

ECOGRAPHY

Research Article

Topography constrains the climatic response of treeline migration in Taiwan's subalpine forests

Kuan-Yu Chen¹, Jonathan Peereman^{1,2}, J. Aaron Hogan³ and Teng-Chiu Lin^{1,4}  

¹Department of Life Science, National Taiwan Normal University, Taipei, Taiwan

²SPHERES Research Unit, University of Liège, Arlon, Belgium

³Department of Biology, Colorado State University, Fort Collins, CO, USA

⁴Department of Natural Resources and Environmental Studies, National Dong Hwa University, Hualien, Taiwan

Correspondence: Teng-Chiu Lin (tclin@ntnu.edu.tw)

Ecography

2026: e08500

doi: 10.1002/ecog.08500

Subject Editor: Eric Post

Editor-in-Chief:

Christine N. Meynard

Accepted 17 April 2026



Treelines are moving upslope, but the rates and drivers differ among different regions, globally. Many studies have examined the relationship between treeline movement and climate change, particularly rising temperature, while the role of topographical factors has received much less attention, despite the longstanding recognition of its importance. We examined treeline dynamics from 1980 to 2021 in two mountain ranges of Taiwan, the Yushan Mountain Range (YMR) and the Central Mountain Range (CMR), in relation to topography and climate using multi-temporal aerial imagery and U-Net deep-learning segmentation. Treeline elevation advanced approximately 60 m on the two mountains and was accompanied by forest area expansion of 197 ha in the YMR and 158 ha in the CMR, which was mainly due to upward forest movement, not tree densification. Elevation, increases in growing-season temperature and minimum temperature, and growing-season precipitation were important predictors of forest area expansion. In contrast, elevation, increases in growing-season precipitation and maximum temperature, and slope steepness were key predictors of treeline movement. Treeline upslope migration was approximately two times greater during the 1980–2001 period (2.1 in the YMR and 1.6 m year⁻¹ in the CMR) compared to the 2001–2021 period (1.0 in the YMR and 0.75 m year⁻¹ in the CMR), likely because forests already occupied most of the suitable habitat, and topographic factors constrained upward movement. Our study highlights the importance of accounting for both climatic and topographic factors in understanding treeline responses to climate change. In addition, our results indicate that treeline advance in mountain island forests, such as those in Taiwan, may be approaching an elevational limit, above which further upward migration is likely to exhibit a more muted response to further warming.

Keywords: climate change, forest expansion, remote sensing, subalpine forests, tree densification, treeline, treeline movement



www.ecography.org

© 2026 The Author(s). Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

High mountain ecosystems are particularly sensitive to climate change because many species, predominantly plants living in these environments, are adapted to very specific, often harsh climates that include low temperatures, short growing seasons, and intense solar radiation (Pauli et al. 2012, Stanchi et al. 2013). Thus, even minor climate changes can significantly impact seedling establishment and growth (Körner 1999, Pauli et al. 2012, Greenwood et al. 2015). Rising temperatures typically drive species migrations to higher elevations, reducing suitable habitat area (Grabherr et al. 2010, Gottfried et al. 2012, Duque et al. 2015, Elsen and Tingley 2015, Feeley et al. 2020).

The treeline is the elevation of an approximate contour line that connects the highest patches of forest within a given slope or series of slopes with similar exposure (Körner 1998, 2012, Greenwood et al. 2015). It is the transition zone (i.e. ecotone) between subalpine forest and alpine tundra. This transition zone is sensitive to climate change, especially warming. Warming affects treeline dynamics via two distinct processes: 1) upslope movement of the treeline ecotone, reflecting changes in the upper elevational limit of tree establishment, and 2) densification within the existing treeline zone, reflecting increased tree cover without an upward shift. These processes may respond differently to climate, disturbance, and topographic constraints, and must be evaluated separately to understand mountain forest responses to warming.

Warming over the past century has allowed trees to expand to higher elevations, pushing treelines higher (Cazzolla Gatti et al. 2019). A meta-analysis reported that from 1901 to 2018, treelines in 127 out of 143 locations ascended in elevation (Lu et al. 2021). Nevertheless, the rate of treeline advancement varied considerably across local and regional scales during this period, ranging from 0.4 to 2.0 m year⁻¹ in the European Alps (Ameztegui et al. 2015, Cudlín et al. 2017, Mietkiewicz et al. 2017), 0.23 and 2.3 m year⁻¹ in the Rocky Mountains (Elliott and Petruccioli 2018, Davis et al. 2020, Trant et al. 2020), and 1.1–11.3 m year⁻¹ in the Himalayas (Yadava et al. 2017, Mohapatra et al. 2019). In addition to driving forests to higher altitudes, climate change can increase tree density in subalpine environments (Trembl et al. 2016, Wang et al. 2016, Morley et al. 2020). Tree densification within treeline ecotones, driven by warming-induced increases in seed germination, seedling establishment, and tree growth, has been documented across many regions worldwide (Wang et al. 2006, Körner 2012, Lett and Dorrepaal 2018, Davis et al. 2020, Du et al. 2021). Yet, in many cases, this densification has occurred without a corresponding upward shift in treeline position (Liang et al. 2011, Mathisen et al. 2014, Devi et al. 2020), highlighting a decoupling between upslope migration and local stand densification in response to climate warming.

Both upslope treeline movement and tree densification can increase forest cover at the treeline ecotone, and they can occur in unison or separately, and often happen at different rates. For example, in the Pyrenees mountains of western

Europe, 40% of treelines showed a mismatch between rates of upslope migration and tree densification (Feuillet et al. 2020). Globally, mismatches between these two processes have been reported for 63% of treelines (Shi et al. 2022). The mismatch can be due to topographic or geological constraints, such as steep slopes (e.g. cliff faces) or unsuitable growing substrates (e.g. rocky soils), which can prevent treeline advancement to higher elevations (Butler et al. 2007, Macias-Fauria and Johnson 2013, Morley et al. 2020). Landscape slope and landform are the main factors affecting tree densification. Generally, concave and gentle slopes are the most suitable for forest colonization (Feuillet et al. 2020, Beloiu et al. 2022). In addition, in regions experiencing drier, warmer climates, forest establishment at higher elevations within the ecotone is environmentally constrained, but tree growth and recruitment often increase at the treeline, leading to greater stand biomass and tree densification (Trembl et al. 2016). Alternatively, the mismatch could result from complex interactions among environmental factors in response to climate change (Corlett and Westcott 2013, Feuillet et al. 2020, Shi et al. 2022). Distinguishing between these processes is essential for interpreting treeline responses in Taiwan, where complex topography and disturbance regimes may decouple upward migration from increases in tree cover.

Trees growing at high altitudes face harsh environmental conditions, including strong winds and intense solar radiation, which reduce sapling growth. Elevation, slope, and aspect interact with local climate, solar irradiance, and substrate stability to further affect tree growth. Thus, when analyzing treeline dynamics, both altitudinal movement and tree densification should be considered in relation to local climate conditions and topographical features (Shi et al. 2022). However, although the role of topographical factors in shaping treeline dynamics has long been recognized (Brown 1994, Elliott and Cowell 2015, Leonelli et al. 2016), most studies have focused solely on climatic factors, particularly temperature (Bhatta et al. 2025).

Taiwan is a mountainous subtropical island with about 60% forest cover. Although the island's mean elevation is 312 m a.s.l, it ranges from 0 to 4000 m a.s.l. Subalpine forests of the island are dominated by Taiwan fir *Abies kawakamii*. The island's rugged topography results in diverse climates and environmental conditions that influence forest distribution. This environmental heterogeneity provides an ideal setting to explore how topographical features modulate climatic influences on treeline dynamics under ongoing warming. Previous treeline studies in Taiwan have applied a range of data sources and analytical approaches to quantify treeline dynamics (Supporting information). Early field-based research inferred episodic upslope advance from tree establishment age and spatial position relative to the current treeline, estimating an increase of 9–18 m every 35–40 years (0.23–0.51 m year⁻¹; Lai 1992, Chuang 1998). More recent studies have used multi-temporal Landsat imagery combined with digital elevation models to quantify forest cover change and extract shifts in treeline elevation, reporting rates of up to 1.43 m year⁻¹ (Chung et al. 2021). High-resolution

aerial-photograph analyses further suggest that tree densification within the treeline ecotone and upslope displacement of the upper forest boundary can occur at different rates, with substantial increases in forest area sometimes accompanied by relatively modest elevational change (Greenwood et al. 2014, Morley et al. 2020). These contrasting approaches provide complementary reference estimates and together indicate that high-mountain forests in Taiwan have generally expanded, accompanied by an upward shift in their upper elevational limits.

Although studies have documented local forest expansion and treeline movement in Taiwan, there are few comprehensive assessments of treeline dynamics across different mountain ranges. The findings of studies focusing on a specific mountain or mountain range may not be generalizable to other mountains with different climatic and topographical conditions. Moreover, previous assessments of forest expansion with climate change in Taiwan and in many parts of the world often used climate data from global datasets. However, such coarsely gridded climate data do not capture rapid climate variation along topographic gradients (Potter et al. 2013, Aalto et al. 2017). A thorough understanding of how subalpine forests are expanding over broad areas, and their key drivers, is crucial for biodiversity conservation, ecosystem management, and the development of climate adaptation strategies.

To place Taiwan's treeline responses in a broader context, we distinguish between upslope boundary shifts and densification within the treeline ecotone, two processes that may respond differently to climate warming. We analyzed the spatiotemporal treeline dynamics of the Yushan Mountain Range (YMR) and the Central Mountain Range (CMR) of Taiwan over 40 years using aerial photographs from 1980, 2001, and 2021. By integrating fine-resolution climate data from the Taiwan Climate Change Projection Information and Adaptation Knowledge Platform (TCCIP; <https://tccip.ncdr.nat.gov.tw>) with topographic information, we identify climatic and topographic factors influencing treeline dynamics. We ask: 1) how have forest cover and treeline elevation changed over the past four decades? and 2) what climatic and topographical factors affect treeline migration and stand densification? We hypothesize that, as observed in many mountain regions, forest cover and treeline elevations in the two mountain ranges have increased over the studied period (H_1). In addition, we hypothesize that dynamics of the upper boundary of subalpine forests are mainly driven by temperature increases rather than topographic features (H_2).

