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Dispersal dynamics along river corridors modulate impact of climate change on treeline shift in Hengduan Mountain

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Abstract

Alpine treelines are expected to respond to climate warming, but the magnitude and direction of treeline shifts often vary across mountain landscapes. In the Hengduan Mountains, river corridors may shape how forest expansion is expressed as lateral and elevational treeline shifts, with important implications for future alpine habitat loss. Here, we modified and applied the spatially explicit individual based model LAVESI to simulate treeline dynamics along four major river corridors: the Dadu, Lancang, Nu, and Yalong rivers. Simulations covered the historical period from 1940 to 2020 and the future period from 2020 to 2100 under SSP1-2.6, SSP2-4.5, and SSP5-8.5.

During the historical period, simulated treeline shifts were gradual but river specific. Lateral changes were strongest in the Lancang and Nu rivers, intermediate in the Yalong River, and weak in the Dadu River. Elevational changes were more limited, with the Lancang River showing the clearest upward shift and the Nu River remaining close to stable. After 2020, lateral treeline shifts became stronger and more divergent among river corridors and scenarios. In most rivers, future lateral advance increased, with SSP2-4.5 generally producing relatively high cumulative expansion. Elevational shifts followed a related but not identical pattern: the Lancang River maintained the strongest upward trend, the Dadu and Yalong rivers showed moderate increases, and the Nu River remained weakly responsive. The relationship between lateral and elevational changes therefore varied among rivers, indicating that horizontal boundary reorganization did not always translate into comparable upslope shift.

Treeline invasion potential was also uneven. The Dadu River frequently reached the predefined upper limit, although this result should be interpreted in relation to the shorter simulation extent. In contrast, most simulations for the Lancang, Nu, and Yalong rivers remained below the upper limit by 2100, suggesting incomplete occupation of the available treeline tundra ecotone. Overall, our results indicate that future treeline shifts in the Hengduan Mountains are likely to remain spatially heterogeneous across river corridors, with different implications for alpine habitat vulnerability. This vulnerability should therefore be evaluated at the river corridor scale, where lateral expansion, elevational advance, and local topographic and ecological settings jointly shape the potential for future forest expansion.

1 Introduction

1.1 Alpine treeline dynamics in the Tibetan Plateau

Alpine treeline is primarily constrained by climate and its upward shifts have been widely observed by the increase of growing season temperature (Körner, 2021; Sigdel et al., 2024). Nevertheless, evidence also suggests that the treeline responses to climate are varied and often lag behind climate change due to regional differences and from

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diverse ecosystem compositions such as acting on seed dispersal limitations (Harsch et al., 2009; Holtmeier & Broll, 2005; Kruse et al., 2019; Kruse & Herzschuh, 2022). Where treeline does advance, forest expansion can replace alpine ecosystems and compress high-elevation habitats that are inherently limited in area, with potentially severe consequences for alpine biodiversity (Pauli et al., 2012; Dirnböck et al., 2011; Wang et al., 2022). These dynamics highlight the need to focus on climate-sensitive mountain regions to better understand and predict treeline dynamics under ongoing environmental change.

Alpine treeline patterns on the Tibetan Plateau are highly heterogeneous, reflecting pronounced spatial variation in climate, topography, and ecosystem structure (Chen et al., 2015; Piao et al., 2019). Modern ecological and remote-sensing studies show that treeline responses to recent warming vary across the Tibetan Plateau, and not all treelines have observed upshift (e.g., Wang et al., 2019; Zou et al., 2022; Peng et al., 2024). Palaeoecological studies further indicate that treeline positions on the Tibetan Plateau and its southeastern margin have shifted repeatedly during the Holocene in response to climatic fluctuations, with additional human influence in some areas (e.g., Kramer et al., 2010; Liu et al., 2021; Xu et al., 2025). Hengduan Mountain area, located at the east and south border of Tibetan Plateau, is the worldwide biodiversity hotspot with a rich endemic alpine flora (Ding et al., 2020). This area formed a highly heterogeneous environment and completed alpine altitudinal zonation under the combined effect of monsoon and orogenic uplifts, which plays a key role in species diversification, persistence and dispersal (Li et al.,2014; Antonelli et al., 2018). The widespread alpine treeline area, also known as the high mountain ecotone, is sensitive to climate change and other environmental variables (Di Musciano et al., 2020; Weckworth et al., 2013; Vintsek et al., 2022). Therefore, understanding the driving mechanism of treeline shift and how it is corresponding to climate change is essential for revealing the alpine ecosystem and predicting future changes of endemic species.

1.2 River corridors as dispersal pathways across alpine ecotones

Forest expansion beyond the upper treeline has increasingly led to the replacement of alpine shrublands and meadows, thereby reshaping the structure and functioning of high elevation ecosystems (Wang et al., 2022; Sigdel et al., 2024). The extent and rate of forest alpine replacement vary markedly across regions and are influenced by differences in snow regime, moisture availability, nutrient limitation, and biotic interactions, which can produce delayed, uneven, or locally suppressed treeline advance (Rees et al., 2020; Gustafson et al., 2021; Zheng et al., 2024). Part of this variation may also reflect broader landscape structure. Treeline ecotones are increasingly understood as spatially heterogeneous systems in which topography, treeline form, and local environmental context jointly influence where upward movement occurs and where it remains constrained (Holtmeier and Broll, 2005; Bader et al., 2021; Treml and Chuman., 2015).

Within this landscape framework, river systems may provide an important mechanism through which forest expansion beyond the upper treeline becomes spatially organized. At broad spatial scales, river networks are increasingly recognized as ecological corridors that shape dispersal, connectivity, and biodiversity patterns across landscapes (Rinaldo et al., 2018). For plants, river corridors can influence vegetation composition and regeneration by facilitating water-mediated dispersal, maintaining connected riparian habitats, and generating dynamic microsites through flooding, sediment deposition, erosion, and disturbance (Nilsson et al., 2010;

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Corenblit et al., 2007; Gurnell et al., 2016). In this sense, rivers are not merely passive topographic features but active ecological interfaces between terrestrial and aquatic systems, with important consequences for vegetation structure, ecosystem functioning, and landscape connectivity (Naiman and Décamps, 1997; Riis et al., 2020; Wohl et al., 2017).

For alpine ecotones, river valleys and riparian zones may therefore act both as dispersal pathways and as environmental filters. Connected valley habitats and buffered microclimates may increase opportunities for seed arrival, seedling establishment, and upslope movement, whereas exposed ridges and fragmented terrain may restrict movement and contribute to uneven treeline advance (Rupp et al., 2001; Wei et al., 2013; Holeštová and Douda, 2022; Zhang et al., 2023). However, connectivity alone is unlikely to determine whether forest migration is realized. The establishment and survival of trees beyond the current treeline also depend on topoclimatic buffering, microsite conditions, disturbance regimes, and distance to seed sources (Greenwood et al., 2015; Vitali et al., 2017; Rita et al., 2023; Hamid et al., 2023). The Hengduan Mountains provide a particularly suitable setting for examining these processes, because major north–south river systems, including the Jinsha, Lancang, and Nu rivers, have carved deeply incised parallel valleys through high mountain ranges, producing sharp elevational gradients and strong habitat heterogeneity within short distances (Sherman et al., 2008; Zhang et al., 2021).

1.3 Individual-based models can capture nonlinear treeline responses

Treeline dynamics have been investigated using several modelling frameworks. Empirical statistical models, including generalized linear models and partial least squares regression, have been widely used to identify broad climatic controls on treeline position and change. For example, generalized linear models have been applied to model the potential distribution of the Himalayan treeline species *Betula utilis*, whereas partial least squares regression has been used to analyse large scale treeline dynamics in the Hengduan Mountains (Bobrowski et al., 2017; Tian et al., 2022). More flexible statistical approaches, particularly generalized additive models, are useful for capturing nonlinear responses and environmental thresholds. These approaches have been used to analyse mortality and growth responses at alpine treelines and to assess the relative roles of climate and herbivory in treeline dynamics (Barbeito et al., 2012; Mienna et al., 2020). In parallel, machine learning approaches and species distribution models have become increasingly common because they can characterize complex environmental relationships and estimate potential distribution changes under future climates. For instance, support vector machines and XGBoost have been used to analyse deviations between actual and thermal treelines on Yulong Snow Mountain, while MaxEnt based studies have been widely applied in the Himalaya to estimate climatic suitability for treeline forming species (Lin et al., 2024; Bobrowski et al., 2021). However, because these approaches are primarily correlative, they are less well suited to representing the demographic processes that ultimately govern treeline advance, stability, or retreat.

