Peer Community In
Ecology

Forest microclimate in mountains and its impact on plant community: Still a question of shade, but this time it's not coming from the canopy

Romain Bertrand *based on peer reviews by* ***Martin Macek*** *and 2 anonymous reviewers*

Jeremy Borderieux, Emiel De Lombaerde, Karen De Pauw, Pieter Sanczuk, Pieter Vangansbeke, Thomas Vanneste, Pieter De Frenne, Jean-Claude Gégout, Josep M. Serra-Diaz (2024) Cool topoclimates promote cold-adapted plant diversity in temperate mountain forests. ecoevorxiv, ver. 3, peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.32942/X2XC8T

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Recently, microclimate has gained significant momentum1, as evidenced by the increasing number of studies and the emergence of a dedicated scientific community coordinating research efforts2. Several factors underpin this trend, including advances in technology that have made microclimate monitoring3 and ecological contextualization4 more accessible, as well as improvements in computational methods that facilitate modeling at unprecedented scales5. But the growing emphasis on microclimate is primarily driven by their ecological relevance, as microclimate represent the actual climate conditions experienced by organisms1. This makes them more suitable than macroclimate data for understanding and predicting biodiversity responses to climate change6. While macroclimate data remain a common tool in ecology, they often represent generalized climatic conditions over large spatial scales. These data are typically derived from statistical models calibrated on observations collected at meteorological stations7, which are usually located at 2 meters above the ground in open areas and at elevations compatible with human activities. Such characteristics limit the applicability of macroclimate data for understanding biodiversity responses, particularly at finer spatial scales.

This is especially true in forest ecosystems, where microclimate results from the filtering of macroclimate conditions by forest habitats8. A simple walk in a forest during summer highlights this filtering, with the cooling effect of canopy shading and tree packing being clearly perceptible. If humans can sense these variations, they likely influence forest biodiversity. In fact, microclimates are crucial for defining the thermal niches of understory plant species9 and understanding plant community reshuffling in response to climate warming10. In mountainous areas, topography adds further complexity to microclimates. The drop in temperature with elevation, known as the elevation-temperature lapse rate, is familiar, but topography also drives fine-scale variations11. Solar radiation hitting forest varies with aspect and hillshade, creating localized temperature differences. For example, equator-facing slopes receive more sunlight, while west-facing slopes are sunlit during the warmest part of the day. Consequently, in the northern hemisphere, southwest-facing slopes generally exhibit warmer temperatures, longer growing seasons, and shorter snow cover durations12. Thus, both topography and forest canopy shape the understory microclimate experienced by organisms in temperate mountainous forests.

Is biodiversity more influenced by topography- or canopy-induced temperature buffering? While this question may not seem particularly interesting at first glance, understanding the underlying mechanisms of microclimate is crucial for guiding biodiversity conservation decisions in the face of climate change13. Poleward-facing slopes, valley bottoms, and dense canopies buffer warm episodes by creating cooler, more humid habitats that can serve as refugia for biodiversity12. Both buffering processes are valuable for conservation, but topography-induced buffering is generally more stable over the long term14. In contrast, canopy buffering is more vulnerable to human management, disturbances, and the ongoing acceleration of climate change, which is expected to drive tree mortality and lead to canopy opening15. Identifying the dominant buffering process in a given area is essential for mapping biodiversity refugia and fully integrating microclimate into conservation strategies. This approach can improve decision-making and actions aimed at promoting biodiversity sustainability in a warming world.

The work of Borderieux and colleagues16 offers new insights into this question through an innovative approach. They focus on temperate forests in a watershed in the Vosges Mountains, where they monitor understory temperature and inventory forest plant communities in separate samplings. Aiming to disentangle the effects of topography and forest canopy on understory temperature and its impact on plant communities, the authors deployed a network of temperature sensors using stratified sampling, balanced according to topography (elevation, aspect, and slope) and canopy cover. They then correlated mean annual temperatures (daily mean and maximum) with topographic factors and canopy cover, considering their potential interactions in a linear model. The contribution of each microclimate component was computed, and their effects on temperatures were mapped. These predictions were then confronted to floristic inventories to test whether topography- and canopy-induced temperature variations explained plant diversity and assemblages.

First, the authors demonstrated that local topographic variations, which determine the amount of solar radiation reaching forests in mountainous areas, outweigh the contribution of canopy shading to understory temperatures. This result is surprising, as many previous studies have emphasized the importance of canopy buffering in shaping forest microclimate conditions8. However, these studies mostly focused on lowland areas or large scales, where terrain roughness has less influence. It is also unexpected because the authors observed that canopy cover varies at a smaller scale than aspect or topographic position in their study area, creating habitat heterogeneity that could reasonably drive local temperature variations. Nevertheless, the authors found that aspect, heat load, and topographic position induced more variation in microclimate than canopy filtering, significantly allowing deviations from the expected elevation-temperature lapse rate. Second, the topographic effect on understory temperature propagated to biodiversity. The authors found that topography-induced temperature offset explained plant diversity and composition, while canopy-induced temperature offset did not. Specifically, cold topoclimates harbored 30% more species than the average species richness across the inventoried plots. This increase in species richness was primarily due to an increase in cold-adapted species, highlighting the role of cold topoclimates as refugia.