Material and methods

Our work included the acquisition and preprocessing of aerial images and environmental data, sample extraction and labeling, U-Net training for tree mapping, and the generation of forest maps for the study sites. Based on the maps and environmental data we then quantified forest area expansion and treeline movement, followed by exploring their environmental drivers using spatial regression models (Fig. 1).

Study sites

The study encompassed high-elevation regions of Taiwan's YMR and CMR (Fig. 2). In the YMR, the study area included the main peak of Yushan and its north, east, south, and west peaks, as well as East Xiaonan Mountain, all of which exceed 3000 m a.s.l. The center of the study domain lies in YMR (23°27'39.6"N, 120°57'28.8"E). In the CMR, the study area included Qilai South Peak, Nanhua Mountain, and Nenggao Mountain, all of which were above 3000 m, with the domain centered in the north-central section of the range (24°02'09.6"N, 121°16'58.8"E). Both regions are characterized by steep, rugged terrain and shallow, rocky soils.

Climatically, the two mountain ranges are cold and humid, with a pronounced dry season from winter to early spring. In the YMR, the mean annual air temperature is 4.6°C, with monthly averages ranging from 0.7°C in January to 8.3°C in July, and a mean annual precipitation of about 2858 mm. In the CMR, mean annual air temperature is 7.6°C, with monthly averages ranging from 0.9°C in January to 10.1°C in July, and annual precipitation of about 2188 mm (obtained from TCCIP). Precipitation is dominated by spring–summer plum-rain events and summer–autumn typhoon-associated storms, together accounting for roughly 70–80% of annual totals.

Strong winds are common, and cloud and fog are frequent, particularly in the afternoon (Climate Observation Data Inquire Service, <https://codis.cwa.gov.tw/StationData>). Air temperatures frequently fall below 0°C from December through April. Snowfall is episodic, occurring mainly during cold-surge events, and no permanent snowline is present. The mean summer environmental lapse rate is approximately 5.5–6.5°C km⁻¹, while winter temperature inversions may occur (Chiu et al. 2014, Lin et al. 2018). Geologically, the YMR is dominated by metamorphosed sandstone and slate, whereas the CMR comprises slate, phyllite, metamorphosed sandstone, and marble. These mountain ranges were selected primarily because fine-resolution imagery with multi-decadal coverage was available.

The treelines of the two mountain ranges are clear boundaries between bamboo grasslands, dwarf shrubs, and subalpine forests. The subalpine forests consist of Taiwan fir, with occasional occurrences of Taiwan hemlock *Tsuga chinensis* var. *formosana*, Taiwan red pine *Pinus taiwanensis*, and Taiwan white pine *Pinus armandii* var. *mastersiana*. The alpine grasslands and dwarf shrubs comprise *Yushania niitakayamensis*, *Juniperus squamata*, *Juniperus formosana* var. *formosana* and several species of *Rhododendron* (Li et al. 2013). The two mountain ranges are regularly exposed to tropical cyclones and occasional landslides.

Aerial images

We used 1:5000 aerial orthophotos of the study areas taken in the winters of 1980, 2001, and 2021. The Aerial Survey and Remote Sensing Division of Taiwan Forestry and Nature Conservation Agency produced these images. The images from 1980 are in black-and-white, while those from 2001 and 2021 are in true color (RGB bands), including an additional

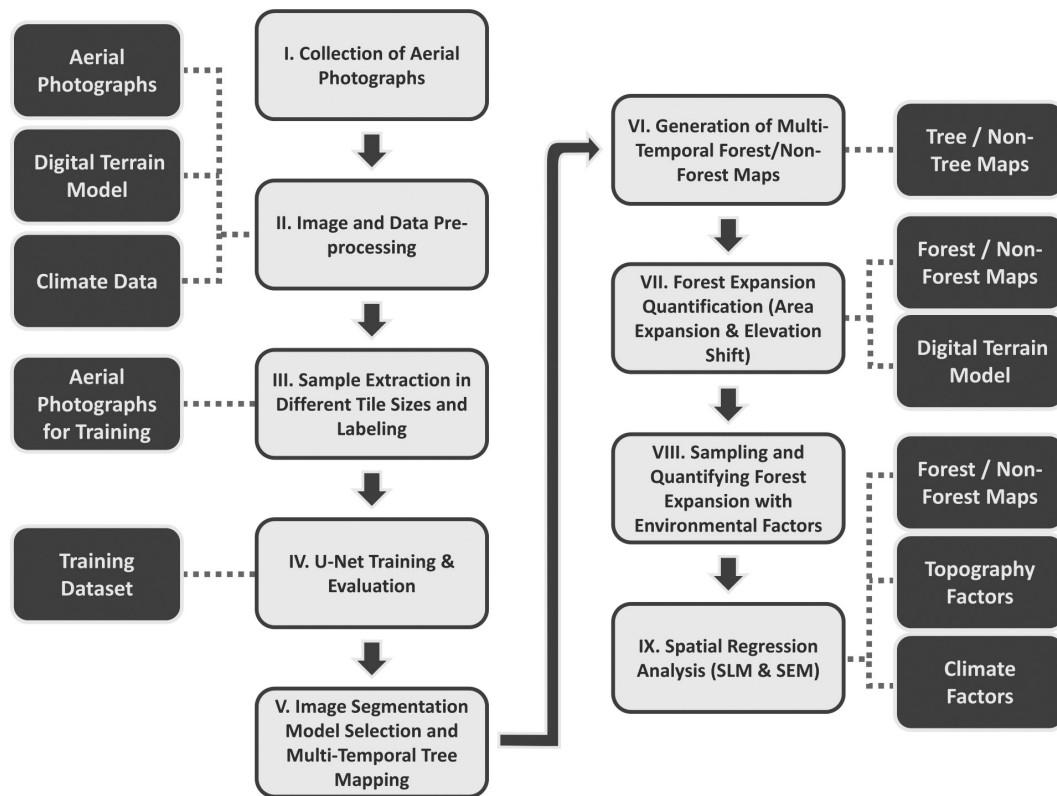


Figure 1. Workflow of data collection, model training, segmentation, and analysis. SLM: spatial lag model; SEM: spatial error model.

near-infrared (NIR) band for 2021. All images were taken on the same day of the year, except for the images of YMR in 1980 and CMR in 2001 (108 and 33 days apart from other images, respectively).

Image preprocessing

The images were geometrically corrected and spatially aligned, and resampled to a spatial resolution of 0.5 m because their ground resolutions ranged from 0.25 to 0.5 m. We employed the deep learning toolkit (Train Deep Learning Model) in ArcGIS Pro (ver. 3.2.1) for image classification. This tool processes a maximum of three channels during model training. Consequently, we reconfigured the four-band images from 2021 into a three-band NIR+R+G image. NIR is effective for vegetation classification, and the NIR+R+G spectral combination yields better automatic image interpretation than the R+G+B combination (Persson et al. 2018, Song et al. 2022).

Climate, topographic, and vegetation ground-survey data

Climate data from TCCIP were gridded daily observation measurements from 1980 to 2021 at a 0.05° (approximately 5 km) spatial resolution. The data were spatially down-scaled to 15 m resolution using the TCCIP data interpolation tool clim.regression ver. 2 (detailed methodology in the Supporting information). This tool accounts for the lapse rate effect during downscaling and estimates climatic differences

driven by altitude gradients, thereby increasing the spatial resolution of the data (Lin et al. 2018). Then, we calculated the annual mean temperature and annual precipitation, and rainfall and temperature of the growing season, May–October, for high mountains based on an island-wide assessment of vegetation phenology (Chang and Huang 2016). We utilized the 20-m resolution digital terrain model (DTM) provided by Taiwan Ministry of the Interior (<https://data.gov.tw/dataset/35430>) to describe mountain topography. The DTM was used to calculate slope steepness (°), aspect (0 to 359°), and topographic position index (TPI). TPI values range from −1 to 1: values near 1 indicate ridges, values near −1 indicate valleys, and values around 0 indicate flat areas. Aspect values were converted to the heat load index (HLI) to obtain a linear variable measuring incident radiation (McCune and Keon 2002). We assumed static topography over the 41-year study period. Finally, we collected ground data on forest types and grasslands from the Fourth Forest Resource Survey of Taiwan conducted from 2008 to 2014.

Preparation of segmentation model training samples

We used a U-Net deep learning neural network (Ronneberger et al. 2015), a supervised learning approach, to train an image segmentation model to classify forest and non-forest areas in high-resolution aerial images. The training data were derived from the Fourth Forest Resource Survey, conducted between 2008 and 2014, and processed to produce a forest/non-forest land-cover classification. These

