

Responses to Reviewers

Reviewer 1

General comments

This manuscript extends the spatially explicit individual-based model LAVESI to four major river corridors in the Hengduan Mountains and examines historical and future treeline dynamics using field observations, tree-ring records, multispecies parameterization, and replicate simulations. The distinction between along-corridor displacement and elevational change is potentially useful, and the study represents a substantial modelling and data-collection effort. However, the current design does not yet clearly separate the effects of river-corridor characteristics from those of initialization, model calibration, domain geometry, and climate forcing. Several central interpretations, particularly the claim that river corridors modulate treeline migration and the proposed explanation for the stronger response under SSP2-4.5, therefore require additional support or more cautious framing.

1. The four transects have very different spin-up lengths, whereas seedintro_maxy is fixed at 5000 m in all simulations. Direct seed introduction therefore covers the entire Dadu spin-up zone but only approximately 1.7–2.5% of the other three zones. The long spin-up period and permanent background seed rain may reduce this discrepancy, but the manuscript does not clarify whether the permanent seed input is also restricted by seedintro_maxy, nor does it demonstrate that all four transects had reached comparable equilibrium states by 1940. A simple pre-1940 stability diagnostic is needed; otherwise, the comparison between Dadu and the other rivers should be interpreted more cautiously.

Response:

We thank the reviewer for raising this point. We agree that the distinction between the spin-up section and the seed-introduction zone was not sufficiently clear in the first version of the manuscript.

The parameter seedintro_maxy = 5000 m defines a fixed 5-km seed-introduction zone and was applied consistently across all four river transects. It was not defined as a fixed proportion of the spin-up section. Inspection of the model implementation confirmed that continued external seed input uses the same spatial bounds. Thus, external seed input does not occur uniformly throughout the full simulation domain. Beyond the 5-km seed-introduction zone, population expansion results from seed production by established individuals, wind-driven seed dispersal, establishment, growth, and mortality within LAVESI.

We agree that the duration of the spin-up period alone does not demonstrate that initialization effects had disappeared by 1940. We will therefore add a simple pre-1940 stability diagnostic by examining the behaviour of simulated treeline position during the final part of the spin-up period. The purpose is not to demonstrate identical equilibrium states among the four river transects, which differ substantially in environmental conditions and

simulation-domain length, but to assess whether persistent directional drift remained immediately before the start of the analysed period.

We also agree that the shorter simulation domain of the Dadu transect requires particular caution in cross-river comparisons. We will therefore reduce the emphasis placed on direct comparisons involving Dadu in the main text and provide the corresponding Dadu-specific results and boundary-related diagnostics in the Supplementary Material. The interpretation will be revised accordingly so that differences involving Dadu are not attributed solely to ecological processes when they may also reflect simulation-domain configuration.

2. The authors initially compare simulations with plots 401–472, but the final elevation offset of 900 m is selected using the single best-performing reference plot, plot 404, and then applied to all four river systems. Because this parameter compensates for differences between coarse-resolution climate forcing and local mountain climate, its transferability across climatically and topographically distinct river corridors requires validation. The manuscript should report model performance across the full plot dataset and demonstrate that the main inter-river patterns are not highly sensitive to the chosen offset.

Response:

We thank the reviewer for raising the issue of transferability of the elevation correction. In the preliminary calibration, simulations were compared with field observations for plots 401–472 using plot-specific climate and topographic inputs. After excluding records for which both July temperature and annual precipitation were zero, 57 plots were retained. Six preliminary elevation offsets (0, -200, -400, -600, -800, and -1000 m) were evaluated by comparing simulated maximum tree height with field-recorded height, together with the observed vegetation type.

Plot 404 was selected as the reference for finer calibration because it showed both close agreement with the field observation and relatively stable behaviour across offsets and simulation batches (Fig. R1). Its observed maximum tree height was 18 m, whereas the three simulation batches at -800 m produced maximum heights of 18.792, 16.961, and 20.561 m. Among plots 404, 405, and 406, for which a complete common evaluation grid was available across all six offsets and three batches, plot 404 had the lowest mean relative absolute height error across the tested offset range (27.62%) and the lowest relative between-batch variability (41.49%). A leave-one-batch-out evaluation further showed that all three splits selected -800 m for plot 404, with a mean held-out relative error of 8.13%. We subsequently refined the calibration for plot 404 from -1000 to +1000 m in 50 m increments, which identified -900 m as the setting providing the closest agreement with the field observation.