It is difficult to assess the extent to which these results are influenced by the specific forest context of the study area chosen by the authors, as there is no clear consensus in previous research regarding the role of topoclimate. For example, Macek et al. (2019)17 highlighted the predominance of topography in controlling temperature and, consequently, forest community structure in the Czech Republic, while Vandewiele et al. (2023)18 demonstrated the dominance of canopy control in the German Alps. The forest conditions investigated by Borderieux et al. (2025) were narrow, as they focused mainly on closed forests (more than 80% of the study area and sampling sites exhibiting canopy cover greater than 79%). Given that the canopy buffering effect on temperature increases with canopy cover until plateauing at around 80%19, this may explain why the authors did not find a strong contribution from the canopy. Nevertheless, the methodology and case presented in their study are both innovative and applicable to other mountainous regions. The work of Borderieux et al. (2025) deserves attention for highlighting a frequently overlooked component of forest microclimate, as canopy filtering is typically regarded as the dominant driver. Topoclimate is a critical factor to consider when protecting cold-adapted forest species in the context of global warming, especially since topographic features are less subject to change than canopy cover. Future research should aim to test this hypothesis across a broader range of forest and topography conditions to identify general patterns, as well as assess the long-term effectiveness of these topographic refugia for biodiversity. It remains unclear whether the cooling effect provided by topoclimate will be sufficient to stabilize climate conditions despite the expected acceleration of climate warming in the coming decades, and whether it will be able to preserve cold-adapted species, which are among the most unique but threatened components of mountain biodiversity.

References:

1. Kemppinen, J. et al. Microclimate, an important part of ecology and biogeography. Global Ecology and Biogeography 33, e13834 (2024).

2. Lembrechts, J. J. et al. SoilTemp: A global database of near-surface temperature. Global Change Biology 26, 6616–6629 (2020).

3. Wild, J. et al. Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. Agricultural and Forest Meteorology 268, 40–47 (2019).

4. Zellweger, F., Frenne, P. D., Lenoir, J., Rocchini, D. & Coomes, D. Advances in Microclimate Ecology Arising from Remote Sensing. Trends in Ecology & Evolution 34, 327–341 (2019).

5. Haesen, S. et al. ForestTemp – Sub-canopy microclimate temperatures of European forests. Global Change Biology 27, 6307–6319 (2021).

6. Lembrechts, J. J. et al. Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. Global Ecology and Biogeography 28, 1578–1596 (2019).

7. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315 (2017).

8. De Frenne, P. et al. Global buffering of temperatures under forest canopies. Nat Ecol Evol 3, 744–749 (2019).

9. Haesen, S. et al. Microclimate reveals the true thermal niche of forest plant species. Ecology Letters 26, 2043–2055 (2023).

10. Zellweger, F. et al. Forest microclimate dynamics drive plant responses to warming. Science 368, 772–775 (2020).

11. Rolland, C. Spatial and Seasonal Variations of Air Temperature Lapse Rates in Alpine Regions. (2003).

12. Rita, A. et al. Topography modulates near-ground microclimate in the Mediterranean Fagus sylvatica treeline. Sci Rep 11, 1–14 (2021).

13. Bertrand, R., Aubret, F., Grenouillet, G., Ribéron, A. & Blanchet, S. Comment on "Forest microclimate dynamics drive plant responses to warming". Science 370, eabd3850 (2020).

14. Hylander, K., Greiser, C., Christiansen, D. M. & Koelemeijer, I. A. Climate adaptation of biodiversity conservation in managed forest landscapes. Conservation Biology 36, e13847 (2022).

15. McDowell, N. G. & Allen, C. D. Darcy's law predicts widespread forest mortality under climate warming. Nature Clim Change 5, 669–672 (2015).

16. Borderieux, J. et al. Cool topoclimates promote cold-adapted plant diversity in temperate mountain forests. Ecoevorxiv, ver. 3(2024). Peer-reviewed and recommended by PCI Ecology https://doi.org/10.32942/X2XC8T

17. Macek, M., Kopecký, M. & Wild, J. Maximum air temperature controlled by landscape topography affects plant species composition in temperate forests. Landscape Ecol 34, 2541–2556 (2019).

18. Vandewiele, M. et al. Mapping spatial microclimate patterns in mountain forests from LiDAR. Agricultural and Forest Meteorology 341, 109662 (2023).