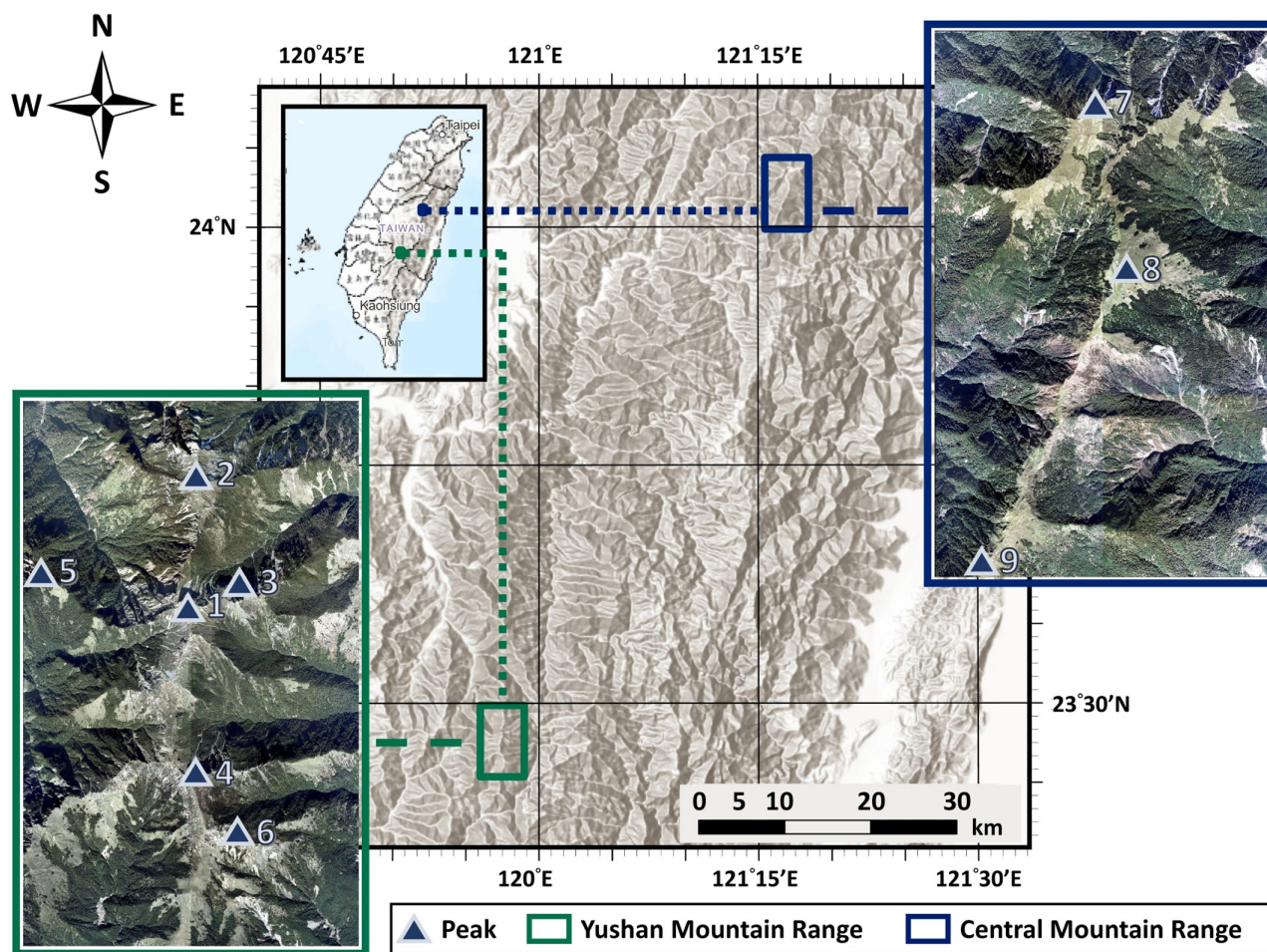


Figure 2. Locations of the study areas within Taiwan. Triangles are mountain peaks, with peaks 1–6 in the Yushan Mountain Range and peaks 7–9 in the Central Mountain Range: 1) Yushan Main Peak; 2) Yushan North Peak; 3) Yushan East Peak; 4) Yushan South Peak; 5) Yushan West Peak; 6) East Xiaonan Mountain; 7) Qilai South Peak; 8) Nanhua Mountain; and 9) Nenggao Mountain.

pre-classified images were then divided into tiles with different user-specified dimensions (256×256 , 512×512 , and 1024×1024) for testing and comparison, and the model with the best performance was selected for subsequent analysis. The forest survey was conducted in years different from the years of the forest images used in this study, and earlier digitized forest survey data were unavailable. Therefore, we manually labeled training data for each year.

Following Ameztegui et al. (2015) and Morley et al. (2020), a cell in the 15×15 m² grid was classified as forest if it had $\geq 10\%$ canopy cover. First, the ground-truthed data for three years were produced through manual digitization. Then, in each mountain range, two of the six maps from each of the three years (1980, 2001, and 2021) were randomly selected as training data, while the remaining four maps were used as test data. In total, 12 images were used for training and 24 for testing across the two mountain ranges over the three years. The images for the training dataset were cut into different combinations of tile and stride sizes (i.e. the image size and step size for the sliding filter, respectively) and used for subsequent model training because different tile sizes and

strides in model training can provide varying feature information (Lee et al. 2022, Cira et al. 2024). Moreover, because the aerial images from the three years varied in spectral information (i.e. single band, RGB, RGB+NIR), we trained image segmentation models for each year. For each year, we evaluated nine configurations combining three tile sizes (256, 512, and 1024 pixels) and three stride sizes (128, 256, and 512 pixels) and selected the combination with the highest predictive performance.

Forest classification models

We trained the U-Net model using the deep learning libraries in ArcGIS Pro (ver. 3.2.1; deep learning libraries ver. 3.2). U-Net is a convolutional neural network (CNN) designed for semantic segmentation and has been widely applied in recent years to land-use and land-cover image segmentation. It features an encoder–decoder architecture with skip connections, which preserves spatial details while capturing contextual information from deeper layers. The encoder extracts hierarchical features by progressively reducing the spatial dimensions of the input image, while the decoder

restores the resolution to produce the segmentation map (Ronneberger et al. 2015). In this study, we employed U-Net with a ResNet-34 backbone and adopted a transfer learning strategy. ResNet-34, pre-trained on large-scale datasets such as ImageNet (He et al. 2016), was used as the feature extraction component of the U-Net architecture, enabling the model to leverage previously learned representations and accelerate convergence during training. This combination is expected to improve the robustness and overall performance of the segmentation results.

Prior to model training, the ArcGIS Pro deep learning libraries require configuring multiple training and validation parameters (the settings are reported in the Supporting information). For model training, we set the maximum number of epochs to 100, following Wagner et al. (2019), and the batch size to eight to ensure that all models were compared under the same training baseline. We did not specify the learning rate because the optimal learning rate is automatically extracted from the learning curve during training. Additionally, 10% of the training dataset was randomly selected as a validation set during each epoch to mitigate overfitting. The training set was used to learn and update model weights, while the validation set evaluated the model's performance on unseen data. Model optimization was based on the default cross-entropy loss function implemented in the deep learning libraries used in this study. We assessed potential overfitting by comparing the training and validation losses. Data augmentation was carried out to increase the size of the training dataset and its heterogeneity by transforming the annotated data (i.e. manually labeled). The parameters for data augmentation were: 50% chance of 1) image rotation by 30°, 2) increasing or decreasing image brightness by 20%, 3) adjusting the contrast to between 0.75 and 1.75 (the default setting, with 1 being the original contrast value), and 4) image enlargement or reduction by 20%.

In this study, 500 checkpoints were taken from the testing dataset to evaluate model performance. They were randomly distributed across the testing dataset. The ground-truth for the checkpoints was conducted by overlaying and manually interpreting digitized data from the Forest Resource Survey, orthoimage basemap of Taiwan, and aerial images. To assess the model's predictive performance, we computed the number of true positives (TP), false positives (FP), false negatives (FN), and true negatives (TN). We calculated the recall rate (Eq. 1), precision rate (Eq. 2), and F1 Score (Eq. 3) and selected the best model based on these metrics.

$$\text{Recall rate} = \frac{\text{TP}}{\text{TP} + \text{FN}} \quad (1)$$

$$\text{Precision rate} = \frac{\text{TP}}{\text{TP} + \text{FP}} \quad (2)$$

$$\text{F1 - score} = \frac{2 \times \text{Recall} \times \text{Precision}}{\text{Recall} + \text{Precision}} \quad (3)$$

Post-model fitting data analyses

We calculated land-cover transition matrices based on the modeled classification of forest and non-forest cover for 1980, 2001, and 2021. To examine treeline movement, we first identified the geographic locations of treelines. Treeline was defined as a forest pixel with at least one other neighboring forest pixel and the highest elevation among its eight surrounding pixels (Ameztegui et al. 2015). To ensure treeline positions reflected ecologically meaningful forest boundaries, areas affected by landslides, valleys, or non-forest edges – where treeline could not be robustly defined – were conservatively excluded (Supporting information).

We selected a 100-m buffer zone around the treeline positions from the 1980 images. Within these buffer zones, 120 sampling points were randomly selected with a minimum 250-m distance between any two points, ensuring that no sampling points overlap. For 1980 imagery, forest cover area within the buffer was ensured to be greater than 5000 m², following the FAO (2012) definition of forest. Forest area expansion and treeline elevation changes between 1980–2001 and 2001–2021, along with changes in environmental factors over the 41 years, were extracted from the buffer zones. Forest expansion was calculated by subtracting the forest area in 1980 from that in 2001, and the forest area in 2001 from that in 2021. Treeline elevation change was quantified following a sensitivity analysis (Supporting information), and with reference to Feuillet et al. (2020), by tracking shifts in the mean of the five highest-elevation values of forest pixels within each buffer zone. Feuillet et al. (2020) used five as a minimum threshold to reduce the influence of isolated artefacts (e.g. a single rocky outcrop above the treeline) while preserving local treeline dynamics. Because we investigated local dynamics, using five values allowed us to reliably track treeline elevation change while avoiding the buffering effect associated with using more pixels. The elevation change was obtained by subtracting the treeline elevation in 1980 from that in 2001, and the elevation in 2001 from that in 2021. Conversion rates of non-forest to forest, and of forest to non-forest cover were derived for the 1980–2001 and 2001–2021 periods.

We used multiple linear regression models to examine the relationships between forest area and treeline elevation changes, and climatic and topographic factors (Supporting information), across the two mountain ranges. Climatic factors included the changes in mean annual temperature and total annual precipitation, growing-season precipitation, growing-season mean temperature, maximum temperature, and minimum temperature between 1976–1980 and 2017–2021 averages. A positive value indicated an increase over the 41-year period. Topographical factors included slope steepness and HLI, elevation, and TPI. All variables were standardized using z-scores. Multicollinearity among predictors was assessed using variance inflation factors (VIF, 'car' R package). Predictors with VIF > 5 were iteratively removed, starting with the highest VIF value (Peereman et al. 2022), until all VIF were < 5. Based on this criterion, changes in mean annual temperature and total annual precipitation were excluded from the final model.

Following Anselin (1988, 2005), an ordinary least squares linear regression model was fitted, and the residuals were tested using Moran's I to assess spatial autocorrelation. Then we conducted a spatial lag model (SLM) and a spatial error model (SEM) because Moran's I was significant for both forest area expansion and treeline elevation change. Model selection was guided by Lagrange multiplier (LM) diagnostics (Anselin 2005). We selected the SLM when LM-lag was significant, but LM-error was not, and the SEM when LM-error was significant. When both LM tests were significant, Robust LM diagnostics were used to discriminate between SLM and SEM; if both robust tests remained significant, both models were fitted and compared. Model fit was evaluated using the Akaike information criterion (AIC).

Results

Accuracy of segmentation models

The accuracy of the nine segmentation models increased while the loss function decreased with the number of iterations (Supporting information). The error matrices for the nine models indicated that the model with a tile size of 256×256 pixels and a stride of 128×128 performed best at classifying forest and non-forest cover across all three years (Supporting information). Particularly for the black-and-white images from 1980, classification performance was significantly lower with large tile and stride sizes (Supporting information).