We agree, however, that these analyses justify the selection of the calibration reference but do not by themselves demonstrate that the same elevation correction is equally transferable across the four river transects. We will therefore revise the manuscript to distinguish more clearly between calibration and spatial validation. The revised Supplementary Material will present the comparisons across the available field plots and the associated calibration diagnostics.

In addition, we will conduct a limited sensitivity analysis around the selected -900 m correction to assess whether the principal inter-river and SSP patterns depend strongly on this choice. Simulations using neighbouring elevation-offset settings will be compared with the baseline -900 m simulations, focusing on the direction and magnitude of treeline advance and on whether the main relative patterns among river transects and SSP scenarios are retained.

We will also clarify in the Discussion that the -900 m value represents a common regional correction applied to all river transects, rather than a river-specific calibration, and that uncertainty in its transferability should be considered when interpreting absolute differences among transects.

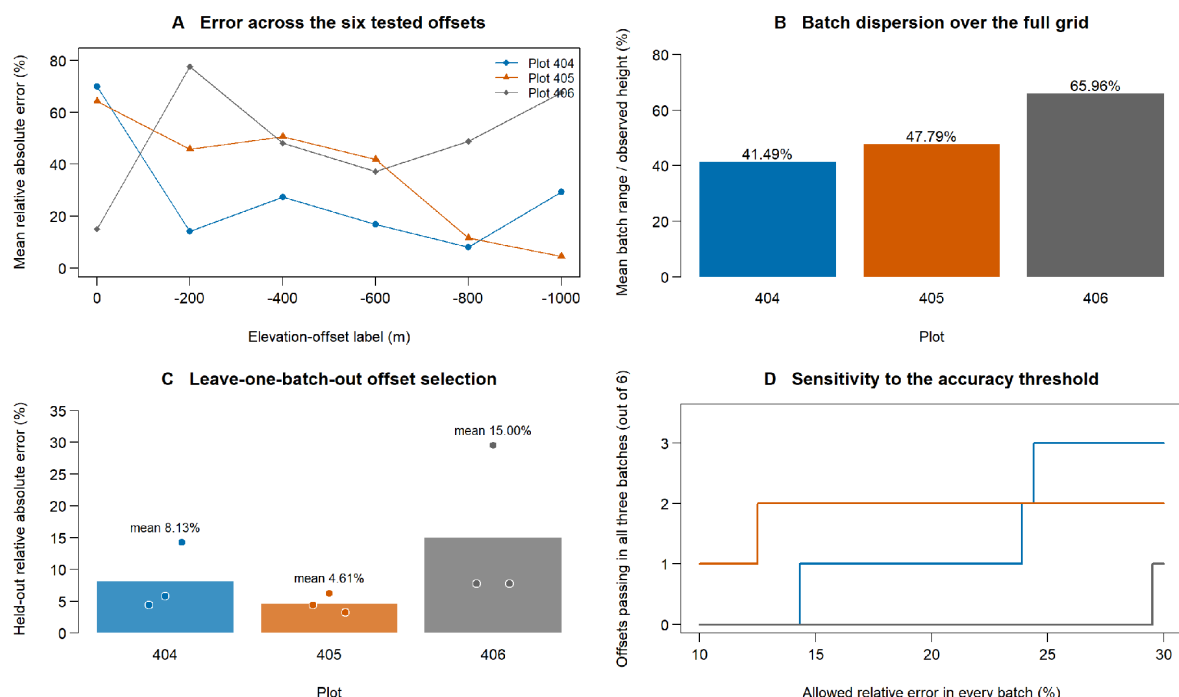


Figure R1. Calibration for selected fitted plots 404, 405 and 406, each with six offsets and three evaluable result batches. Relative absolute error is equal to $|\text{simulated height} - \text{observed height}| / \text{observed height}$.