In this context, individual based process models provide a useful complement to correlative approaches because they can explicitly represent demographic processes such as growth, seed production, dispersal, establishment, and mortality. This makes them better suited to examining transient dynamics, migration lags, and delayed stand responses that are difficult to infer from statistical relationships alone. LAVESI is one such spatially explicit model and has been applied mainly to larch dominated treeline systems to investigate how demographic constraints influence treeline advance, stability, and retreat (Kruse et al., 2016). Subsequent developments

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improved the representation of dispersal and migration and incorporated additional processes including permafrost vegetation interactions and adaptive responses, thereby broadening its potential application under heterogeneous environmental conditions (Kruse et al., 2018; Kruse et al., 2022; Gloy et al., 2023). In the Hengduan Mountains, modelling studies relevant to forests and treelines have so far been dominated by remote sensing, spatial statistics, machine learning, and species distribution models, while process based individual or gap models remain scarce. Remote sensing studies have documented both treeline position shifts and structural densification (Tian et al., 2022; Zou et al., 2022), machine learning has been applied to identify actual treelines and their climatic deviations (Lin et al., 2024), and MaxEnt based studies have been used to project alpine vegetation or tree species suitability under future climates (He et al., 2020; Li et al., 2020). By contrast, process based demographic modelling has so far played a relatively limited role in treeline studies from the Hengduan Mountains, although related gap modelling has been explored in nearby mountain systems, such as a FAREAST application on Gongga Mountain (Huo et al., 2010). In this context, LAVESI provides a useful framework not simply because it has not yet been widely applied in this region, but because its explicit representation of growth, dispersal, establishment, and mortality is well suited to analysing the spatially heterogeneous and potentially lagged treeline dynamics observed here.

Research Objective

Our overarching aim is to understand forest upslope migration and assess how the topography of river corridors influences this process, in order to estimate future rates. Specifically, we address three research questions by developing a new version of LAVESI to simulate forest dynamics along river corridors with contrasting topographic settings in the Hengduan Mountains, driven by climate trajectories from before the Holocene climatic optimum through to multiple future climate change scenarios:

1. To what extent, and over what time scales, will treelines shift in response to historical and contemporary climate change and associated ecological processes along mountain river corridors?
2. How do contrasting river systems mediate treeline migration over the coming decades under different climate change scenarios?
3. Do river corridors constitute climate-sensitive hotspots of future treeline advance and associated alpine habitat loss in the Hengduan Mountains?

2 Materials and Methods

2.1 Study system Hengduan mountains

Located at the southeastern margin of the Tibetan Plateau, the Hengduan Mountains form the longest and widest typical north–south-oriented parallel mountain system in China. Long-term tectonic uplift associated with the Indian-Eurasian collision, together with intense river incision, has produced a highly dissected landscape characterized by closely spaced high mountains and deeply incised valleys (Integrated Scientific Expedition to Qinghai-Tibet Plateau, Chinese Academy of Sciences, 1997; Xing and Ree, 2017). This strong topographic relief creates pronounced elevational and climatic gradients, ranging from warm, low-elevation valleys to cold subalpine and alpine zones above the treeline (Fig. 1). The major river systems, including the Nu, Lancang, Yalong, and

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Dadu rivers, are embedded within the north south-oriented mountain valley terrain and connect headwater areas with downstream valleys across pronounced elevational, climatic, and vegetation gradients. These features make the Hengduan Mountains an ideal region for examining spatial variation in alpine treeline patterns across complex mountain-river systems.

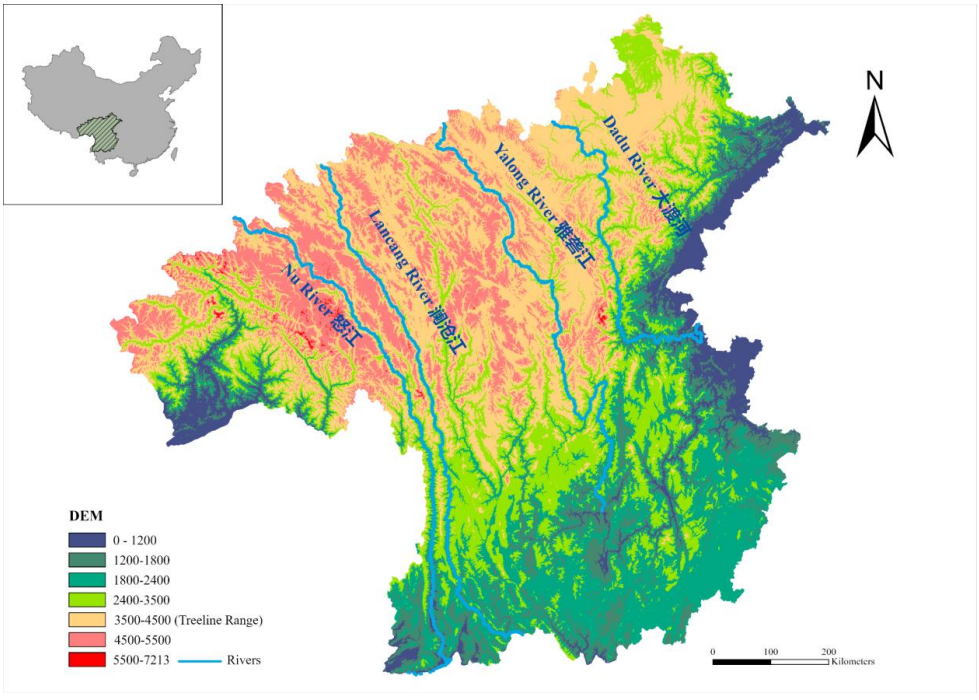

Figure 1. Digital elevation model of the study area showing elevation zones, the treeline range, and major river systems. The inset map in the upper left shows the location of the study area within mainland China.

2.2 The LAVESI model and setup

2.2.1 Model description

In this study, we used the individual-based, spatially explicit model LAVESI (Large Vegetation Simulator, Fig. 2) (Kruse et al., 2016), which was originally developed for *Larix gmelinii* in northeastern Siberia and simulates the full life cycle of larch species. Each simulation step represents one year and includes a series of ecological processes implemented sequentially as submodules. At the start of each annual cycle, an environmental update is conducted. Monthly mean temperature, monthly precipitation sums, and a weather index are used to derive daily environmental conditions, while competition is assessed using an annually updated map of tree population density. The model then simulates seed production, seed dispersal, seedling establishment, and competition-dependent tree growth, followed by ageing and mortality. LAVESI already incorporates many of the key factors affecting treeline migration and has been further extended to include wind-related seed dispersal (Kruse et al., 2018), landscape topography and additional boreal tree species (Kruse et al., 2022).

The detailed model processes and equations summarized in this section follow the original LAVESI model

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descriptions by Kruse et al. (2016, 2019). They are presented here to clarify the model implementation used in this study, while the species parameterization and simulation settings were adapted for the Hengduan Mountain.

Initialisation: The environmental information (elevation, slope, terrain water index) of the simulated area is read in and filled in the model's structures. The weather provided in monthly temperature and precipitation values is read for a given number of years. Each simulation run starts with an empty area and seeds are introduced to the area during a spin-up period at the start of the model.