19. Zellweger, F. et al. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. Global Ecology and Biogeography 28, 1774–1786 (2019).

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.32942/X2XC8T
Version of the preprint: 2

Authors' reply, 19 December 2024

Dear Editor,

Thanks for you last revision and comments. We replied and took them into account, we deleted some minor comments by accident, but added the related changes in yellow.

Thanks again for the revision,

Jeremy Borderieux

Download tracked changes file

Decision by Romain Bertrand, posted 17 December 2024, validated 17 December 2024

Dear Jeremy and co-authors,

I have now finished to read the new version of your manuscript as well as the response to my comments and the one from the three reviewers. Thank you for the hard work!

I feel very happy with the new version. At this point, I have only minor comments (or maybe more suggestions) to improve the clarity of some parts. I try to do this work carefully, so please try to account the most of them during your final revision, but of course feel free to accept or not. I made my comments (and some propositions of text edition) directly in your manuscript that I attached to this message. I don't ask for a point by point response letter to my minor comments. You can directly address my comments in your manuscript only if you feel it's important (some of them don't need any answer).

Your work will not be reviewed by the external referees anymore. When you will submit your revised manuscript, I will read it before to definitely recommend it.

Thank you for submitting to PCI Ecology.

Best regards,

Romain

Download recommender's annotations

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.32942/X2XC8T

Version of the preprint: 1

Authors' reply, 27 November 2024

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Decision by Romain Bertrand, posted 09 August 2024, validated 09 August 2024

Dear Jeremy Borderieux and Co-authors,

Three reviewers and I have now completed the evaluation of your manuscript. We all believe that your work has the potential to make a significant contribution to ecology by enhancing our understanding of how elevation lapse rate, topography, and forest habitat drive local temperatures in mountain forest ecosystems, as well as how these factors influence floristic diversity and the adaptation of plant assemblages to local temperature conditions. However, the referees have raised several concerns that I also share. Below, I list some points that I consider important (this list is not exhaustive, and other comments from the referees should also be addressed):

- The title does not seem appropriate, as your study does not investigate macroclimate.

- Using a linear model to explore the determinants of species richness is not appropriate, as species richness cannot be negative and is likely to follow a Poisson distribution.

- Working on residuals to correct for the bioindicated-pH effect on CTI or species richness, instead of modeling CTI or species richness in a multivariate model that accounts for pH, lapse rate, topoclimate, and habitat, could lead to misleading results. This approach might underestimate the effect of elevation lapse rate, as there is likely a correlation between elevation and bioindicated-pH. Of course, this suggested analysis needs to consider multicollinearity. If multicollinearity is present (which I suspect), you will need to use statistical approaches that are less sensitive to this issue or at least conduct additional analyses to demonstrate that multicollinearity does not challenge your results.

- Is elevation considered part of topoclimate or topography? Based on previous studies, I think the answer is yes. I understand and appreciate your effort to disentangle elevation lapse rates from other topographic factors, as they drive temperature variations at different scales or resolutions. However, the terms "topography" or "topoclimate" do not seem entirely appropriate. Perhaps "physiography" would be a better term.

- "Topoclimate cooling" may not be the most accurate term. In my view, it is more of a topoclimate effect that either cools or warms the local climate depending on local topographic conditions.

In addition to the valuable comments provided by the three reviewers, I have three main concerns:

1. I understand that 348 species were inventoried, but only 30 were associated with a thermal optimum value (STI) and used to compute CTI. Is that correct? If so, this means a significant amount of information is lost, with only 8.6% of the species inventoried being covered that are used compute CTI. I suspect this could have a substantial influence on the CTI estimate, even if these 30 species are the most common.

2. If CTI is based on STI computed from macroclimate conditions, could this explain why CTI is not influenced by canopy cooling? Additionally, could canopy cooling be underestimated due to the limited range of forest cover conditions you sampled? I suspect that canopy shading have a higher impact when canopy cover is low (conditions that you did not sample if I understand correctly).

3. Methods for computing topography and canopy cooling:

- Topoclimate estimates: Why did you predict for 90% canopy cover (line 258)? Fixing canopy cover to predict topoclimate effect is only relevant if there are interactions between canopy closure and "topography" considered in the model, but this is not the case in the model used to map understory temperature.

- Temperature predictions extrapolation: You mentioned that temperature predictions were extrapolated for the 20% of pixels with a canopy closure lower than 79%. This is quite significant. What proportion of floristic surveys involved temperature predictions that had to be extrapolated?

- Cooling restriction: You stated, "We restrained the minimal cooling to -1.5°C; however, some pixels displayed lower values up to 0°C due to low to no canopy closure." Why was this done? It seems like this could bias the predictive effect towards a higher cooling effect.