3. The finding that SSP2-4.5 often produces greater cumulative advance than SSP5-8.5 is potentially important. The discussion already offers plausible explanations involving local environmental constraints, species-specific climatic suitability, and nonlinear responses to warming. However, these explanations remain inferential. Because LAVESI explicitly represents growth, establishment, competition, and mortality, a limited process-level analysis should be used to determine whether the weaker response under SSP5-8.5 is actually associated with reduced growth or establishment, increased drought stress, or greater mortality. Otherwise, these explanations should be presented explicitly as hypotheses.

Response:

We thank the reviewer for this suggestion. We agree that the mechanisms underlying the cumulative treeline advance under SSP5-8.5 should be examined more directly. Because each LAVESI simulation is computationally intensive, repeating the complete simulation ensemble with additional process-level output would not be feasible. Instead, we will rerun a limited number of representative simulations under SSP2-4.5 and SSP5-8.5 and examine relevant model processes, particularly establishment, growth, and mortality, together with moisture-related limitation where the corresponding model output is available near the advancing treeline.

This analysis is intended to provide a qualitative assessment of whether the contrasting cumulative advance under the two scenarios is consistent with reduced establishment or growth and/or increased mortality under stronger warming, rather than a full quantitative attribution of the mechanism. Where the process-level results do not clearly support a particular mechanism, we will revise the Discussion to present the proposed explanations explicitly as hypotheses rather than as demonstrated causal mechanisms.

4. The current experimental design does not isolate a river-corridor effect. All simulations are conducted within narrow domains extending only 30 m on either side of the river centreline, and seeds leaving one lateral boundary are reintroduced from the opposite side. This geometry constrains long-distance movement primarily along the transect. In addition, there is no non-river control, such as a ridge or non-valley slope, and hydrological dispersal, flooding, and riparian disturbance are not explicitly represented. River-specific topography, climate, wind forcing, simulation length, and spin-up length also vary simultaneously. The results therefore demonstrate heterogeneous dynamics among four river-aligned transects, but do not by themselves show that river corridors enhance or modulate treeline migration relative to non-river landscapes. The causal language in the title, abstract, and conclusions should either be supported by an appropriate control or moderated accordingly.

Response:

We thank the reviewer for this important clarification. We agree that the current experimental design does not isolate a causal river corridor effect relative to non-river landscapes.

Our aim was to simulate treeline dynamics along river-valley transects in the Hengduan Mountains, rather than to represent river hydrology explicitly or to test whether rivers themselves enhance treeline migration. The river valleys were used to define the spatial framework of the simulation domains, while hydrological seed dispersal, flooding, and riparian disturbance were not represented in LAVESI.

We recognise that some wording in the title, Introduction, Discussion, and Conclusions could nevertheless be interpreted as implying that river corridors themselves were demonstrated to promote or modulate treeline migration. We will therefore revise these sections to distinguish more clearly between treeline dynamics simulated along river-valley transects and causal effects attributable to rivers. In particular, statements implying that river corridors enhance migration will be replaced by descriptive language referring to differences in treeline dynamics among the four river-valley transects.

We will also explicitly acknowledge that topography, climate forcing, wind forcing, simulation-domain length, and other environmental characteristics vary among transects and

that no non-river control was included. The present simulations therefore cannot separate a specific river corridor effect from these covarying factors.

5. Future temperature and precipitation are taken from a single climate model, MPI-ESM1.2-LR. The simulations therefore represent differences among SSPs under one model realization, but do not account for structural uncertainty among climate models. This is particularly relevant because the non-monotonic ordering of SSP2-4.5 and SSP5-8.5 may depend on the regional temperature–precipitation response of the selected model. The authors should justify the choice of MPI-ESM1.2-LR and make clear that the projections are conditional on this forcing. If a multimodel sensitivity analysis is not feasible, the potential model dependence of the scenario ranking should at least be discussed.

Response:

We thank the reviewer for highlighting this source of uncertainty. Future temperature and precipitation forcing in the present simulations was based on MPI-ESM1-2-LR under SSP1-2.6, SSP2-4.5, and SSP5-8.5. MPI-ESM1-2-LR was used because its future temperature and precipitation data for the three SSP scenarios were already available. We will clarify this in the Methods and state explicitly that the projected treeline responses are conditional on this forcing.