Environment: As density map is calculated for the area in which the density influence is recorded for the trees. The competition between trees is calculated based on the basal diameter in a given area of the density map (Eq. (1)). The active-layer depth is estimated based on the number of days exceeding 0°C.

$$density\ influence(x\_coord, y\_coord) = \frac{diameter_{basal}}{\sqrt{x_{coord}^2 + y_{coord}^2} + 1} \quad (1)$$

Growth: The maximal growth is calculated based on an average of ten years' climate data. The basal growth (Eq. (2)) of one individual for the year is then derived from this by including the density index of the tree. Based on the diameter, the tree height is estimated (Eq. (3)).

$$Growth_{max,diameter} = \left(precipitation * Growth_{standard,diameter} * \left(\frac{1}{f_{AATNDD}} * AATI + \left(1 - \frac{1}{f_{AATNDD}}\right) * net\ degree\ days\right)\right) * (1 - TDEI) \quad (2)$$

$$height = \begin{cases} 44.43163 * diameter_{basal}, height < 1.3\ m \\ \left(7.02 * \sqrt{diameter_{breast}}\right)^2 + 130, height \geq 1.3\ m \end{cases} \quad (3)$$

Seed dispersal: Seeds that are still within cones are dispersed, the direction and distance are randomly determined influenced by wind data (Eq. (4)). When seeds leave the extent of the transect to either the east or west, they are reintroduced from the opposite site, to simulate a larger forest and avoid the loss of many seeds.

$$distance = sqrt\left(2\left(release\ height * wind\frac{speed}{fall}speed\right)^2 * \left(-log(rand)\right) + \frac{1}{2}distance\ ratio * rand^{-1.5}\right) \quad (4)$$

Seed production: Once a tree has reached the height of maturation, based on a pre-generated distribution randomly assigned, it produces seeds. The amount produced in each year is based on the height of the tree, competition, and the weather (Eq. (5)).

$$seeds\ produced = \lfloor factor\_s * Diameter\_basal * (1.0 - (height/(50\ m))\text{^}(-1.0)) \rfloor \quad (5)$$

Establishment: Seeds that are on the ground germinate based on weather conditions (Eq. (6)).

$$probability\ to\ germinate(year) = background\ germination\ rate + \quad (6)$$

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$$\left(weather\ quality\ factor * \frac{Growth_{(max,basal)(year)}}{Growth_{standard,basal}}\right)$$

Mortality: The probability of death is calculated for each tree and, based on that, it is semi-randomly determined whether the tree dies and is removed from the simulation. The calculation is based on long-term weather values, the calculated drought strength, competition of sur rounding trees, the age and size of the tree, and a base mortality rate. For each of these a mortality value is calculated, these are then summed up and compared to a randomly generated number. If the sum of death probabilities is larger the tree dies. The death of seeds is determined at this step as well, although the mortality rate for these is fixed.

Ageing: The last step is an increase in the age of both the seeds and the trees. Since every year is simulated, the age is advanced by once each cycle. The seeds are removed once they have reached a certain (3 years) age limit.

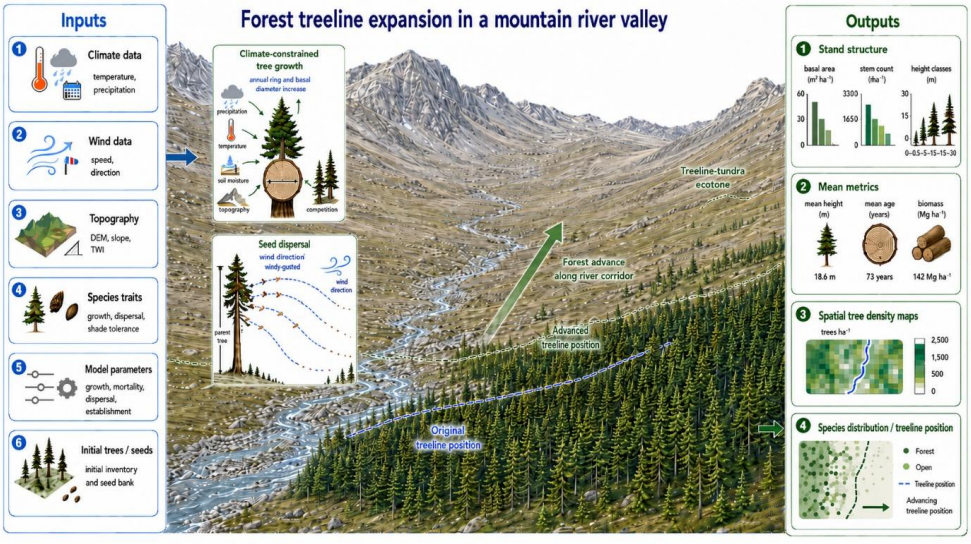

Figure 2. Conceptual framework of simulated forest treeline expansion in a mountain river valley. (This figure was created with the assistance of an AI-based image generation tool and subsequently reviewed and edited by the authors to ensure conceptual accuracy.)

2.2.2 Hengduan species parameter set

The initial version of LAVESI focused on genus *Larix* (Kruse et al. 2016). This conifer species forms the treeline in Eurasian arctic treelines. Therefore, we decided to extend the range of application especially to include Hengduan Mountain treeline forming species by selecting species based on local floristic records. We summarized species lists from the Flora Xizangica (Integrated Scientific 195 Expedition to Qinghai-Tibet Plateau, Chinese Academy of Sciences, 1983–1987), the Flora of Sichuan (Gao et al., 1981), and the Flora of Yunnan (Kunming Institute of Botany, Chinese Academy of Science, 1977-2006), and identified the shared gymnosperm species among these regions, yielding a total of 50 species. For the necessary parameters, we collected them from trait

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datasets, handbook, Flora and expert experiences (Table S1).

Based on field surveys conducted in the Hengduan Mountains in 2023 and 2024, we collected measurements of individual trees from plot records along the selected river system area, including tree height and stem diameter. To describe the relationship between tree height and stem size, we built height–diameter models for each target species. We first selected records for the target species and removed observations with missing or zero values for height or diameter. Tree height was converted to cm, and diameter was converted to mm. Depending on the dataset (Jin et al.,2026), diameter was represented by diameter at breast height (DBH) or basal diameter.

Because the relationship between height and diameter was nonlinear, both variables were transformed using the natural logarithm before model fitting. We then fitted a logistic nonlinear model in log space:

$$ln(H) = \frac{A}{1 + exp(\frac{x_m - ln(D)}{s})} \quad (7)$$

where H is tree height, D is DBH or basal diameter, A is the upper asymptote, x_m is the midpoint parameter, and s is the scale parameter (Eq. (7)).

Initial parameter values were obtained with a self-starting Logistic function. Final parameter estimates were then fitted using generalized nonlinear least squares (GNLS) with function “gnls” from R-package “nlme” (Pinheiro et al. 2026). The fitted model was used in LAVESI to estimate tree height for the observed and simulated diameter range and to draw height–diameter curves for each species.

We collected tree ring data from published datasets archived in the International Tree Ring Data Bank (ITRDB) (Grissino-Mayer and Fritts, 1997). The data were accessed through the NOAA World Data Service for Paleoclimatology. We restricted the search to sites within China and then queried the database using the Latin names of the target conifer species Finally, we found 10958 individual ring-width series for 21 species (Table S2).

Radial growth was modelled as an exponential quadratic function of stem size:

$$G(D) = exp(a + b \cdot D + c \cdot D^2) \quad (8)$$

where G(D) is the annual radial increment at stem size D, a is the intercept (gdbasalconst), b is the linear size effect (gdbasalfac), and c is the quadratic size effect (gdbasalfacq) (Eq. (8)). The quadratic term allows growth to increase at small sizes and decline again at larger sizes, thus representing a unimodel growth trajectory.

