, NY, USA: Cambridge University Press.

Johnson, D. M., & Smith, W. K. (2007). Limitations to photosynthetic carbon gain in timberline Abies lasiocarpa seedlings during prolonged drought. *Canadian Journal of Forest Research*, *37*(3), 568–579. https://doi.org/10.1139/x06-246

Jump, A. S., Huang, T.-J., & Chou, C.-H. (2012). Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography*, *35*, 204–210. https://doi.org/10.1111/j.1600-0587.2011.06984.x

Jump, A. S., Mátyás, C., & Peñuelas, J. (2009). The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, *24*(12), 694–701. https://doi.org/10.1016/j.tree.2009.06.007

Klasner, F. L., & Fagre, D. B. (2002). A half century of change in alpine treeline patterns at glacier national park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, *34*(1), 49–56. https://doi.org/10.2307/1552508

Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, *115*(4), 445–459. https://doi.org/10.1007/s004420050540

Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, *31*(5), 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x

Leuschner, C., & Schulte, M. (1991). Microclimatological investigations in the tropical alpine scrub of maui, hawaii: evidence for a drought-induced alpine timberline!. *Pacific Science*, *45*(2), 152–168.

Liang, E., Wang, Y., Eckstein, D., & Luo, T. (2011). Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytologist*, *190*(3), 760–769. https://doi.org/10.1111/j.1469-8137.2010.03623.x

Lumley, T. (2018). Survey: Analysis of complex survey samples. R Package Version, 3.34.

Luo, G., & Dai, L. (2013). Detection of alpine tree line change with high spatial resolution remotely sensed data. *Journal of Applied Remote Sensing*, *7*(1), 073520. https://doi.org/10.1117/1.JRS.7.073520

MacDonald, D., Crabtree, J. R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., … Gibon, A. (2000). Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management*, *59*(1), 47–69. https://doi.org/10.1006/jema.1999.0335

Malanson, G. P., Resler, L. M., Bader, M. Y., Holtmeier, F.-K., Butler, D. R., Weiss, D. J., … Fagre, D. B. (2011). Mountain treelines: A roadmap for research orientation. *Arctic, Antarctic, and Alpine Research*, *43*(2), 167–177. https://doi.org/10.1657/1938-4246-43.2.167

Mathisen, I. E., Mikheeva, A., Tutubalina, O. V., Aune, S., & Hofgaard, A. (2014). Fifty years of tree line change in the Khibiny Mountains, Russia: Advantages of combined remote sensing and dendroecological approaches. *Applied Vegetation Science*, *17*(1), 6–16. https://doi.org/10.1111/avsc.12038

McNown, R. W., & Sullivan, P. F. (2013). Low photosynthesis of treeline white spruce is associated with limited soil nitrogen availability in the Western Brooks Range. *Alaska. Functional Ecology*, *27*(3), 672–683. https://doi.org/10.1111/1365-2435.12082

Millar, C. I., Westfall, R. D., & Delany, D. L. (2007). Response of high-elevation limber pine (Pinus flexilis) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. *Canadian Journal of Forest Research*, *37*(12), 2508–2520. https://doi.org/10.1139/x07-097

Morley, P. J., Donoghue, D. N. M., Chen, J.-C., & Jump, A. S. (2018). Integrating remote sensing and demography for more efficient and effective assessment of changing mountain forest distribution. *Ecological Informatics*, *43*, 106–115. https://doi.org/10.1016/j.ecoinf.2017.12.002

Olofsson, P., Foody, G. M., Stehman, S. V., & Woodcock, C. E. (2013). Making better use of accuracy data in land change studies: Estimating accuracy and area and quantifying uncertainty using stratified estimation. *Remote Sensing of Environment*, *129*, 122–131. https://doi.org/10.1016/j.rse.2012.10.031

Olofsson, P., Holden, C., Bullock, E., & Woodcock, C. (2016). Time series analysis of satellite data reveals continuous deforestation of New England since the 1980s. *Environmental Research Letters*, *11*, 064022. https://doi.org/10.1088/1748-9326/11/6/064002

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., … Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*(5), 424–430. https://doi.org/10.1038/nclimate2563

Pickering, J., Stehman, S. V., Tyukavina, A., Potapov, P., Watt, P., Jantz, S. M., … Hansen, M. C. (2019). Quantifying the trade-off between cost and precision in estimating area of forest loss and degradation using probability sampling in Guyana. *Remote Sensing of Environment*, *221*, 122–135. http://dx.doi.org/10.1016/j.rse.2018.11.018

R Core Team, (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B. O., Holt, B. G., Morueta-Holme, N., … Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, *365*(6458), 1108–1113. https://doi.org/10.1126/science.aax0149

Resler, L. M., Fonstad, M. A., & Butler, D. R. (2004). Mapping the alpine treeline ecotone with digital aerial photography and textural analysis. *Geocarto International*, *19*, 37–44. https://doi.org/10.1080/10106040408542297

Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., … Dullinger, S. (2018). Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences*, *115*(8), 1848–1853. https://doi.org/10.1073/pnas.1713936115

Stehman, S. V. (2013). Estimating area from an accuracy assessment error matrix. *Remote Sensing of Environment*, *132*, 202–211. https://doi.org/10.1016/j.rse.2013.01.016

Steinbauer, M. J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., … Beierkuhnlein, C. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, *25*(9), 1097–1107. https://doi.org/10.1111/geb.12469

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., … Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*(7700), 231–234. https://doi.org/10.1038/s41586-018-0005-6

Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B., & Thomas, C. D. (2011). Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, *120*(1), 1–8. https://doi.org/10.1111/j.1600-0706.2010.18270.x

Sullivan, P. F., Ellison, S. B. Z., McNown, R. W., Brownlee, A. H., & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, *96*(3), 716–727. https://doi.org/10.1890/14-0626.1

Treml, V., & Chuman, T. (2015). Ecotonal dynamics of the altitudinal forest limit are affected by terrain and vegetation structure variables: An example from the sudetes mountains in central Europe. *Arctic, Antarctic, and Alpine Research*, *47*(1), 133–146. https://doi.org/10.1657/AAAR0013-108

Vetaas, O., & Grytnes, J.-A. (2002). Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, *11*(4), 291–301. https://doi.org/10.1046/j.1466-822X.2002.00297.x

Weiss, D. J., Malanson, G. P., & Walsh, S. J. (2015). Multiscale relationships between alpine treeline elevation and hypothesized environmental controls in the Western United States. *Annals of the Association of American Geographers*, *105*(3), 437–453. https://doi.org/10.1080/00045608.2015.1015096

BIOSKETCH

The authors are an interdisciplinary group focusing on integrating remote sensing data into assessments of global environmental change impacts, with an emphasis on forest systems. Their research has a strong focus on quantifying forest change and understanding the spatial heterogeneity of the impacts of climate change on plant populations.

Authors contribution: P.M., D.D, J-C.C. & A.J. designed the study, P.M. performed the analyses which were verified by D.D. and A.J. P.M. wrote the manuscript with input from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Morley PJ, Donoghue DNM, Chen J-C, Jump AS. Montane forest expansion at high elevations drives rapid reduction in non-forest area, despite no change in mean forest elevation. *J Biogeogr*. 2020;00:1–12. https://doi.org/10.1111/jbi.13951