To place this forcing in a broader climate-model context, we added a supplementary comparison of projected temperature and precipitation changes at the median simulated lateral treeline position from DEM in 2020 along the four river transects (Table. R1). Mean near-surface air temperature was compared using monthly CMIP6 tas from MPI-ESM1-2-LR and 23 other models. Annual precipitation change was compared using downscaled CMIP6 precipitation data from WorldClim v2.1 for MPI-ESM1-2-LR and 22 other models. The temperature comparison used each model's own 1970–2000 historical baseline, whereas the precipitation comparison used the WorldClim 1970–2000 baseline.

These comparisons show that, at the assessed locations, MPI-ESM1-2-LR generally lies toward the lower-warming and lower-precipitation-change part of the compared model sets (Fig. R2). In the tas comparison, MPI projected smaller warming than the median of the other models in all evaluated river-scenario period combinations. In the precipitation comparison, MPI also showed smaller changes than the median of the other models across the evaluated combinations. Lower precipitation change here generally indicates a smaller increase relative to the historical baseline, rather than a decrease in precipitation in every case.

This additional comparison helps to place MPI-ESM1-2-LR projections in a broader climate-model context, but it does not constitute a multi-GCM LAVESI sensitivity analysis and does not demonstrate that the simulated treeline responses or the SSP ranking are robust to climate-model choice. We will therefore revise the Discussion to make clear that the non-monotonic scenario response, including the greater cumulative advance observed in some cases under SSP2-4.5 than under SSP5-8.5, remains conditional on the temperature and precipitation trajectories represented by MPI-ESM1-2-LR.

River	Longitude(°)	Latitude(°)
Dadu	100.437785	33.554595
Lancang	94.580125	33.791018
Nujiang	91.551988	31.814634
Yalong	97.590275	34.036313