2.2.3 River transect simulation setup

We selected four representative river transects in the Hengduan Mountains, as major rivers in this region are predominantly oriented along a north–south axis and traverse a large proportion of the landscape. Acting as key

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ecological corridors, they play a crucial role in maintaining ecosystem stability and facilitating species migration. Based on the Tibetan treeline range defined by Xu (2025), we determined the longitudinal extent of the simulation area for each river according to its elevational range (Table 1). Xu *et al*. suggested that the regional treeline occurs approximately between 3500 and 4500 m. Therefore, for each river, we defined the lower-elevation section extending from the downstream starting point to the upper limit of this treeline range as the spin-up and seed introduction zone (Fig. A1). This zone allowed the model to establish a stable initial vegetation state and seed availability before entering the target treeline-tundra ecotone. The remaining upstream section, generally located above the treeline range, was then treated as the treeline-tundra ecotone simulation zone. We then applied a 30 m buffer on both sides of the river centreline, which defined the width of the simulation area. In addition, a spin up and seed introduction zone was included before the treeline-tundra ecotone to allow the simulated forest to establish under continuous seed input and approach a near stable state. The extent of this zone was defined according to the spatial range in which most simulated species were concentrated in the model output. All spatial operations were carried out in ArcGIS Pro.

Table 1. Basic information for selected river transects.

River	Full Length in Simulation(m)	Spin-up and Seed Introduction Length(m)	Treeline-tundra Ecotone Length(m)
Dadu 大渡河	26625	5000	21625
Lancang 澜沧江	252355	200000	52355
Nu 怒江	339730	290000	49730
Yalong 雅砻江	308035	280000	28035

2.3 Forcing data

2.3.1 Past and historical climate data

LAVESI requires monthly mean temperature, monthly mean precipitation data, and 6-hourly wind speed and direction as input data. Temperature, precipitation and wind data were derived from the transient MPI ESM_Glac1d-P3 data (Max Planck Institute for Meteorology Earth System Model, 1.875° resolution) (Kapsch et al., 2022). Past temperature and precipitation data was downscaled and bias corrected to monthly values using the CRU TS data (years 1901-present, 0.5° resolution) which was derived by interpolating weather station observations (Harris et al., 2020). Wind speed and direction was downscaled to four daily values using the Copernicus ERA5 (European ReAnalysis) dataset and adding monthly variation patterns. This global dataset (0.25° resolution) covers data from 1940 to present at 10 m height (Hersbach et al., 2020). Specially, to the wind data in future phase from 2021-2100, we performed random sampling based on the high resolution data from 1940 to 2020 in order to reduce the influence of the lower data resolution in the future phase.

2.4.2 Future climate data

Future temperature, precipitation and wind data were derived from MPI-ESM 1.2 LR (Max Planck Institute for Meteorology Earth System Model version 1.2 low resolution, 1.875°). This data was generated for the Coupled

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Model Intercomparison Project Phase 6 (CMIP 6) (Wieners et al., 2019). To represent future climate forcing, three Shared Socioeconomic Pathway scenarios were used, namely SSP1-2.6, SSP2-4.5, and SSP5-8.5. These scenarios span a range from relatively low to high future radiative forcing and are widely used to assess climate related ecological responses under contrasting future conditions (Meinshausen et al., 2020).

2.3.3 Environment

To apply LAVESI to the study areas of this thesis, environmental variables including elevation, slope, and surface moisture were derived from a 30 m resolution digital elevation model (Ho et al., 2025). The digital elevation model was used to calculate slope and the Topographic Wetness Index (TWI), while water bodies were excluded through masking. These spatial processing steps were carried out in ArcGIS Pro to generate ready to use input files for LAVESI. The buffered river shapefiles were used as masks, from which the corresponding elevation, slope, and TWI were extracted. The data package will be made publicly available at final publication on Zenodo.

2.3.4 Model adjustments

The local version extends LAVESI-WIND specifically for treeline simulations in the Hengduan Mountains and river transects. On the input side, it no longer relies only on fixed DEM, slope, and TWI files as in the official version; instead, it uses “weatherchoice” codes to identify river transects such as the Dadu, Lancang, Nu, and Yalong rivers, and automatically reads the corresponding treeline environmental inputs, including DEM, slope, and TWI, together with specific Hengduan climate and wind data. On the output side, it adds customized treeline outputs, such as “maxposition”, which records, by species, the maximum position reached by individuals taller than 1.3 m, allowing direct tracking of treeline advance. It also produces simplified datatrees files at selected years, retaining key variables such as Y-position, species, and tree height, which can be used for further analysis in summary treeline tables.

2.4 Simulation tests

2.4.1 Parameters setting

All simulations were forced with the same parameter settings and climate input structure. The difference among the four river simulations was the topographical setting of the river corridors, which determined the spatial configuration of the simulation area and the associated environmental context. Therefore, differences in simulated treeline dynamics can be interpreted primarily in relation to the different corridor settings rather than to changes in model parameterization. The relevant parameters that were used for all simulations are listed in Table 2.

Table 2. Important parameters setting.

Parameter	Value	Description
elevationoffset	900	Tuning variable for adjusting the baseline height of the topography.
weatherchoice	1000X00404	Setting for the different scenarios and

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		rivers. X here represents different river selections.
lastyearweatherdata	25151	Determined by the available input data series (final year + 1), setting of year 25151 allows the final simulation year to be 2100 CE
simduration	15150	Duration of the simulation period, shorter than lastyearweatherdata means starting later in time
seedintro	1	Binary switch to enable seed input to the simulated area
yearswithseedintro	1000	Years of seed introduction at the beginning of each simulation
seedintronumber	510	Number of seeds introduced per ha per year (for eachyearswithseedintro)
seedintropermanent	1	Binary switch to enable introduction of a low number of seeds into the simulation area as background seed rain
seedintronumberpermanent	51	The number of seeds introduced per ha per year and plot if switched on
seedwinddispersalmode	2	Setting to determine the positions for introduced seeds that is randomly into the simulated area in our case
seedintro_maxy	5000	The setting of the maximum position of introduced seeds in m, starting at the lowest points of the river corridor

2.4.2 Calibration based on plot datasets

To identify the most suitable climatic setting for the simulations, we calibrated the parameter weatherchoice, which represents different combinations of climate input data, using all available plot data (plots 401–472). For each plot, local climate and topographic information were first extracted from its spatial location and used as model input. We then ran simulations under a range of elevation offset values. The elevation offset is a tuning parameter that adjusts the climatic conditions represented in the simulation area instead of directly applying a uniform lapse rate allowing fine tuning especially in topographically complex topographies where the local climate differs likely from the mean that is provided by the data sources as a mean value over a larger area. Model performance was evaluated by comparing simulated outputs with field observations in two steps. First, we assessed whether the simulated community type matched the observed plot type, that is, whether the plot was represented as forest, shrubland, or meadow. Second, we compared the maximum height of the three tallest observed trees in each plot with the height of the tallest simulated tree individual. The observed and simulated results were visualized and compared using ggplot2 (Wickham, 2016), and plot 404 showed the best overall agreement between field observations and simulation output. It was therefore selected as the reference plot for further calibration. Based on this plot, the elevation offset was varied from −1000 m to +1000 m in increments of 100 m in order to determine which setting most closely reproduced the observed composition and structure of the

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real treeline ecotone.

2.4.3 Simulation of treeline expansion

To reduce stochastic effects, each river corridor was simulated with 100 replicate runs on the high performance computing platform. Each run covered 15,150 model years and extended to the year 2100 CE. The initial time phase acted as the spin-up phase, and we analysed only the final 160 years of each simulation, corresponding to 1940–2100 CE.

For each year and species, the model output recorded the maximum simulated position. Lateral (upslope, along the river corridor) treeline position was then derived from these annual outputs using a rule-based definition. We first selected species with more than 1000 individuals, then scanned the spatial distribution using a 100 m moving window. A window was considered valid when it contained at least 100 individuals, and a treeline was accepted only if such valid windows formed a continuous segment of at least 100 m. The uppermost position satisfying these criteria was defined as the annual lateral treeline.