Based on the evaluation metrics (Supporting information), for 1980, the model using 256×256 tiles with a $128 \times$

128 stride achieved the highest F1 score (0.973), which was much higher than those for 512×512 (0.861) and 1024×1024 (0.864) tile-stride combinations. Similar patterns were observed in 2001 and 2021: the smallest tile-stride combination consistently produced the highest performance, with F1 scores of 0.983 and 0.976, respectively, whereas larger tile and stride sizes resulted in noticeably lower performance.

Spatial distribution of forest cover expansion

There was a clear trend toward forest area expansion through upslope treeline migration at both sites over the last four decades, primarily around the treelines of 1980 (Table 1, Fig. 3a–b), supporting H_1 . In the YMR, 22% of the non-forest area transitioned to forest over the 1980–2001 period, while 5% of the forest area transitioned to non-forest. This resulted in a net increase of 115 ha in forest area (Table 1). Between 2001 and 2021, 18% of the non-forest area transitioned to forest, while 3% of the forest area became non-forest, mostly due to landslides. This represented a net increase of 82 ha in forest area (Table 1). Overall, forest area increased from 3095 ha in 1980 to 3210 ha in 2001 and to 3292 ha in 2021, representing increases of 4% between 1980 and 2001, and 2.55% between 2001 and 2021.

In the CMR, the transition rate from non-forest to forest was 32% between 1980 and 2001, while the rate of forest to non-forest was 3%, resulting in a net increase of 165 ha (Table 1). Between 2001 and 2021, the transition rate of non-forest to forest was 21%, while the rate of forest to non-forest was 4%, leaving a net decrease of 7 ha in forest cover (Table 1).

Table 1. The area and probability transition matrix of forest and non-forest cover in the Yushan Mountain Range (YMR) and Central Mountain Range (CMR) from 1980 to 2021.

Site	Year	Cover	Area (ha)			Probability (%)	
			Forest	Non-forest	Total	Forest	Non-forest
YMR	1980	Forest	2948	147	3095	95	5
		Non-forest	262	912	1174	22	78
		Total	3210	1060	4270		
	2001	Forest	3106	103	3210	97	3
		Non-forest	186	874	1060	18	82
		Total	3292	977	4270		
	2021	Forest	2985	110	3095	96	4
		Non-forest	307	867	1174	26	74
		Total	3292	977	4270		
	1980	Forest	3300	107	3407	97	3
		Non-forest	272	570	843	32	68
		Total	3572	677	4250		
CMR	2001	Forest	3420	152	3572	96	4
		Non-forest	145	632	677	21	79
		Total	3565	684	4250		
	2021	Forest	3272	135	3407	96	4
		Non-forest	293	549	843	35	65
		Total	3565	684	4250		

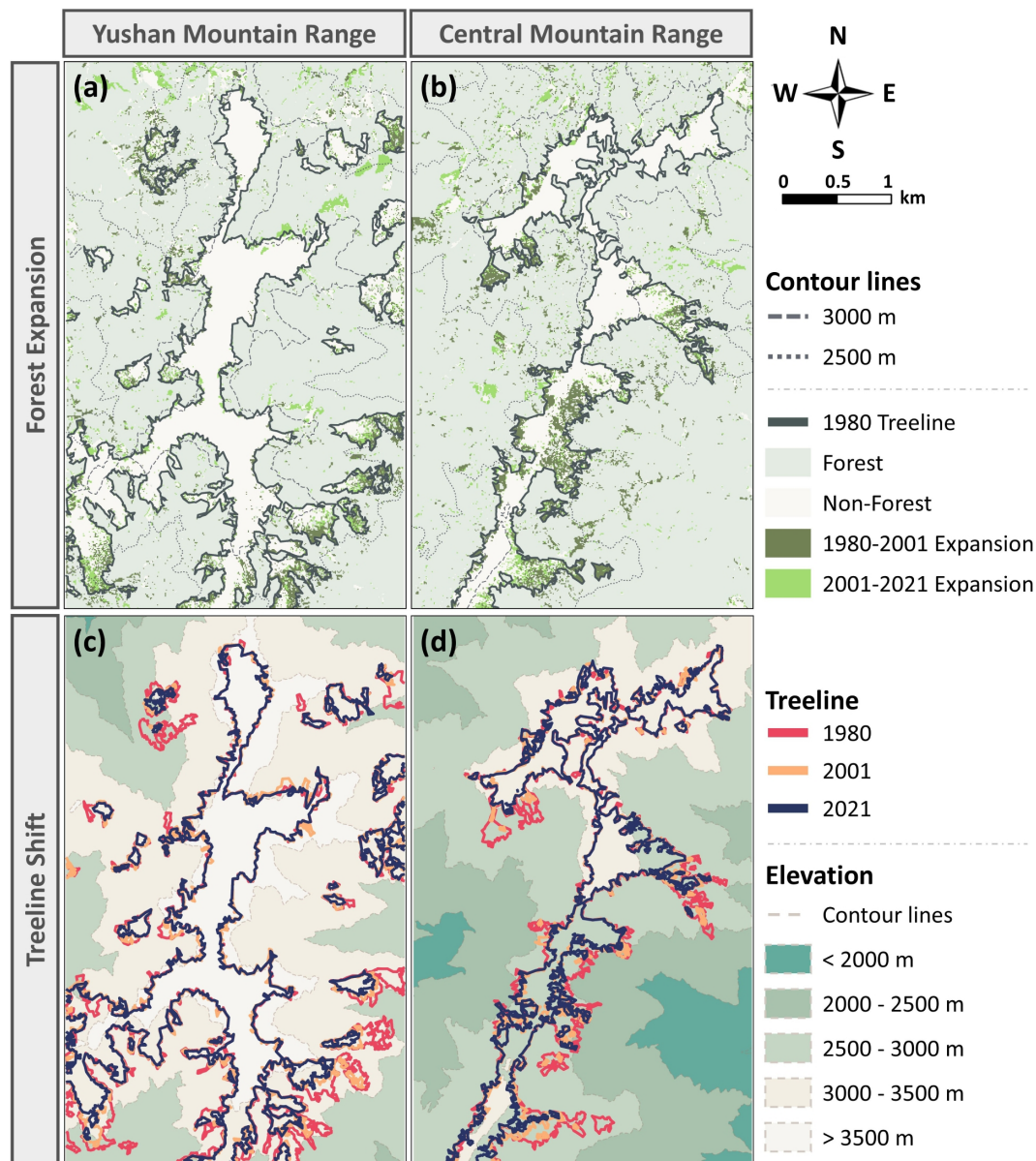


Figure 3. Spatial and elevational patterns of forest expansion and treeline shift in Taiwan. Panels (a) and (b) show forest expansion in the Yushan and Central Mountain Ranges, respectively, during 1980–2001 (dark green) and 2001–2021 (light green). Panels (c) and (d) show the elevational distributions of treeline positions in the Yushan and Central Mountain Ranges in 1980 (red), 2001 (orange), and 2021 (blue). Background shading from green to tan indicates elevational gradients from < 2000 to > 3500 m.

Overall, forest cover increased from 3407 ha in 1980 to 3572 ha in 2001 and slightly decreased to 3565 ha in 2021. This represented a change rate of 5% for 1980–2001, and of approximately -0.2% for 2001–2021. Despite the overall forest expansion, forest contraction was scattered across the two mountain ranges, particularly for the 2001–2021 period, and tended to concentrate around stream channels (Table 1).

Treeline has moved upslope in the two mountain ranges over the studied period (Fig. 3c–d, 4). In the YMR, the average elevation of the treeline progressed from 3312 (1980) to 3355 (2001), and 3375 m in 2021, meaning an increase of 63 m in elevation, and an average annual upslope migration rate

of 2.1 in the first two decades and 1.0 m year^{-1} in the second two decades. Minimum treeline elevation was 2628, 2770, and 2826 m in 1980, 2001, and 2021, respectively, indicating an upslope shift of roughly 198 m over 41 years. However, the maximum treeline elevation showed little change over the 41 years, from 3741 m in 1980 and 2001 to 3744 m in 2021. In the CMR, treeline average elevation was 2918, 2952, and 2977 m in 1980, 2001, and 2021, respectively, showing an increase of 59 m over 41 years, and an average annual upslope migration of 1.6 in the first two decades and 0.75 m year^{-1} in the second two decades. Minimum treeline elevation was 2303, 2408, and 2427 m in 1980, 2001, and

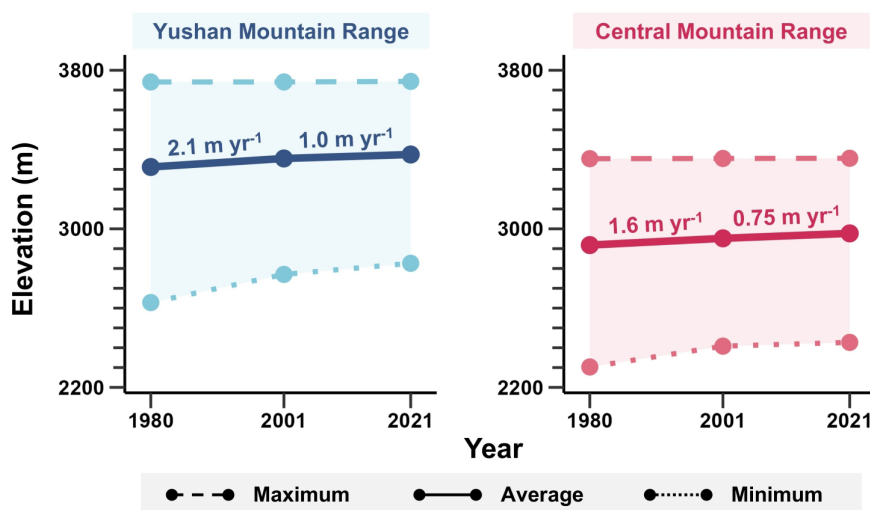


Figure 4. The minimum, mean, and maximum treeline elevations (m) in the Yushan Mountain Range and the Central Mountain Range for 1980, 2001, and 2021, along with the average treeline elevation shift rates for the 1980–2001 and 2001–2021 periods.

2021, respectively, indicating an upslope shift of 124 m. The maximum treeline elevation of the CMR showed virtually no change over time, remaining at 3354 in 1980, 3355 in 2001, and 3356 m in 2021. Across the two mountain ranges, the treeline elevation shift and forest area expansion were significantly but weakly correlated (Supporting information).