Table R1. Reference treeline position for each river

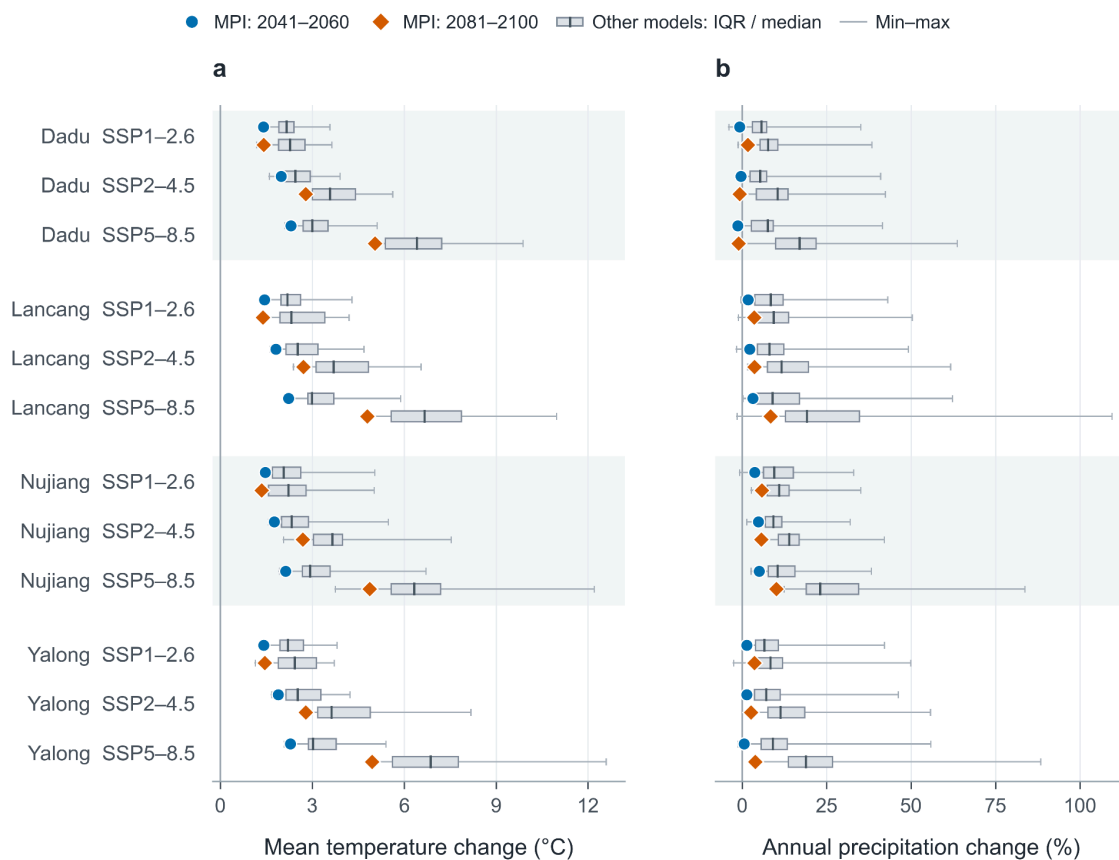


Figure R2. Projected changes in (a) annual mean near-surface temperature (tas) and (b) annual precipitation relative to 1970–2000 at four candidate river reference locations under

the forward DEM interpretation. Symbols indicate MPI-ESM1-2-LR; grey boxes, central ticks and whiskers represent other models' interquartile ranges, medians and full ranges. Temperature comparisons use 23 other CMIP6 models on their respective archive grids and historical baselines; precipitation comparisons use 22 other models on the WorldClim 10' grid and baseline.

6. Future wind fields are generated by resampling historical winds from 1940–2020. The manuscript explains that this was done to avoid the lower spatial resolution of future wind data, but the resulting stationarity assumption is not discussed. Because wind speed and direction directly determine seed dispersal, the authors should clarify whether the resampling preserves seasonality, the joint distribution of wind speed and direction, and temporal persistence. It should also be stated whether the three SSPs use identical or statistically equivalent wind forcing.

Response:

We thank the reviewer for raising this point. We rechecked the procedure used to generate the future wind forcing and have clarified it in the revised Methods. Future wind data were generated by annual block resampling from the available historical wind record. For each target year outside the reference set, one complete reference year was selected at random and the entire annual wind data file was copied to the target year. Wind speed and wind direction were therefore not sampled independently, nor were individual months, days, or time steps resampled separately.

This procedure preserves the within-year seasonal structure, the joint temporal pairing of wind speed and direction, and the temporal persistence contained within each sampled annual sequence. However, because reference years were sampled independently for different target years and the same reference year could be selected more than once, interannual temporal persistence and long-term trends in wind climate were not explicitly preserved. The same resampled wind series was used for SSP1-2.6, SSP2-4.5, and SSP5-8.5, so the comparison was not affected by differences in prescribed wind forcing among scenarios.

The simulations therefore do not represent systematic future changes in wind climate, it is only a conservative estimate.

7. The supplementary material substantially improves the transparency of the multispecies parameterization by providing parameter values and tree-ring data sources. Nevertheless, several missing parameters are transferred from congeners as "educated guesses, and many demographic parameters are shared across species. The manuscript should briefly explain the most important parameter transfers and discuss whether uncertainty in dispersal, establishment, drought sensitivity, and mortality parameters could affect the relative results among rivers. A full new parameter table is not required, but the consequences of parameter sharing should be acknowledged.

Response:

We thank the reviewer for highlighting the need to clarify the basis and implications of parameter transfer and sharing. Our multispecies parameterization combines field measurements of tree height and stem diameter from the Hengduan Mountains, ITRDB tree-ring records, plant-trait databases, floristic information, and other published sources. Species-specific information remains incomplete for several regional conifers. Missing parameter values were therefore supplemented using congeneric proxies where appropriate, based on similarities in ecological characteristics and life-history traits.

Two aspects of this approach should be distinguished. Some parameters are shared within genera, including height–diameter coefficients among *Picea* species and among *Pinus* species in Table S1. Several demographic coefficients governing seed production, background germination, and components of mortality are also shared across species as common modelling assumptions. These coexist with species-specific parameters such as seed terminal velocity and climatic and soil-water thresholds.