Elevational treeline position was derived by mapping the simulated lateral treeline positions onto the digital elevation model using R-version 4.3.3 (R core team,2023). For each annual treeline position, the corresponding elevation value was extracted from the 30 m DEM, allowing us to reconstruct yearly changes in treeline elevation.

3 Results

3.1 Lateral treeline dynamics during the historical period

During the historical period from 1940 to 2020, all rivers showed gradual lateral shifts of the treeline, although the magnitude of change differed markedly among river systems (Fig. 3). Based on the mean cumulative trajectories, the Dadu River remained nearly stable, with only very small cumulative advance and retreat throughout this period. In contrast, the Lancang River and Nu River exhibited much stronger cumulative advances, both reaching about 200 m by 2020. In these two rivers, the increase became more pronounced after around 1980, although the overall trend remained progressive rather than abrupt. The Yalong River showed an intermediate pattern, with cumulative advance reaching approximately 60 m by 2020 and a smoother trajectory than those of the Lancang River and Nu River.

At the same time, all rivers showed weak but persistent cumulative retreat during the historical period. Although retreat remained much smaller than advance, its presence indicates that lateral treeline dynamics were not expressed as a purely one directional expansion. Instead, the historical period was characterized by modest but bidirectional boundary change, with advance dominating over retreat in all four rivers.

The 25–75% quantile bands (Fig. 3) showed that uncertainty differed substantially among rivers. Historical variability was relatively small in the Dadu River, but much larger in the Lancang River, Nu River, and Yalong River, indicating that even under the same historical forcing, the magnitude of simulated lateral shift varied strongly among simulation runs.

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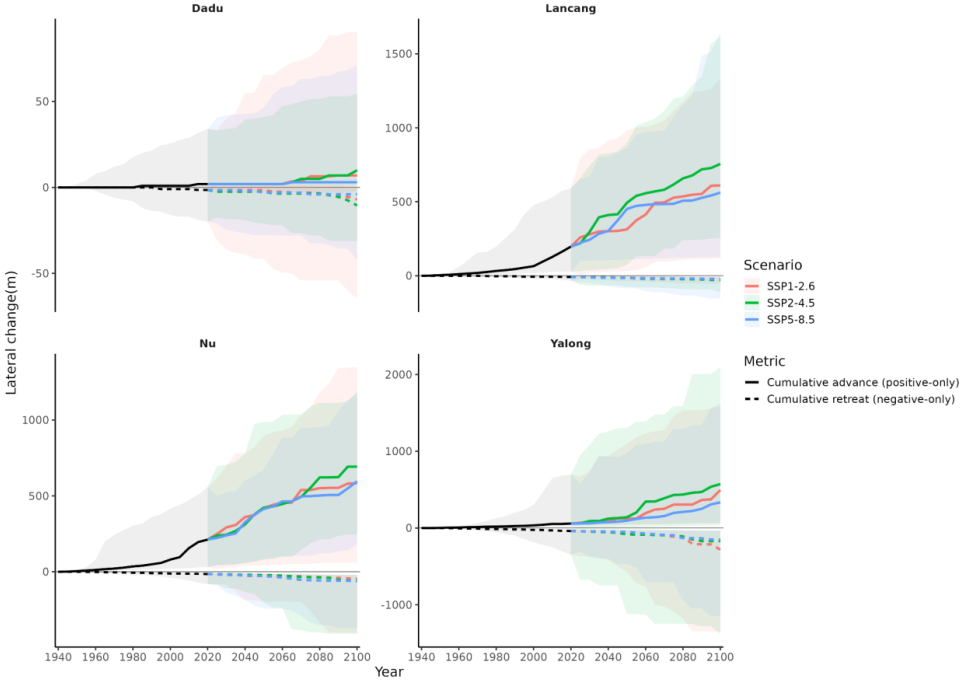

Figure 3. Cumulative lateral treeline advances and retreat across rivers under SSP scenarios, with 25–75% quantile bands, for 1940–2100 CE. Solid lines show cumulative advance (positive only), and dashed lines show cumulative retreat (negative only). The historical period (1940–2020) is merged and shown in black, whereas future trajectories (2020–2100) are shown separately for SSP1-2.6, SSP2-4.5, and SSP5-8.5

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Figure 4. Treeline elevational change across rivers under SSP scenarios, with 25–75% quantile bands, for 1940–2100 CE. The historical period (1940–2020) is merged and shown in black, whereas future trajectories (2020–2100) are shown separately for SSP1-2.6, SSP2-4.5, and SSP5-8.5

3.2 Lateral treeline dynamics during the future period

During the future period from 2020 to 2100, lateral treeline trajectories became increasingly divergent among scenarios and river systems (Fig. 4). All rivers showed stronger lateral shifts than during the historical period, indicating a transition to a more dynamic phase of treeline change. In most rivers, the mean cumulative advance reached around 500 m by 2100. Among the three scenarios, SSP2-4.5 generally produced the strongest mean cumulative advance, with maxima reaching about 560 m, whereas SSP1-2.6 and SSP5-8.5 showed lower maxima of approximately 438 m and 385 m, respectively.

The largest increases occurred in the Lancang River and Nu River, where the mean cumulative advance reached about 446 m and 412 m by 2100. In both rivers, the increase was rapid and sustained throughout the future period. The Yalong River also showed substantial advance, reaching about 409 m by 2100, but its trajectory exhibited a more abrupt acceleration around the 2060s compared with those of the Lancang River and Nu River. By contrast, the Dadu River remained much more stable, with the mean cumulative advance reaching only about 5 m by 2100, indicating a much weaker future response relative to the other rivers.

Mean cumulative retreat also increased across all rivers during the future period, although its magnitude remained lower than that of cumulative advance. By 2100, retreat values ranged from about 6 to 160 m, with particularly clear increases under SSP1-2.6 and SSP2-4.5 in some river systems. The 25–75% quantile bands showed that uncertainty widened substantially after 2020, especially in the Lancang River, Nu River, and Yalong River (Fig. 4). This indicated that future lateral treeline change is characterized not only by stronger average expansion, but also by greater variation among simulation runs. Overall, the results showed that lateral treeline dynamics shift from a relatively slow and convergent historical pattern to a faster and increasingly divergent future pattern.

3.3 Elevational treeline dynamics across river systems

Elevational changes in treeline position differed markedly among river systems (Fig. 4). During the historical period from 1940 to 2020, treeline elevation changed only gradually in most rivers, but the magnitude of change varied substantially. The strongest elevational increase occurred in the Lancang River, where treeline elevation rose continuously over the 80-year period and had already increased by more than 10 m by around 2020. In contrast, the Dadu River and Yalong River showed only modest upward changes, with cumulative increases of roughly 1–2 m during the same period. The Nu River exhibited the weakest elevational response, remaining close to stable with only slight fluctuations.

During the future period from 2020 to 2100, scenario specific divergence became more evident. The Lancang River maintained the strongest upward trend under all future scenarios, with the largest increase under SSP2-4.5 and a cumulative elevational gain exceeding 20 m by 2100. The Dadu River also continued to rise, but with a much smaller magnitude and stronger variation among scenarios. The Yalong River showed an intermediate response, with continued but moderate elevational increases under all scenarios. By contrast, the Nu River

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remained the least responsive in elevational terms, with only minor changes and a slight negative trend under SSP1-2.6 toward the end of the century.

The 25–75% quantile bands showed that uncertainty differed substantially among rivers and became greater after 2020(Fig. 4). Quantile ranges were especially large in the Dadu River and Lancang River, indicating considerable variation among simulation runs in future elevational responses. In the Yalong River, the quantile bands also showed a broader range during the future period, although the mean upward trend remained moderate. By contrast, the Nu River showed relatively small mean changes but still displayed a notable spread around zero, indicating that its future elevational response remained weak and uncertain rather than strongly directional. Overall, clear spatial differences were observed in treeline elevational change across the Hengduan Mountains, with the Lancang River showing the largest increase, the Dadu Rive and Yalong River showing moderate increases, and the Nu River showing the smallest overall change.