Relationships between climate and topography, and the changes in forest area and treeline elevation

Across the two mountain ranges, Moran's I was 0.27 for forest area expansion and 0.11 for treeline elevation change, both statistically significant (p -values < 0.001), indicating positive spatial autocorrelation in forest dynamics. Accordingly, we evaluated the need for spatial regression using LM diagnostics. For forest area expansion, the LM-error test was significant (LM-error=5.287, p -value=0.02), whereas LM-lag was not (LM-lag=2.785, p -value=0.10), supporting a spatial error specification; the SEM further indicated significant error dependence (λ =0.386, p -value=0.04). In contrast, for treeline elevation change, both standard LM tests were non-significant (LM-lag=0.175, p -value=0.68; LM-error=0.336, p -value=0.56), and the Robust LM diagnostics likewise indicated no residual spatial dependence (Robust LM-lag=0.023, p -value=0.88; Robust LM-error=0.184, p -value=0.67). Accordingly, the non-spatial MLR achieved the best fit (with the lowest AIC), suggesting that spatial structure was adequately accounted for by the included covariates.

Based on the selected models, the three climatic variables (changes in growing-season temperature and precipitation, and minimum temperature) and elevation were significant factors explaining forest area expansion in the regression model (Table 2). Forest area expansion increased with changes in growing-season precipitation, temperature, and minimum temperature, indicating that increases in these factors contributed to the expansion of forest cover. However,

the negative effect of elevation captured the observed pattern of greater forest expansion at lower treeline edges than at higher ones. Then, according to the second regression model, increases in growing-season precipitation, slope steepness, and maximum temperature were positively associated with forest elevation shift, whereas elevation was negatively associated (Table 2).

Discussion

The effectiveness of the U-Net model for subalpine forest segmentation

The U-Net models performed well during training and converged stably, as indicated by increasing accuracy and decreasing loss with iteration (Supporting information), providing confidence in our detection of subalpine forest and treeline dynamics from aerial imagery. The high classification performance associated with smaller tile-stride combinations (Supporting information) likely reflect the larger number of training samples generated, allowing the model to better capture fine-scale canopy heterogeneity. Such local details, including shadows, textures, and crown structure, are critical for distinguishing forest from non-forest cover in heterogeneous alpine landscapes (Chen et al. 2014). Compared with traditional manual interpretation and conventional machine-learning classifiers, U-Net-based semantic segmentation typically achieves higher accuracy and is particularly effective for high-resolution aerial photographs, including historical black-and-white imagery, where spectral information is limited. In addition, relative to field-based surveys, this approach enables consistent, landscape-scale assessments of treeline dynamics across extensive and rugged terrain that would be difficult to sample comprehensively on the ground. We acknowledge that the random selection of samples across both ranges may inflate validation metrics, and future work

could employ spatially independent training and validation datasets. Nevertheless, the approach remains suitable for highly heterogeneous imagery because it allows the model to learn fine-scale spatial features essential for reliable forest classification.

Subalpine forest distribution and expansion

Our finding of an overall expansion of forest cover along the subalpine treeline ecotone over the past four decades echoes results of previous studies of subalpine environments of Taiwan (Lai 1992, Chuang 1998, Greenwood et al. 2014, 2015, Tseng 2015, Morley et al. 2020, Chung et al. 2021). Moreover, the upslope migration rates of treelines we report (2.1 and 1.6 m year⁻¹ from 1980 to 2001 and 1.0 and 0.75 m year⁻¹ from 2001 to 2021 for YMR and CMR, respectively) are consistent with global trends (i.e. the global average of 1.2 m year⁻¹ from 2000 to 2010) (Harsch et al. 2009, He et al. 2023). However, despite the overall increase in forest cover in the treeline ecotone, the rate of upslope migration was approximately two times greater during the 1980–2001 period (2.1 in the YMR and 1.6 m year⁻¹ in the CMR) compared to the 2001–2021 period (1.0 in the YMR and 0.75 m year⁻¹ in the CMR). Notably, there was a slight decrease in forest cover (~ -0.2%) in the CMR between 2001 and 2021. This may be happening because forests are approaching mountain peaks, or because there is minimal forest edge area to allow for forest establishment into alpine grasslands. In other words, most of the areas suitable for tree growth may have already been covered with trees by 2001, and the remaining areas are mostly unsuitable for forest expansion, even when minimum temperature is no longer a limiting factor (Rehm and Feeley 2015 for tropical cloud forests), for instance, because of competition (Dial et al. 2016). Alternatively, in some treeline ecotones of central-south Taiwan, fires are known to play a key role in competition between subalpine forest and grassland, favoring subalpine grassland (Chiu et al. 2015). However, Greenwood et al. (2014) reported no evidence of widespread fire or changes in fire frequency in the Hehuanshan Mountain Range, along with treeline movement and tree densification. Nonetheless, our study points to the possibility of an elevational threshold in Taiwan mountain forests, beyond which warming may no longer drive treeline migration.

Because land area decreases with elevation, the overall area of subalpine forests will shrink sharply if the lower elevation boundary also migrates upslope. A recent climate-based modeling study predicted that subalpine forests in Taiwan will experience area reductions under a warming climate (Lin et al. 2020). The suitable habitat range of the Taiwan fir, the dominant tree species along Taiwan's treelines, is predicted to decrease by 90% in area if temperature rises by 2.0°C, mainly due to habitat loss at lower elevations (Chiu et al. 2022). Consequently, the upslope migration of subalpine forests implies that non-forest habitats above treeline, such as that of the dwarf shrub *J. squamata*, may gradually be lost. It has been estimated that if temperatures increase by 1–2°C, the suitable habitat for *J. squamata* in the two mountains

we studied will decline by 60–90% due to forest encroachment (Hsu 2016). A reduction of *J. squamata* habitat area by 90% will leave only 11 ha of suitable habitat left in the two mountain ranges (CMR and YMR), suggesting that warming may have even greater impacts on vegetation above subalpine forests than on subalpine trees themselves. Future studies should examine the lower boundary of subalpine forests to determine whether the upslope treeline migration is accompanied by a shift in subalpine forest distribution from lower to higher elevations.

Upslope movement and densification of subalpine forests

In our study areas, the upslope treeline migration was more pronounced at treeline edges located at low elevations such that the maximum elevation of treelines barely changed (Fig. 4). The upslope treeline migration at high elevations was likely limited by environmental constraints because areas near mountain peaks and ridgelines are exposed to greater wind and temperature changes are unfavorable for tree growth. Furthermore, on high mountain peaks, the weathering and disintegration of exposed bedrock forms harsh habitats, which likely limit seed germination, seedling establishment, and tree growth, and thus effectively create a landscape barrier that limits treeline movement (Körner 1998, 2012, Chiu et al. 2010, Trembl and Migoñ 2015, Körner and Hoch 2023).

We found that the forest area expansion concentrated around the treeline of 1980, with most of the expansion taking place above it (Fig. 3a–b). As a result, the expansion was accompanied by the upslope advancement of forests (Fig. 3c–d). However, some expansion took place near or below the 1980 treeline (Fig. 3a–b), suggesting tree densification in the treeline ecotone. Greenwood et al. (2014, 2015) and Morley et al. (2020) reported that tree densification was the major type of forest expansion in the Hehuanshan Mountain Range of Taiwan. This contrasts with our findings for CMR and YMR, which showed that treeline migration was the main type of forest area expansion, while tree densification in the treeline ecotone occurred only in localized areas. Different forest area expansion patterns may be due to varying environmental conditions, such as elevation and the orientation of the mountain range relative to the prevailing wind direction. For example, the maximum height of the two mountain ranges we studied is several hundred meters higher than that of the Hehuanshan Mountain Range, such that upslope movement is more limited in Hehuanshan, leading to more pronounced tree densification. At similar latitudes and montane elevations, comparable heterogeneity has also been documented on subtropical oceanic islands. On Tenerife (Canary Islands), treeline change has been characterized by increased tree density accompanied by relatively slow elevational advance (Bello-Rodríguez et al. 2019). In the Hawaiian Islands, a 40-year resurvey documented upslope shifts in the upper elevational distributions of vascular plants (Koide et al. 2017). Overall, these island comparisons suggest that the relative prominence of upslope migration versus

densification can vary widely across subtropical island montane forests in response to local topographic and climatic constraints.

Moreover, anthropogenic disturbances and land-use legacies may be another factor influencing treeline dynamics and could help explain the differences between our findings and those of other studies in Taiwan. We acknowledge that this interpretation is speculative, as we did not collect direct data on human disturbance. Nonetheless, differences in anthropogenic pressures likely contribute to differences in the main type of forest area expansion between the two mountain ranges we studied and Hehuanshan Mountain Range. Hehuanshan is Taiwan's most visited peak above 3000 m; while popular hiking trails and mountain lodges exist in the CMR and YMR, neither range sees as much human development or tourist traffic. Smaller anthropogenic pressures may lead to greater upslope treeline migration in our study than in the Hehuanshan Mountain Range due to tree densification. Human disturbance has been reported to be an essential factor influencing treeline dynamics in the Pyrenees (Batllori and Gutiérrez 2008). In the Swiss Alps, treeline dynamics are the result of both land-use and climate change (Bolli et al. 2007). Thus, under similar climate conditions, subalpine forest expansion patterns can differ under contrasting environmental conditions and human land use.

Factors regulating subalpine forest expansion and elevation shift

The modest correlation ($r=0.35$) between subalpine forest elevation upshifts and area expansion (Supporting information) suggests that lateral infilling and upslope advance are partially decoupled processes. One explanation is geometric: area-based metrics are strongly influenced by terrain steepness and hypsometry, such that small vertical shifts on gentle slopes can produce large increases in forest area, whereas equivalent elevational changes on steep slopes yield minimal areal gain. Therefore, when assessing the impact of climate change on treeline dynamics, localized responses to microclimate changes should also be considered (Mathisen et al. 2014, Greenwood et al. 2015, Wielgolaski et al. 2017, Feuillet et al. 2020). The topographic scaling effect, noted in montane systems elsewhere (Elsen and Tingley 2015, Hooshyarkhah et al. 2025), underscores that area and elevation are not directly comparable indicators of treeline change. Significant spatial error further indicates the influence of unmeasured spatially structured processes, such as disturbance legacies, microclimatic heterogeneity, typhoon exposure gradients, or historical land use. Because analyses were conducted within a fixed buffer surrounding the 1980 treeline, some scale-dependent effects may influence estimates of change. However, the use of a 100-m buffer allowed detection of both forest advance and recession within the ecotone, reducing the likelihood that the design systematically favored upslope shifts. The occurrence of localized forest retreat further indicates that the 1980 boundary functioned as a neutral reference rather than a fixed benchmark, enabling bidirectional assessment of treeline dynamics.