We acknowledge that uncertainty in these parameters may influence seed arrival, establishment, growth, and survival and therefore the rate and extent of simulated treeline advance. Sensitivity analyses by Haupt et al. (2025) identified important, site-dependent responses to factors including seedbed availability, seedling establishment, reproductive maturation, and wind-mediated seed dispersal. In our study, applying the same parameter settings across the four river transects provides a consistent modelling framework, but parameter effects may differ under the contrasting environmental conditions of each transect. Parameter transfer and sharing will therefore be acknowledged explicitly when interpreting the magnitude and relative differences of simulated treeline responses among transects.

Future parameterization will prioritise direct species-specific estimates for parameters currently represented by congeneric proxies or shared values.

Reviewer 2

General comments

This study applies the spatially explicit individual-based model LAVESI to simulate treeline dynamics along four major river corridors (Dadu, Lancang, Nu, Yalong) in the Hengduan Mountains over the historical period (1940–2020) and future scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5, 2020–2100). Treeline changes are decomposed into lateral (along-corridor) and elevational dimensions, revealing strong heterogeneity among river systems. Key findings include: slow but river-specific historical shifts; stronger lateral advance under SSP2-4.5 than SSP5-8.5 in some rivers; decoupling between lateral and elevational changes; limited invasion potential in most corridors; and spatially uneven alpine habitat loss. The paper highlights the critical role of river corridor topography in modulating treeline responses.

Major Issues

1. The definition of lateral treeline relies on arbitrary thresholds (>1000 individuals, 100 m window, ≥100 m continuous segment). No sensitivity analysis is performed.

Changing these thresholds could alter the magnitude or even ranking of lateral shifts among rivers. Justification for threshold choices should be added.

Response:

We thank the reviewer for requesting clarification of these criteria. Our approach aims to identify a representative lateral treeline position supported by the population of treeline species. This is done via applying a systematic, literature-informed assessment of treeline position to ensure that the modelling results are interpretable and comparable across the study. Previous applications of LAVESI used stand-density criteria to derive treeline and forestline positions from simulated populations (Kruse and Herzsich, 2022). In the present study, the >1,000-individual threshold serves as an annual species-inclusion criterion within each simulation domain. It therefore serves as an annual abundance criterion, restricting the analysis to population states with sufficient numerical representation to assess the species' potential contribution to the treeline.

The sliding-window criterion defines the spatial expression of this population boundary: local abundance must meet the specified threshold at 100 consecutive window-start positions spaced 1 m apart. This provides an operational definition of a lateral treeline position supported by local abundance across neighbouring window positions. The approach is conceptually motivated by the identification of treeline from the uppermost tree groups (Körner, 2007; Mainali et al., 2020) and by our field observations.

The annual abundance criterion and the consecutive-window criterion therefore serve complementary purposes: the former determines which population states are included in the analysis, whereas the latter determines the spatial support required to identify the lateral treeline position. To assess sensitivity to spatial scale, we will compare 50 m and 150 m windows with corresponding minimum counts of 50 and 150 individuals, maintaining the same abundance threshold per unit distance along the longitudinal transect axis.

2. Calibration relies on a single plot (plot 404) by tuning elevation offset. Given the strong environmental heterogeneity across the Hengduan Mountains, one plot cannot represent all four river corridors. Cross-validation with at least one plot per river or reporting fit statistics for other plots, is recommended.

Response:

We thank the reviewer for raising this concern. We selected plot 404 as the reference for further calibration based on comparisons between simulated vegetation and field observations across preliminary elevation-offset settings. These comparisons and the additional quantitative analyses described below provide the basis for this choice.

The preliminary comparison covered 72 plots from 401 to 472, using the climate and topographic inputs corresponding to each plot. We compared simulated maximum tree height with field-recorded height and considered the observed vegetation type (forest, shrubland, or meadow) alongside these height comparisons. The comparison included six preliminary elevation-offset settings: 0, -200, -400, -600, -800, and -1000 m. The retained dataset comprised 57 plots after excluding records for which both July temperature and annual precipitation were zero.

Plot 404 was selected from these preliminary comparisons. Its field-recorded maximum tree height was 18 m. At an elevation offset of -800 m, the three simulation batches produced maximum tree heights of 18.792, 16.961, and 20.561 m. Figure R3 shows the simulated height response of plot 404 across the six preliminary elevation-offset settings relative to the observed height. These comparisons provided the initial empirical basis for selecting plot 404 as the calibration reference.