We compared lateral treeline change with elevational treeline change across 5-year windows (Fig. 5). The relationship differed markedly among river systems, with the strongest positive coupling in the Lancang River, almost no elevational response in the Nu River, and intermediate patterns in the Dadu River and Yalong River.

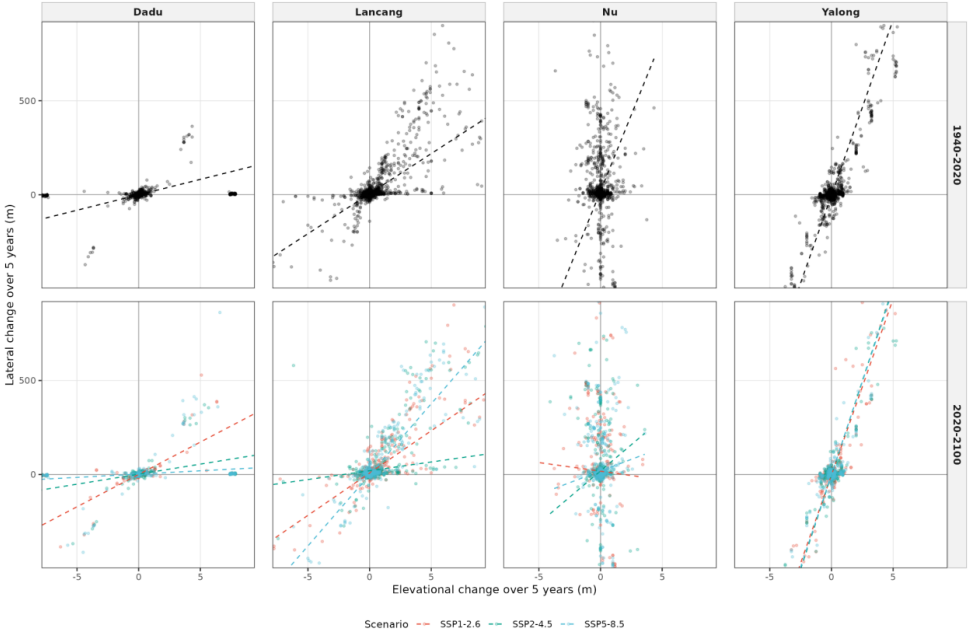

Figure 5. Relationship between lateral and elevational treeline change across four river systems over 5-year windows. Historical windows (1940-2020) are shown in black, and future windows (2020-2100) are shown separately for SSP1-2.6, SSP2-4.5, and SSP5-8.5. Panels are arranged by river corridor, with the upper row showing the historical period and the lower row showing the future period. Each point represents one 5-year window. Axis ranges were limited to improve the visibility of the main point distributions; extreme values outside the plotting range are not shown. Dashed lines indicate fitted linear

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relationships and should be interpreted as visual summaries.

3.4 Treeline states across rivers and scenarios

To further compare river specific differences in treeline behaviour, we summarized the final simulated treeline states into three categories: runs that kept advancing to the predefined upper limit ("Stable limit"), runs that reached the limit briefly but then retreated ("Temporary overshoot"), and runs that never reached the limit ("Below limit") (Fig. 6).

The Dadu River was the most consistent case. Under all three SSPs, 100% of runs remained in the category "Stable limit", indicating that all versions reached and maintained the predefined upper limit. In contrast, the other three rivers were dominated by runs that never reached the limit. In the Lancang River, about 50–58% of runs belonged to the category "Below limit", whereas 41–48% remained in "Stable limit". In the Nu River and Yalong River, the dominance of "Below limit" was even clearer, accounting for about 65–74% of runs depending on scenario, while only about 23–33% remained in "Stable limit".

The category "Temporary overshoot" was always small, generally ranging from 0 to 6%. This indicated that temporary reaching of the upper limit followed by retreat occurred only in a few runs. Dadu River was consistently able to maintain the upper limit, whereas most runs in Lancang River, Nu River, and Yalong River did not reach that limit by the end of the simulation.

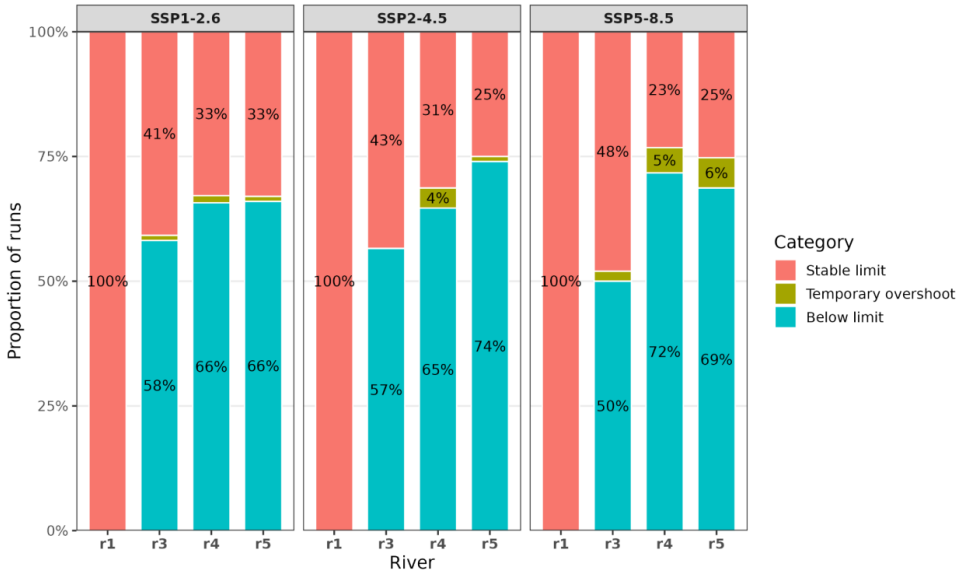

Figure 6. Treeline state composition across rivers and scenarios. Stacked bars show the proportion of simulation runs in three treeline states: Stable limit, Temporary overshoot, and Below limit. Bars are grouped by future scenarios (SSP1-2.6, SSP2-4.5, and SSP5-8.5). River codes correspond to the four study corridors: r1 = Dadu River, r3 = Lancang River, r4 = Nu River,

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and r5 = Yalong River. Percentages within each river × scenario sum to 100%.

4 Discussion

4.1 Historical and future treeline lateral dynamics

During the historical period (1940–2020), simulated forest treeline dynamics were generally slow, but differed markedly among river systems. The Dadu River showed only weak cumulative advance and retreat, indicating a comparatively stable forest boundary, whereas the Lancang and Nu rivers already exhibited substantial cumulative advance before 2020, and the Yalong River showed intermediate but clearly dynamic behaviour. This pattern is consistent with the broader view that historical treeline responses are spatially heterogeneous and are not always expressed as simple upslope shifts (Harsch et al., 2009; Schickhoff et al., 2015). In the Hengduan Mountains, recent landscape observations similarly showed that treeline position often remained broadly stable while vegetation cover increased across most treeline areas, suggesting that historical responses may first appear as structural infilling or boundary adjustment rather than obvious positional displacement (Zou et al., 2022).

The contrast among river corridors is ecologically plausible given the strong environmental heterogeneity of the Hengduan Mountains. Differences in valley morphology, disturbance history, vegetation composition, riverine connectivity, and local topographic setting may all contribute to river-specific forest boundary dynamics. For example, forest change in the upper Dadu River watershed has been influenced by deforestation, rehabilitation, and degradation processes, whereas vegetation patterns in the Lancang and Nu valleys are strongly shaped by riverine landscapes, topographic gradients, and local environmental filtering (Yan et al., 2005; Li et al., 2012; Liu et al., 2014; Zhao et al., 2023). Previous phylogeographic work also suggests that the Yalong River has played an important role in plant dispersal and divergence in the Hengduan Mountains, which is consistent with the relatively dynamic boundary behaviour simulated here (Jian et al., 2016). Altogether, the historical results suggest that forest treeline dynamics in the Hengduan Mountains are better understood as modest but spatially heterogeneous forest boundary changes, rather than as a single regionally homogeneous treeline shift.