We demonstrate how climate has a significant effect on subalpine forest dynamics. Both the elevation change and forest area expansion were positively related to increases in rainfall and temperature, with some nuance about how different temperature parameters affected treeline dynamics. However, we acknowledge that although the upscaling method used to produce finer-resolution climate data addressed the elevation gradient, it did not account for albedo and cold-air drainage, which could affect microclimate variations. Nevertheless, our results highlight that although minimum temperatures at the global scale largely constrain the upper boundaries of forest distribution (Körner 1998, Harsch et al. 2009), they cannot fully explain local-scale treeline dynamics and their responses to climate change.

Additionally, we suggest that temperature and precipitation exert different influences on forest expansion in treeline ecotones. For example, among studies on the range expansion of Taiwan fir, minimum summer temperature was identified as the most crucial factor in one study (Lai 1992), while mean annual temperature was suggested to be more critical in another (Li 2011). Growing-season temperature was argued to be the most predictive factor by yet another (Wang 2013). It can be expected that different temperature and precipitation metrics can have different impacts on tree growth and survival, and that they integrate into complex microclimate–tree performance relationships that play out in unique ways over tree lifetimes. For example, maximum summer temperature may be related to primary productivity during the growing season, increases in spring temperature may lead to an early onset of growth, or increases in winter temperature may extend the growing season. Increases in precipitation during the growing season likely have a greater impact on tree growth than similar increases outside the growing season. Thus, it is essential to examine multiple aspects of temperature and precipitation when assessing the effect of climate change on forest expansion.

Our results that increases in rainfall positively affect forest expansion are consistent with previous studies on subalpine forests in Taiwan and with studies across many parts of the world. Droughts reduce the growth of Taiwan fir (Wang 2013), and warming and prolonged drought events have led to large-scale Taiwan fir dieback in Hehuanshan (Hsu 2014). In addition, temperature increase accelerates Taiwan fir growth at forest edges, but drought increases the mortality of old trees and negatively affects seedling establishment (Tseng 2015). Around the world, studies have found that while rising temperatures favor tree growth, frequent droughts deplete soil moisture and hinder tree development, potentially restricting forest area expansion and causing tree line retreat (Nemani et al. 2003, Zhao and Running 2010, Lyu et al. 2019, Elliott et al. 2020, Bailey et al. 2021, Beloiu et al. 2022). Ultimately, the balance between climate change-driven warming and drying affects forest dynamics (Hogan et al. 2024), and our results show that subalpine forest dynamics at the treeline ecotone are not different in this regard.

Topography plays a key role in forest area expansion and treeline elevation change. Elevation had a negative effect

and a high explanatory power for both forest dynamics (Supporting information). This suggests that although warming can relieve minimum temperature constraints, lateral and upslope forest expansion are geographically constrained near mountain peaks. Moreover, although steep slopes are generally associated with harsh conditions (Fazlollahi Mohammadi et al. 2016, Morley et al. 2020, Beloiu et al. 2022), we found a positive relationship between treeline migration and slope steepness (Fig. 3c–d, Table 2) that may be explained by the fact that most slopes in CMR and YMR are less than 45° while Taiwan fir readily inhabits slopes of up to about 55° (Huang and Lee 1998). In addition, slopes less than 30° in our study areas are mostly found at high elevations (Supporting information), which are unfavorable for tree establishment (Blumthaler et al. 1997, Holtmeier and Broll 2010, Beloiu et al. 2022). Thus, the limited area with slopes too steep for Taiwanese subalpine forests and the distribution of gentle slopes at high elevations likely contributed to the positive relationship between slope steepness and treeline elevation change.

Treeline responses to climate warming are increasingly understood to be mediated by seasonal climate effects, demographic constraints, and terrain rather than by temperature increases alone. Warmer growing seasons can enhance tree growth and recruitment, yet winter cold, frost damage, and snow dynamics frequently limit seedling survival, creating a demographic bottleneck that slows upslope advance (Rees et al. 2020, Lu et al. 2021). Global syntheses further show that treeline advance often lags the pace of climate warming due to episodic recruitment, dispersal limitation, and site-specific constraints (Xu et al. 2022, Lu et al. 2025). Topography plays a central filtering role by shaping microclimates, snow accumulation, soil development, and safe-site availability, with sheltered concave slopes favoring densification while steep, wind-exposed ridges inhibit colonization. These terrain-mediated effects can also decouple area expansion from elevational shifts via hypsometric scaling, helping to explain the weak correlations between forest expansion and treeline elevation change (Peng et al. 2024). Our findings from Taiwan are consistent with these global patterns: forest expansion occurred alongside uneven and partially decoupled treeline advance, indicating strong topographic and microsite controls. At the same time, this study provides new insight from a subtropical high-mountain system, where typhoon disturbance, persistent cloud cover, and steep terrain interact with warming to shape treeline dynamics. By combining multi-decadal aerial imagery with fine-resolution climate and topographic data, and by explicitly distinguishing between upslope boundary shifts and densification, our results help clarify how terrain-filtered processes govern treeline responses in regions that remain underrepresented in global syntheses.

Although our results align with global reports of treeline advance, extending these inferences requires attention to the distinctive environments of islands. On many subtropical and tropical high-elevation islands, trade-wind inversions can create high-elevation aridity, such that treelines may be limited by water availability rather than temperature alone

(Crausbay et al. 2014, Irl et al. 2016). In addition, mass elevation effects differ between continental mountain systems and small island peaks: large landmasses retain heat and elevate climatic treelines, whereas weaker effects on islands lower potential treeline elevations (Körner 1998, Irl et al. 2016, Karger et al. 2019). Remaining contrasts, especially on oceanic islands, likely reflect biogeographic constraints, including limited pools of cold-tolerant treeline species (Karger et al. 2019). Taiwan represents a comparatively cool subtropical island where cold-tolerant conifers dominate the upper treeline ecotone, whereas similarly subtropical oceanic islands such as Hawaii and the Canary Islands support treelines near ~ 2500 m dominated by more drought-tolerant, less cold-tolerant species (Crausbay et al. 2014, Bello-Rodríguez et al. 2019). Together, these factors highlight that treeline responses to warming are context dependent and that moisture limitation, climatic scaling, and biogeographic history are essential for interpreting Taiwan's patterns within a global framework.

Conclusion

From 1980 to 2021, treelines in Taiwan's Yushan and Central Mountain Ranges shifted upslope and expanded in area, but rates of advance slowed in later decades. This deceleration is likely to reflect increasing topographic and environmental constraints as forests approach upper elevational limits and suitable habitat becomes scarce. Forest expansion within the treeline ecotone was associated with warmer and wetter conditions, but remained moderated by harsh high-elevation environments. These findings suggest that, as warming continues, treeline advances in many mountain systems may increasingly depend on terrain, substrate, and remaining suitable habitat rather than temperature alone. Integrating fine-scale topographic controls into global models will improve predictions of alpine biodiversity and ecosystem change.

Acknowledgements – We thank Dr Chung-Te Chang and Dr Cheng-Tao Lin for their comments on the MSc thesis of the first author, from which this paper was developed.

Funding – This study was financially supported by the National Science and Technology Council of Taiwan (grant no. 110-2811-B-003 -502, 112-2313-B-003 -001 -MY3).

Conflict of interest – The authors declare no conflict of interest.

Author contributions

Kuan-Yu Chen: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jonathan Peereman:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Validation (equal); Visualization (supporting); Writing – review and editing (equal). **J. Aaron Hogan:** Writing – review and editing

(equal); Validation (supporting); Visualization (supporting). **Teng-Chiu Lin**: Writing – review and editing (lead); Methodology (supporting); Data curation (supporting); Conceptualization (supporting); Funding acquisition (lead).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/ecog.08500>.

Data availability statement

The data supporting the findings of this study are derived from both publicly accessible and restricted sources. The multi-temporal aerial photographs were obtained from the Aerial Survey and Remote Sensing Branch (ASRSB), Taiwan Image Services, Supplier, and System (www.asrs.gov.tw). These images are not open-access and must be purchased through the platform. Climate data (temperature and precipitation from 1976 to 2021) were obtained from the Taiwan Climate Change Projection Information and Adaptation Knowledge Platform (TCCIP), National Science and Technology Center for Disaster Reduction (<https://dx.doi.org/10.3390/w14030358>). Topographic data were retrieved from the open data platform of the Ministry of the Interior, Taiwan (<https://data.gov.tw/dataset/35430>), and data from the Fourth National Forest Resource Survey were also obtained from the same platform (<https://data.gov.tw/dataset/57873>). These open-access datasets were appropriately referenced throughout the manuscript and used in accordance with the terms of use provided by the respective sources. Furthermore, the specific file names of the aerial images used in the analysis are provided in the Supporting Information, facilitating traceability and ease of access for future reference.

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ncjsxkt8x> (Chen et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aalto, J., Riihimäki, H., Meineri, E., Hylander, K. and Luoto, M. 2017. Revealing topoclimatic heterogeneity using meteorological station data. – *Int. J. Climatol.* 37: 544–556.

Ametztegui, A., Coll, L., Brotons, L. and Ninot, J. M. 2015. Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. – *Global Ecol. Biogeogr.* 25: 263–273.

Anselin, L. 1988. *Spatial econometrics: methods and models*. – Kluwer.

Anselin, L. 2005. *Exploring spatial data with GeoDa: a workbook*. – CSISS.

Bailey, S. N., Elliott, G. P. and Schliep, E. M. 2021. Seasonal temperature–moisture interactions limit seedling establishment at upper treeline in the southern Rockies. – *Ecosphere* 12: e03568.

Batllore, E. and Gutiérrez, E. 2008. Regional tree line dynamics in response to global change in the Pyrenees. – *J. Ecol.* 96: 1275–1288.

Bello-Rodríguez, V., Cubas, J., Del Arco, M. J., Martín, J. L. and González-Mancebo, J. M. 2019. Elevational and structural shifts in the treeline of an oceanic island (Tenerife, Canary Islands) in the context of global warming. – *Int. J. Appl. Earth Obs. Geoinf.* 82: 101918.