To quantify performance across elevation-offset settings and simulation batches, we added a comparison using a common evaluation grid. Plots 404, 405, and 406 had complete evaluable records for all six offsets and three batches. Across this grid, plot 404 had the lowest mean relative absolute height error: 27.62%, compared with 36.49% for plot 405 and 49.07% for plot 406. It also had the smallest mean relative height range across batches: 41.49%, compared with 47.79% and 65.96%, respectively. These results support the selection of plot 404 based on its performance across the tested elevation-offset range and its consistency across simulation batches.

We also conducted a leave-one-batch-out evaluation, in which two simulation batches were used to select the elevation offset and the remaining batch was used for evaluation. All three splits selected -800 m for plot 404. The held-out relative errors were 4.40%, 5.77%, and 14.23%, giving a mean of 8.13%. The corresponding mean errors were 4.61% for plot 405 and 15.00% for plot 406. This evaluation distinguishes performance across the full elevation-offset range from accuracy after offset selection; it does not establish plot 404 as the best-performing plot under every metric.

After selecting plot 404, we refined the elevation-offset calibration from -1000 to +1000 m in 50 m increments. Comparison with field observations identified -900 m as the setting providing the closest agreement, and we adopted this value for subsequent simulations. This finer scan refined the calibration beyond the 200 m spacing used in the preliminary comparisons. These analyses document the selection of the calibration reference and elevation offset; they do not constitute independent spatial validation across the four river transects.

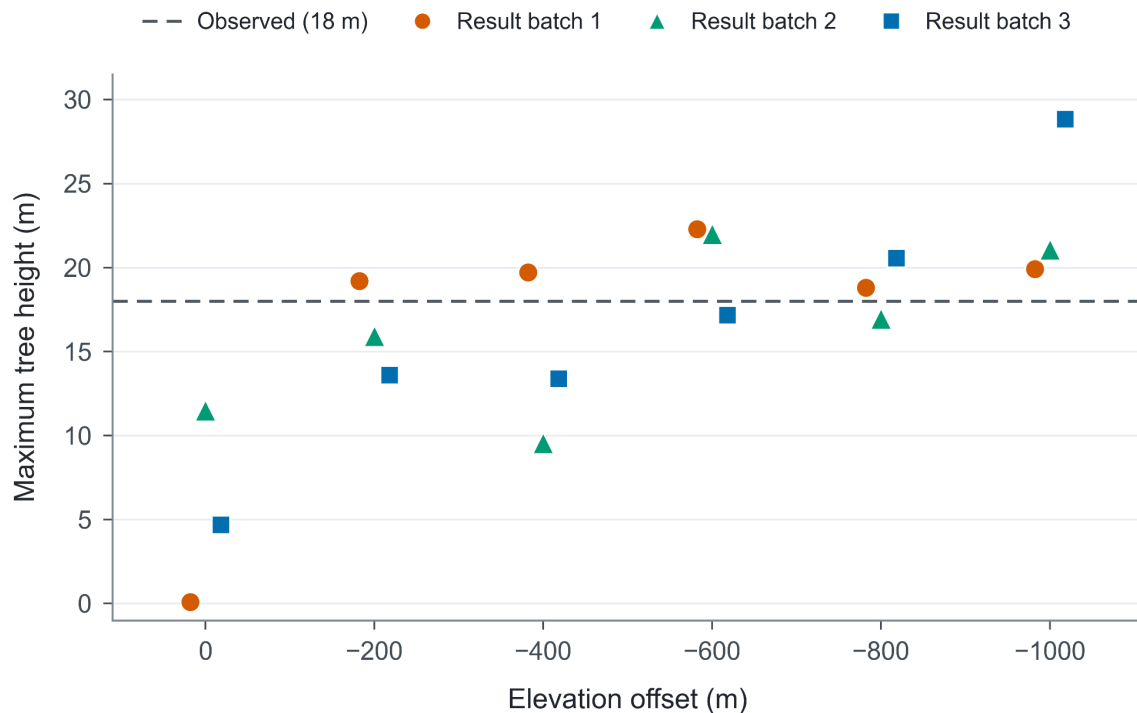


Figure R3. Maximum simulated tree height for plot 404 at the six preliminary elevation-offset settings. The grey dot line indicates the 18 meters tree height.