After 2020, simulated treeline dynamics became much more active across all four river systems, with stronger cumulative advance and clearer divergence among future scenarios. This transition from a relatively constrained historical phase to a more dynamic future phase agrees with treeline studies showing that warming can intensify treeline and ecotone dynamics, although the magnitude and direction of change remain strongly modulated by ecological processes and landscape context (Dullinger et al., 2004; Zheng et al., 2021). In our simulations, the Lancang and Nu rivers showed the strongest cumulative advance, the Dadu River remained weakly responsive, and the Yalong River displayed both substantial advance and retreat. This indicates that future forest treeline change cannot be reduced to a simple monotonic expansion signal. Instead, simultaneous advance and retreat along different boundary segments, especially in the Yalong River, suggest ongoing reorganization within the treeline ecotone.

Such an interpretation is consistent with recent work emphasizing that future treeline responses are likely to involve not only positional change, but also ecotone restructuring, forest expansion into alpine habitats, and nonlinear responses driven by dispersal, density dependence, and local site conditions (Kruse et al., 2023; Kumar and Khanduri, 2024). More generally, future vegetation projections from the Himalaya and other mountain regions indicate that suitable habitats and forest boundaries at higher elevations may shift and reorganize under continued warming, often with strong scenario-dependent divergence and important consequences for alpine habitat availability (Chhetri et al., 2018; Barredo et al., 2020). Therefore, our results support the view that future treeline dynamics in the Hengduan Mountains will be characterized not simply by upward or outward expansion, but by increasingly divergent and spatially heterogeneous forest boundary dynamics across river corridors.

The scenario responses further suggest that warming intensity alone did not determine lateral treeline expansion. Warmer conditions are generally expected to promote treeline advance because low temperature is widely regarded as a major constraint on tree establishment and persistence near upper treeline limits (Körner, 2021).

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Many studies have shown that warming can facilitate upward forest expansion or woody encroachment into open alpine and subalpine habitats (Albert et al., 2008; Piccinelli et al., 2020; Wang et al., 2022). However, our simulations did not show a simple monotonic increase from SSP1-2.6 to SSP5-8.5. Instead, SSP2-4.5 produced the strongest cumulative advance in several cases, particularly in the Lancang, Nu, and Yalong rivers. This pattern suggests that realized treeline expansion in the Hengduan Mountains was shaped by the interaction between climate forcing and local ecological constraints, rather than by warming intensity alone.

Similar conclusions have been reached in other mountain systems, where upslope forest advance can remain strongly constrained by topographic conditions even under warming (Macias-Fauria et al., 2013). Studies from mountain grassland and treeline ecotone systems also show that woody encroachment depends on land-use legacy, colonization opportunities, and local site conditions, in addition to climate (Albert et al., 2008; Piccinelli et al., 2020). Species-specific responses may further complicate this relationship, as dominant Himalayan treeline species can respond differently to climate change (Mainali et al., 2020). From this perspective, intermediate scenarios may remain closer to the suitable climatic space of particular treeline-forming species, whereas stronger warming may generate mixed or locally constrained responses rather than continuous lateral expansion.

4.2 River specific differences in elevational treeline change

Elevational treeline change added an important constraint to the interpretation of lateral treeline dynamics. Although lateral forest expansion was evident in several river corridors, it was not always accompanied by a comparable upward shift in treeline elevation. During the historical period, most river corridors showed only limited elevational advance. The Lancang River was the main exception, showing a sustained increase in treeline elevation, whereas the Dadu and Yalong rivers showed only modest gains and the Nu River remained nearly stable. This contrast suggests that lateral reorganization of the forest boundary and upslope displacement of the upper treeline represent related but distinct dimensions of treeline change.

Future projections reinforced this distinction. Elevational trajectories became more differentiated among river corridors, with the Lancang River maintaining the clearest upward trend, the Dadu and Yalong rivers showing more moderate increases, and the Nu River remaining weakly responsive, including a slight decline under SSP1-2.6 near the end of the century. These results suggest that warming may amplify existing differences in elevational sensitivity, but does not produce a uniform upslope response across the Hengduan Mountains. Positive coupling between lateral and elevational change was most evident in the Lancang and Yalong rivers, whereas the Nu River showed weak elevational change despite lateral dynamics. Such river-specific differences likely reflect variation in topographic configuration, local terrain constraints, regeneration conditions, and species interactions, all of which can moderate treeline responses to climate warming (Schickhoff et al., 2015; Liang et al., 2016; Wang et al., 2022).

These findings support a cautious interpretation of treeline advance. Lateral change describes the horizontal redistribution and infilling of forest along the treeline ecotone, whereas elevational change indicates whether the upper forest boundary has shifted upslope. In this study, these two dimensions were coupled in some river corridors but were not interchangeable. This distinction is consistent with recent evidence that increased tree density within treeline ecotones can be partly decoupled from upward movement of the upper treeline (Feuillet et al., 2020; Shi et al., 2022). Field observations from the Central Alps similarly show that recent increases in tree abundance may largely reflect infilling below or near the former treeline rather than true upward advance of the

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upper boundary (Frei et al., 2023). Therefore, fitted relationships between lateral and elevational change should be interpreted as visual summaries rather than evidence of a single, consistent mechanism. This distinction is important for assessing future alpine habitat vulnerability, because forest expansion within the treeline ecotone may continue to reduce alpine shrubland and meadow habitats even where mean treeline elevation changes only weakly.

4.3 Treeline invasion potential and implications for alpine habitat loss

The upper limit results suggested that most river corridors remained relatively conservative in terms of treeline invasion potential. In the majority of simulations, especially outside the Dadu River, treeline advance did not reach the predefined upper limit, indicating that forest expansion into the full treeline tundra ecotone was often incomplete by the end of the simulation period. This suggests that future treeline advance in the Hengduan Mountains may be substantial, but in most corridors, it is still unlikely to occupy all potentially colonizable space within the simulated domain. Such a pattern is consistent with earlier studies showing that warming does not automatically translate into full or rapid invasion of alpine habitats, because realized expansion is often constrained by recruitment, micrositе availability, land use history, and topographic setting (Albert et al., 2008; Macias-Fauria et al., 2013; Piccinelli et al., 2020). The Dadu River represented a notable exception, as simulated treelines more frequently reached and maintained the upper limit. However, this result should be interpreted cautiously. It may reflect not only a stronger effective response in this corridor, but also the comparatively shorter simulation extent, which makes the predefined limit easier to attain within the current model setup. The apparent invasion potential of a corridor therefore depends not only on ecological response, but also to some degree on how the simulation area is defined.

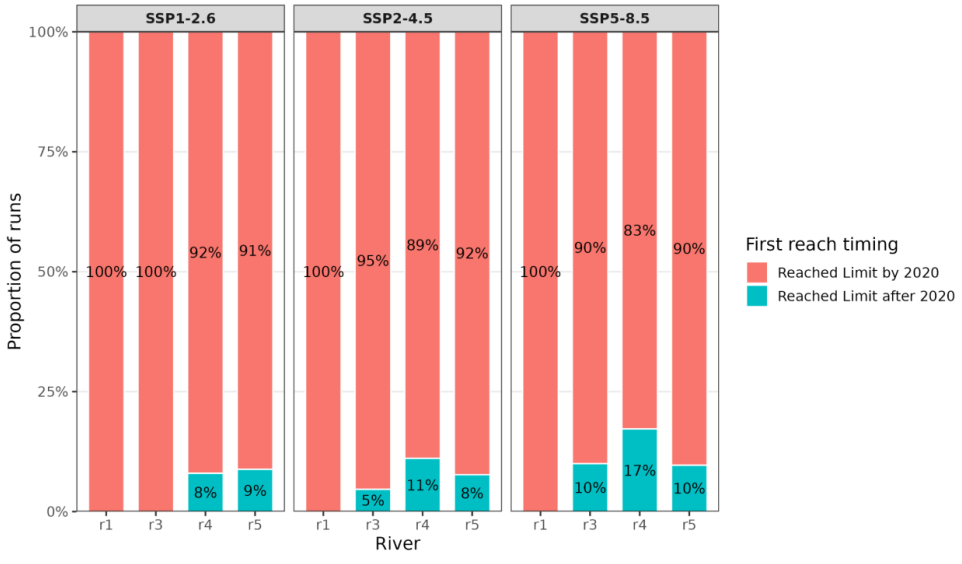

Figure 7. Timing of first reaching the predefined upper limit among simulation runs that reached the limit at least once. Bars show the proportion of runs within each river corridor and future scenario, separated into runs that first reached the limit by 2020 and runs that first reached it after 2020. Percentages within each river and scenario sum to 100% among runs that ever

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reached the limit. River codes indicate r1 = Dadu River, r3 = Lancang River, r4 = Nu River, and r5 = Yalong River.