Beloiu, M., Poursanidis, D., Tsakirakis, A., Chrysoulakis, N., Hoffmann, S., Lymberakis, P., Barnias, A., Kienle, D. and Beierkuhnlein, C. 2022. No treeline shift despite climate change over the last 70 years. – *For. Ecosyst.* 9: 100002.

Bhatta, S., Chandani, K. C., Chauhan, R., Aryal, S., Khadka, D. and Sapkota, R. P. 2025. Geospatial assessment of treeline shifting in response to climate change in Langtang National Park, central Nepal. – *Environ. Chall.* 19: 101155.

Blumthaler, M., Ambach, W. and Ellinger, R. 1997. Increase in solar UV radiation with altitude. – *J. Photochem. Photobiol. B: Biol.* 39: 130–134.

Bolli, J. C., Rigling, A. and Bugmann, H. 2007. The influence of changes in climate and land-use on regeneration dynamics of Norway spruce at the treeline in the Swiss Alps. – *Silva Fenn.* 41: 55.

Brown, D. G. 1994. Comparison of vegetation–topography relationships at the alpine treeline ecotone. – *Phys. Geogr.* 15: 125–145.

Butler, D. R., Malanson, G. P., Walsh, S. J. and Fagre, D. B. 2007. Influences of geomorphology and geology on alpine treeline in the American West – more important than climatic influences? – *Phys. Geogr.* 28: 434–450.

Cazzolla Gatti, R., Callaghan, T., Velichevskaya, A., Dudko, A., Fabbio, L., Battipaglia, G. and Liang, J. 2019. Accelerating upward treeline shift in the Altai Mountains under last-century climate change. – *Sci. Rep.* 9: 7678.

Chang, C. T. and Huang, C. Y. 2016. Spatial patterns of vegetation phenology based on MODIS time-series data in Taiwan applying TIMESAT. – *JPRS* 20: 1–14.

Chen, J. C., Yeh, J. Y., Teng, K. D. and Chen, C. T. 2014. Interpretation of stereo image pair for 12 major conifers tree species in Taiwan. – *Q. Jour. Chin. For.* 47: 193–213.

Chen, K. -Y., Peereman, J., Hogan, J. A. and Lin, T. -C. 2026. Data from: Topography constrains the climatic response of treeline migration in Taiwan's subalpine forests. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.ncjsxkt8x>.

Chiu, C. A., Tseng, Y. H., Wang, C. C., Liao, M. C. and Tzeng, H. Y. 2010. Deliberation of Taiwanese alpine tundra vegetation and its possible position based on an ecoclimatic viewpoint. – *Q. J. Chin. For.* 32: 89–102.

Chiu, C. A., Lin, P. S. and Tsai, C. Y. 2014. Spatio-temporal variation and monsoon effect on the temperature lapse rate of a subtropical island. – *Terr. Atmospheric Ocean. Sci.* 25: 203.

Chiu, C. A., Chen, W. C., Tseng, Y. H., Liao, M. C., Wang, W. and Tzeng, H. Y. 2015. Vegetation recovery after fire of subalpine grassland on the East Peak of Mt. Shei. – *Q. Jour. Chin. For.* 37: 5–18.

Chiu, C. A., Tzeng, H. Y., Lin, C. T., Chang, K. C. and Liao, M. C. 2022. Spatial distribution and climate warming impact on *Abies kawakamii* forest on a subtropical island. – *Plants* 11: 1346.

Chuang, K. Y. 1998. A study on the age structure of Taiwan fir forests and the grassland migration in Hehuan Mountain. – MSc thesis, Natl Dong Hwa Univ., Taiwan.

- Chung, M. E., Doyog, N. D. and Lin, C. 2021. Monitoring of the trend of timberlines in Taiwan amidst climate change through multi-temporal satellite images. – 2021 IEEE International Geoscience and Remote Sensing Symposium (IGARSS) 6488–6491.
- Cira, C. I., Manso-Callejo, M. Á., Yokoya, N., Sălăgean, T. and Badea, A. C. 2024. Impact of tile size and tile overlap on the prediction performance of convolutional neural networks trained for road classification. – Remote Sens. 16: 2818.
- Corlett, R. T. and Westcott, D. A. 2013. Will plant movements keep up with climate change? – Trends Ecol. Evol. 28: 482–488.
- Crausbay, S. D., Frazier, A. G., Giambelluca, T. W., Longman, R. J. and Hotchkiss, S. C. 2014. Moisture status during a strong El Niño explains a tropical montane cloud forest's upper limit. – Oecologia 175: 273–284.
- Cudlín, P. et al. 2017. Drivers of treeline shift in different European mountains. – Clim. Res. 73: 135–150.
- Davis, E. L., Brown, R., Daniels, L., Kavanagh, T. and Gedalof, Z. 2020. Regional variability in the response of alpine treelines to climate change. – Clim. Change 162: 1365–1384.
- Devi, N. M., Kukarskih, V. V., Galimova, A. A., Mazepa, V. S. and Grigoriev, A. A. 2020. Climate change evidence in tree growth and stand productivity at the upper treeline ecotone in the Polar Ural Mountains. – For. Ecosyst. 7: 7.
- Dial, R.J., Scott Smeltz, T., Sullivan, P.F., Rinas, C.L., Timm, K., Geck, J.E., Carl Tobin, S., Golden, T.S. and Berg, E.C. 2016. Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. – Global Change Biol. 22: 1841–1856.
- Du, H., Li, M.-H., Rixen, C., Zong, S., Stambaugh, M., Huang, L., He, H. S. and Wu, Z. 2021. Sensitivity of recruitment and growth of alpine treeline birch to elevated temperature. – Agric. For. Meteorol. 304–305: 108403.
- Duque, A., Stevenson, P. R. and Feeley, K. J. 2015. Thermophilization of adult and juvenile tree communities in the northern tropical Andes. – Proc. Natl Acad. Sci. USA 112: 10744–10749.
- Elliott, G. P. and Cowell, C. M. 2015. Slope aspect mediates fine-scale tree establishment patterns at upper treeline during wet and dry periods of the 20th century. – Arct. Antarct. Alp. Res. 47: 681–692.
- Elliott, G. P. and Petrucci, C. A. 2018. Tree recruitment at the treeline across the continental divide in the Northern Rocky Mountains, USA: the role of spring snow and autumn climate. – Plant Ecol. Divers. 11: 319–333.
- Elliott, G. P., Bailey, S. N. and Cardinal, S. J. 2020. Hotter drought as a disturbance at upper treeline in the southern Rocky Mountains. – Ann. Am. Assoc. Geogr. 111: 756–770.
- Elsen, P. R., and Tingley, M. W. 2015. Global mountain topography and the fate of montane species under climate change. – Nat. Clim. Change 5: 772–776.
- FAO 2012. FRA, 2015 terms and definitions. Forest resources assessment working paper 180. – Food and Agriculture Organization of the United Nations.
- Fazlollahi Mohammadi, M., Jalali, S. G. H., Kooch, Y. and Said-Pullicino, D. 2016. Slope gradient and shape effects on soil profiles in the northern mountainous forests of Iran. – Eurasian Soil Sci. 49: 1366–1374.
- Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez and T. M., Zuleta, D. 2020. Climate-driven changes in the composition of new world plant communities. – Nat. Clim. Change 10: 965–970.
- Feuillet, T., Birre, D., Milian, J., Godard, V., Clauzel, C. and Serano-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? – J. Biogeogr. 47: 1056–1068.
- Gottfried, M. et al. 2012. Continent-wide response of mountain vegetation to climate change. – Nat. Clim. Change 2: 111–115.
- Grabherr, G., Gottfried, M. and Pauli, H. 2010. Climate change impacts in alpine environments. – Geogr. Compass. 4: 1133–1153.
- Greenwood, S., Chen, J. C., Chen, C. T. and 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 Biol. 20: 3756–3766.
- Greenwood, S., Chen, J. C., Chen, C. T. and Jump, A. S. 2015. Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline. – J. Veg. Sci. 26: 711–721.
- Harsch, M. A., Hulme, P. E., McGlone, M. S. and Duncan, R. P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. – Ecol. Lett. 12: 1040–1049.
- He, K., Zhang, X., Ren, S. and Sun, J. 2016. Deep residual learning for image recognition. – Proc. IEEE Comput. Soc. Conf. Comput. Vis. Pattern Recognit., 770–778.
- He, X., Jiang, X., Spracklen, D. V., Holden, J., Liang, E., Liu, H., Xu, C., Du, J., Elsen, P. R. and Zeng, Z. 2023. Global distribution and climatic controls of natural mountain treelines. – Global Change Biol. 29: 7001–7011.
- Hogan, J. A., Domke, G. M., Zhu, K., Johnson, D. J. and Lichstein, J. W. 2024. Climate change determines the sign of productivity trends in US forests. – Proc. Natl Acad. Sci. USA 121: e2311132121.
- Holtmeier, F.-K. and Broll, G. 2010. Wind as an ecological agent at treelines in North America, the Alps, and the European subarctic. – Phys. Geogr. 31: 203–233.
- Hooshyarkhah, B., Johnson, D. L., Spencer, L., Ryait, H. S., and Chegoonian, A. 2025. Mapping four decades of treeline ecotone migration: remote sensing of alpine ecotone shifts on the eastern slopes of the Canadian Rocky Mountains. – Remote Sens. 17: 4004.
- Hsu, C. J. 2014. Spatial patterns and factors influencing the mortality of *Abies kawakamii* (Hayata) Ito snags in Hohuanshan Area. – MSc thesis, Natl Pingtung Univ. of Science and Technology, Taiwan.
- Hsu, H. M. 2016. Patterns of genetic variation and genetic structure in *Juniperus morrisonicola* Hayata in Taiwan Mt Sheishan and Mt Nanhu. – MSc thesis, Natl Pingtung Univ. of Science and Technology, Taiwan.
- Huang, K. Y. and Lee, M. M. 1998. Application of digital terrain model data to investigate the characteristics of spatial distribution of *Abies kawakamii* in the Hohuan Mountain area. – J. Expt. Forest of NCHU 20: 111–124.
- Irl, S. D. H., Anthelme, F., Harter, D. E. V., Jentsch, A., Lotter, E., Steinbauer, M. J. and Beierkuhnlein, C. 2016. Patterns of island treeline elevation: a global perspective. – Ecography 39: 427–436.
- Karger, D. N., Kessler, M., Conrad, O., Weigelt, P., Kreft, H., Koenig, C. and Zimmermann, N. E. 2019. Why tree lines are lower on islands – climatic and biogeographic effects hold the answer. – Global Ecol. Biogeogr. 28: 839–850.
- Koide, D., Yoshida, K., Daehler, C. C. and Mueller-Dombois, D. 2017. An upward elevation shift of native and non-native vas-