3. Dadu River's total simulation length is only 25 km, while others exceed 250 km. Dadu's frequent limit-reaching likely reflects its short domain rather than high invasion potential. Although noted in Discussion, no standardization is applied in Results. Comparison using proportion (advance/total available length) would be fairer.

Response:

We thank the reviewer for highlighting this important limitation. We agree that the substantially shorter simulation domain for Dadu may truncate simulated treeline advance and complicate direct comparisons among the four river transects. We therefore plan to move the detailed Dadu results to the Supplementary Material and clarify the limitations associated with its shorter simulation domain. We also recognise that expressing treeline advance relative to the available forward distance could provide a useful complementary comparison.

Minor Issues

1. The term "lateral treeline shift" is used frequently from the Abstract onward, but the Introduction provides only ecological context without an operational definition. Readers must wait until Section 2.4.3. A brief definition at the end of the Introduction would improve clarity.

Response:

We thank the reviewer for this suggestion. We will add a brief operational definition of 'lateral treeline shift' at the end of the Introduction so that the metric is clear before its detailed description in Section 2.4.3.

2. To elevate the study from a descriptive modelling exercise to a mechanistically grounded analysis, I strongly recommend that the authors incorporate highly relevant empirical studies on critical thresholds for xylogenesis on the Tibetan Plateau, such as Li et al. (2017), Science Bulletin 62: 804–812 and Ren et al. (2018), Annals of Botany 121: 617–624.

Response:

We thank the reviewer for recommending these studies. We will incorporate the empirical studies on xylogenesis thresholds by Li et al. (2017) and Ren et al. (2018) to strengthen the physiological background and to place the simulated treeline responses in a more appropriate physiological context.

3. The caption in Figure 5 states that fitted lines are visual summaries, but the main text (lines 427–428) describes coupling strength qualitatively (“strongest positive coupling in Lancang”, “almost no elevational response in Nu”), which may imply statistical significance. Correlation coefficients or p-values should be provided, or language softened.

Response:

We thank the reviewer for identifying this inconsistency. We will soften the wording in the main text and report statistical results only where formal statistical comparisons are performed. We will also ensure that the interpretation is consistent with the caption of Figure 5 and that visual differences among fitted lines are not presented as statistically supported differences in coupling strength.

References

- Haupt, S., Gloy, J., Farkas, L., Schildt, K., Trimborn, L., and Kruse, S.: The significant role of snow in shaping alpine treeline responses in modelled boreal forests, *Biogeosciences*, 22, 6811–6839, <https://doi.org/10.5194/bg-22-6811-2025>, 2025.
- Körner, C.: Climatic treelines: conventions, global patterns, causes, *Erdkunde*, 61, 316–324, <https://doi.org/10.3112/erdkunde.2007.04.02>, 2007.
- Li, X., Liang, E., Gričar, J., Rossi, S., Čufar, K., and Ellison, A. M.: Critical minimum temperature limits xylogenesis and maintains treelines on the southeastern Tibetan Plateau, *Sci. Bull.*, 62, 804–812, <https://doi.org/10.1016/j.scib.2017.04.025>, 2017.
- Mainali, K., Shrestha, B. B., Sharma, R. K., Adhikari, A., Gurarie, E., Singer, M., and Parmesan, C.: Contrasting responses to climate change at Himalayan treelines revealed by population demographics of two dominant species, *Ecol. Evol.*, 10, 1209–1222, <https://doi.org/10.1002/ece3.5968>, 2020.

Ren, P., Rossi, S., Camarero, J. J., Ellison, A. M., Liang, E., and Peñuelas, J.: Critical temperature and precipitation thresholds for the onset of xylogenesis of *Juniperus przewalskii* in a semi-arid area of the north-eastern Tibetan Plateau, *Ann. Bot.*, 121, 617–624, <https://doi.org/10.1093/aob/mcx188>, 2018.

Kruse, S. and Herzsuh, U.: Regional opportunities for tundra conservation in the next 1000 years *eLife* 11:e75163, <https://doi.org/10.7554/eLife.75163>, 2022.