An additional result is that, even when potential invasions occurred, they usually took place early rather than being newly generated under future scenarios (Fig. 7). Among runs that ever reached the upper limit, the first attainment occurred predominantly before 2020 in all rivers and scenarios. Reaching the limit for the first time after 2020 remained rare and generally accounted for only a small fraction of runs. This indicates that future climate forcing more often modified or extended an already established invasion tendency than initiated a completely new one. Current ecotone structure and pre-existing demographic conditions can strongly shape how treelines respond to subsequent warming (Camarero et al., 2017), which may explain why scenario effects were secondary to the broader contrast between corridors that already had the potential to reach the limit and those that remained constrained throughout the simulation.

These results have direct implications for alpine habitat loss, but the implication is not a simple uniform loss across all river corridors. Climate based projections from European mountains suggest that alpine tundra climate space may contract substantially under future warming, with stronger losses under higher warming levels (Barredo et al., 2020). Our results point in a similar general direction, but they also suggest that habitat loss in the Hengduan Mountains is likely to be uneven. Corridors with higher invasion potential may face greater pressure from forest expansion into the treeline tundra ecotone, whereas corridors with weak or incomplete advance may retain more alpine habitat within the simulated period. Therefore, future alpine habitat vulnerability in this region should be interpreted as spatially heterogeneous and corridor specific, rather than as a uniform consequence of regional warming.

5 Conclusions

This study modified and used the spatially explicit individual based model LAVESI to examine how treeline dynamics respond to historical and future climate forcing along major river corridors in the Hengduan Mountains. The results showed that treeline dynamics were already detectable during the historical period, but their magnitude and timing differed strongly among rivers. Lateral advance remained limited before 2020 in most systems, with the Dadu River showing only weak boundary displacement, the Yalong River showing an intermediate response, and the Lancang and Nu rivers showing the clearest cumulative advance. In elevational terms, the Lancang River displayed the strongest historical upward shift, whereas the Nu River remained nearly stable. These results indicate that historical to modern treeline change along river corridors was gradual rather than abrupt, and that ecological processes and local environmental settings strongly mediated how climate forcing was translated into boundary movement.

The future simulations showed that river specific migration trajectories will diverge more strongly after 2020 under different climate change scenarios. In most rivers, lateral advance accelerated during the future period, with SSP2-4.5 generally producing relatively high cumulative expansion. The Lancang River and Nu River showed the greatest future lateral advance, whereas the Dadu River remained comparatively stable and the Yalong River combined substantial advance with substantial retreat, indicating boundary reorganization rather than simple one directional expansion. Elevational change followed a related but not identical pattern: the Lancang River maintained the strongest upward shift under all scenarios, the Dadu and Yalong rivers showed moderate increases,

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and the Nu River remained the least responsive, with only weak changes and a slight negative trend under SSP1-2.6. Thus, future treeline migration in the Hengduan Mountains is unlikely to follow a single regional pattern, but will instead depend strongly on river specific ecological and topographic settings.

Furthermore, these findings suggest that future treeline advance in the Hengduan Mountains is likely to be uneven across river corridors. The Lancang River showed a relatively strong and sustained response in both lateral and elevational dimensions, indicating a higher potential for forest expansion into the treeline tundra ecotone. In contrast, the Dadu River and especially the Nu River in elevational terms showed more constrained responses. Alpine habitat loss is therefore unlikely to occur evenly across the region. The greatest vulnerability may occur where lateral expansion is strong, upslope movement is sustained, and simulated treeline advance approaches the available treeline tundra ecotone. In general, alpine habitat vulnerability should be evaluated at the corridor scale rather than inferred from a single regional treeline response.

Appendix A

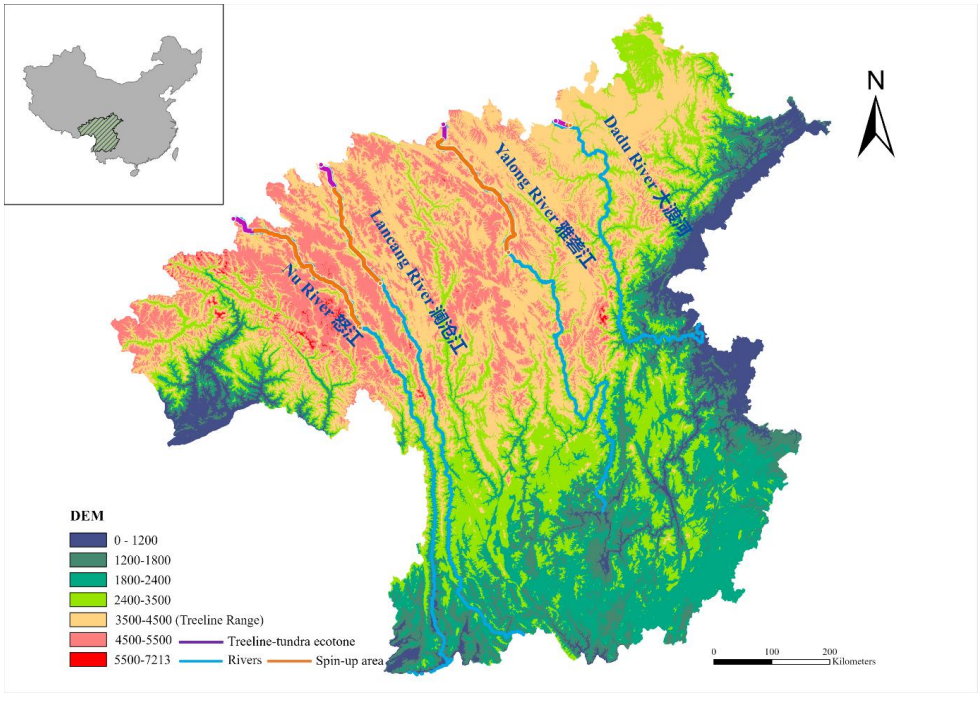

Figure A1. Digital elevation model of the study area showing elevation zones, the treeline range, and major river systems. The simulated area along river systems was marked with orange and purple line, which represents spin-up area and treeline-tundra ecotone respectively.

Code and Data availability

The source code of host model is publicly available from github https://github.com/StefanKruse/LAVESI. The updated version created in this study will receive a tag and final publication at Zenodo after acceptance of the

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manuscript for publication (current commit https://github.com/StefanKruse/LAVESI/tree/dd10208a9923b0310e5b8a9210951132de01ce23).

Supplement link

Check the file link.

Author contributions

LW: Conceptualisation; methodology; software; validation; formal analysis; investigation; resources; data curation; writing original draft; writing review & editing; visualisation. SK: Conceptualisation; methodology; software; validation; formal analysis; investigation; resources; data curation; writing review & editing; supervision; project administration; funding acquisition. JN: Writing review & editing; supervision. XC: Writing review & editing.

Competing interests

The contact author has declared that none of the authors has any competing interests.

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