- cular plants over 40 years on the island of Hawai'i. – *J. Veg. Sci.* 28: 1132–1142.
- Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. – *Oecologia* 115: 445–459.
- Körner, C. 1999. *Alpine plant life*. – Springer.
- Körner, C. 2012. *Alpine treelines*. – Springer.
- Körner, C. and Hoch, G. 2023. Not every high-latitude or high-elevation forest edge is a treeline. – *J. Biogeogr.* 50: 838–845.
- Lai, G. X. 1992. Dynamic structures of ecotones between subalpine coniferous forests and grasslands in Taiwan. – PhD thesis, Natl Chung Hsing Univ, Taiwan.
- Lee, Y., Sim, W., Park, J., and Lee, J. 2022. Evaluation of hyperparameter combinations of the U-Net model for land cover classification. – *Forests* 13: 1813.
- Leonelli, G., Masseroli, A. and Pelfini, M. 2016. The influence of topographic variables on treeline trees under different environmental conditions. – *Phys. Geogr.* 37: 56–72.
- Lett, S. and Dorrepaal, E. 2018. Global drivers of tree seedling establishment at alpine treelines in a changing climate. – *Funct. Ecol.* 32: 1666–1680.
- Li, G. W. 2011. Climate change influence on a sub-alpine *Abies kawakamii* forest stand in central Taiwan. – MSc thesis, Natl Chung Hsing Univ, Taiwan.
- Li, C. F., Chytrý, M., Zelený, D., Chen, M. Y., Chen, T. Y., Chiou, C. R., Hsia, Y. J., Liu, H. Y., Yang, S. Z., Yeh, C. L., Wang, J. C., Yu, C. F., Lai, Y. J., Chao, W. C. and Hsieh, C. F. 2013. Classification of Taiwan forest vegetation. – *Appl. Veg. Sci.* 16: 698–719.
- Liang, E., Wang, Y., Eckstein, D. and Luo, T. 2011. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. – *New Phytol.* 190: 760–769.
- Lin, H. Y., Hu, J. M., Chen, T. Y., Hsieh, C. F., Wang, G. and Wang, T. 2018. A dynamic downscaling approach to generate scale-free regional climate data in Taiwan. – *Taiwania* 63: 251–266.
- Lin, H. Y., Li, C. F., Chen, T. Y., Hsieh, C. F., Wang, G., Wang, T. and Hu, J. M. 2020. Climate-based approach for modeling the distribution of montane forest vegetation in Taiwan. – *Appl. Veg. Sci.* 23: 239–253.
- Lu, X., Liang, E., Wang, Y., Babst, F. and Camarero, J. J. 2021. Mountain treelines climb slowly despite rapid climate warming. – *Global Ecol. Biogeogr.* 30: 305–315.
- Lu, X., Zheng, X., Liang, E., Piao, S., Babst, F., Elliott, G. P., Sigdel, S. R., Wang, T., Wang, Y., Li, X., Gao, S., Zhang, L., Sun, J., Li, J., Zhu, H., Rossi, S., Peñuelas, J. and Camarero, J. J. 2025. Patterns, dynamics and drivers of alpine treelines and shrublines. – *Nat. Rev. Earth Environ.* 6: 489–502.
- Lyu, L., Zhang, Q. B., Pellatt, M. G., Büntgen, U., Li, M. H. and Cherubini, P. 2019. Drought limitation on tree growth at the Northern Hemisphere's highest tree line. – *Dendrochronologia* 53: 40–47.
- Macias-Fauria, M. and Johnson, E. A. 2013. Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. – *Proc. Natl Acad. Sci. USA* 110: 8117–8122.
- Mathisen, I. E., Mikheeva, A., Tutubalina, O. V., Aune, S. and Hofgaard, A. 2014. Fifty years of tree line change in the Khibiny Mountains, Russia: advantages of combined remote sensing and dendroecological approaches. – *Appl. Veg. Sci.* 17: 6–16.
- McCune, B. and Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. – *J. Veg. Sci.* 13: 603–606.
- Mietkiewicz, N., Kulakowski, D., Rogan, J. and Bebi, P. 2017. Long-term change in sub-alpine forest cover, tree line and species composition in the Swiss Alps. – *J. Veg. Sci.* 28: 951–964.
- Mohapatra, J., Singh, C. P., Tripathi, O. P. and Pandya, H. A. 2019. Remote sensing of alpine treeline ecotone dynamics and phenology in Arunachal Pradesh Himalaya. – *Int. J. Remote Sens.* 40: 7986–8009.
- Morley, P. J., Donoghue, D. N. M., Chen, J. C. and Jump, A. S. 2020. Montane forest expansion at high elevations drives rapid reduction in non-forest area, despite no change in mean forest elevation. – *J. Biogeogr.* 47: 2405–2416.
- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., Myneni, R. B. and Running, S. W. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. – *Science* 300: 1560–1563.
- Pauli, H. et al. 2012. Recent plant diversity changes on Europe's mountain summits. – *Science* 336: 353–355.
- Peereman, J., Hogan, J. A. and Lin, T. C. 2022. Disturbance frequency, intensity and forest structure modulate cyclone-induced changes in mangrove forest canopy cover. – *Global Ecol. Biogeogr.* 31: 37–50.
- Peng, X., Feng, Y., Zang, H., Zhao, D., Zhang, S., Cai, Z., Wang, J. and Peng, P. 2024. Climate warming has contributed to the rise of timberlines on the eastern Tibetan Plateau but slowed in recent years. – *Atmosphere* 15: 1083.
- Persson, M., Lindberg, E. and Reese, H. 2018. Tree species classification with multi-temporal sentinel-2 data. – *Remote Sens.* 10: 1794.
- Potter, K. A., Arthur Woods, H. and Pincebourde, S. 2013. Microclimatic challenges in global change biology. – *Global Change Biol.* 19: 2932–2939.
- Rees, W. G., Hofgaard, A., Boudreau, S., Cairns, D. M., Harper, K., Mamet, S., Mathisen, I., Swirad, Z. and Tutubalina, O. 2020. Is subarctic forest advance able to keep pace with climate change? – *Global Change Biol.* 26: 3965–3977.
- Rehm, E. M. and Feeley, K. J. 2015. The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. – *Ecography* 38: 1167–1175.
- Ronneberger, O., Fischer, P. and Brox, T. 2015. U-net: convolutional networks for biomedical image segmentation. – In: *Medical image computing and computer-assisted intervention MICCAI 2015: 18th international conference*. Springer, pp. 234–241.
- Shi, H., Zhou, Q., He, R., Zhang, Q. and Dang, H. 2022. Climate warming will widen the lagging gap of global treeline shift relative to densification. – *Agric. For. Meteorol.* 318: 108917.
- Song, C. E., Wang, U. H., Lin, G. S., Wang, P. J., Jan, J. F., Chen, Y. C. and Wang, S. F. 2022. Establishing automatic classification models for forest cover using airborne hyperspectral and LiDAR data. – *Taiwan J. For. Sci.* 37: 121–143.
- Stanchi, S., Freppaz, M., Godone, D. and Zanini, E. 2013. Assessing the susceptibility of alpine soils to erosion using soil physical and site indicators. – *Soil Use Manage.* 29: 586–596.
- Trant, A., Higgs, E. and Starzomski, B. M. 2020. A century of high elevation ecosystem change in the Canadian Rocky Mountains. – *Sci. Rep.* 10: 9698.
- Trembl, V. and Migoń, P. 2015. Controlling factors limiting timberline position and shifts in the Sudetes: a review. – *Geogr. Pol.* 88: 55–70.
- Trembl, V., Šenfeldr, M., Chuman, T., Ponocná, T. and Demková, K. 2016. Twentieth century treeline ecotone advance in the Sudetes Mountains (central Europe) was induced by agricul-

- tural land abandonment rather than climate change. – *J. Veg. Sci.* 27: 1209–1221.
- Tseng, Y. L. 2015. Using aerial photography to investigate the effects of climate change on the growth and decline for *Abies kawakamii* vegetation in Hehuan Mountain. – MSc thesis, Natl Pingtung Univ. of Science and Technology, Taiwan.
- Wagner, F. H., Sanchez, A., Tarabalka, Y., Lotte, R. G., Ferreira, M. P., Aïdar, M. P. M., Gloor, E., Phillips, O. L. and Aragão, L. E. O. C. 2019. Using the U-net convolutional network to map forest types and disturbance in the Atlantic rainforest with very high resolution images. – *Remote Sens. Ecol. Conserv.* 5: 360–375.
- Wang, S. H. 2013. Reconstruction of 232 years montane climate of Taiwan from stable oxygen isotope ratios in *Abies kawakamii* tree ring. – MSc thesis, Natl Taiwan Univ.
- Wang, T., Zhang, Q. B. and Ma, K. 2006. Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. – *Global Ecol. Biogeogr.* 15: 406–415.
- Wang, Y., Pederson, N., Ellison, A. M., Buckley, H. L., Case, B. S., Liang, E. and Camarero, J. J. 2016. Increased stem density and competition may diminish the positive effects of warming at alpine treeline. – *Ecology* 97: 1668–1679.
- Wielgolaski, F. E., Hofgaard, A. and Holtmeier, F. K. 2017. Sensitivity to environmental change of the treeline ecotone and its associated biodiversity in European mountains. – *Clim. Res.* 73: 151–166.
- Xu, D., An, D. and Zhu, J. 2022. Dynamics of the alpine treeline ecotone under global warming: a review. – *J. Resour. Ecol.* 13: 476–482.
- Yadava, A. K., Sharma, Y. K., Dubey, B., Singh, J., Singh, V., Bhutiyani, M. R., Yadav, R. R. and Misra, K. G. 2017. Altitudinal treeline dynamics of Himalayan pine in western Himalaya, India. – *Quat. Int.* 444: 44–52.
- Zhao, M. and Running, S. W. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. – *Science* 329: 940–943.