- Linearity between temperature and topography/canopy closure: Please provide plots to better justify the expected linearity between temperature and topography or canopy closure.

Additionally, please clarify the following:

- Classification of cold, intermediate, and warm classes: Please provide more details about the method used to define these classes. You mentioned in the figures that these are topoclimate classes, so how were they separated based on your topoclimate estimates?

- Lines 278-281: It would be helpful to provide results as supplementary material.

- Lines 317-329: These lines seem to mix methods and discussion rather than presenting results.

- Lines 482-487: I'm not sure you can draw the conclusions as stated, given that you did not test different microclimate variables. Additionally, topographic position, which you assumed to rely on hydrography, is only investigated here as a factor driving temperature.

- Lines 522-524: We don't know enough about this. For instance, a cold topoclimate may be insufficient to buffer and sustain cold-adapted populations against expected future warming acceleration. This mainly depends on the extent of decoupling between macro- and topoclimate, which is still uncertain and how it will be impacted by future climate change remains largely unknown.

For all these reasons, I believe your manuscript merits revision before a recommendation can be considered.

Best regards,

Romain Bertrand

Reviewed by Martin Macek, 16 July 2024

This study work with original dataset consisting of 48 sites with in-situ measured temperatures and independent set of 306 vegetation plots. This case study undoubtely contribute to our understanding of vegetation patterns with relation to microclimate (topoclimate) and is well written, research questions are clearly presented, results are properly tested and discussed in the context of recent advances. However, I have several concerns regarding methodology which needs to be solved (see my comments below) and some suggestions for manuscript improvements.

Title is not matching – topoclimate does not buffer from macroclimate (the manuscript does not work with macroclimate at all), but rather enhance (or decouple) this variability in space.

Major comments – relative contribution of different temperature drivers to explained variability depends largely on their variability within taining dataset, which is determined by sampling design and may not reflect correctly their relative contribution within the study area, as the sampling was not random but stratified. Can you provide similar measure of their relative importance for the whole study area?

The concept of „Topoclimatic cooling" is confusing to me. First, I'm not sure, if this is a proper term. As „cooling" I consider some active process like cooling by evapotranspiration. This term is not used elsewhere in scientific literature. You selected extreme south facing slopes on the ridge as a reference value, which is not very natural reference - I would expect flat terrain/midslope position as a reference, which would also better stick to discretization of plots to cold/moderate/warm topoclimate.

l. 68 –It is not clear from the statement in previous sentence why southwest and not south slopes display warmer mean temperatures. Please explain it bit more in detail.

l. 79 Increase in winter temperatures near the ground is mostly due to snow insulation, effect of canopy insulation (namely in deciduous forests) on winter temperatures is limited. Cited references haven't found any significant effects of canopy on winter temperatures.

l. 93 – maybe reference to (Haesen et al 2023) would be more appropriate here?

l. 117 check punctation in "m.a.s.l" – commonly used is "m a.s.l." or "m.a.s.l."

l. 130 – move reference to DEM directly after "digital elevation models", at the and of sentence it seems like reference to topographical indices.

l. 134-136 – consider using abbreviations for heat load index and topographic index, which appears multiple times throughout the manuscript.

l. 136 – Heat load index does not account for topographic shading (see McCune and Keon 2002, p . 605)

l. 138 – This is uncommon definition of topographic position index. What software/function you used to calculate topographic position index?

l. 146 bilinear interpolation is a downscaling technique, for upscaling, mean (median) aggregation is preffered.

l. 156 why did you choose threshold value of 0.75 to separate north from south facing slopes, when flat land has a heat load index of 0.66?

l.174 what was the angle of view (zoom)/model of the smartphone?

l. 210 – What is "thermal optimum value" from ClimPlant? Such value is not defined in this paper. Is it a mean mean annual temperature over its geographic range?

l. 212 should be 300, not 30?

l. 238 – Have you checked the assumption of linearity? Zellweger reports nonlinear relation between canopy cover and tempertures. But I understand, that with 48 points, one should avoid overfitting using higher-polynoms.

l. 270 – Generalized poisson regression model would be definitely more appropriate for species richness (see also negative pH-corrected species richness in Figure 3). This needs to be fixed!

l. 282 – more details about variance partitioning are needed – are values displayed in Table 1 unique effects or shared effects?

l. 285 – you can define abbreviation for growing season in methods on line 188.

l. 285 – Are GS temperature values for 2005-2020 period and 2022 switched?

l. 298 and elsewhere – check spacing before °C.

https://www.nist.gov/pml/owm/writing-si-metric-system-units

Table 1 –maybe effect size should be an absolute value?

Table 1 - explained variation is exactly the same for Heat load index and Topographic position – is this a mistake? (same apply to Table S1 with much different effect estimates).

l. 346 – correlations with R2 ~0.3 are considered as moderate, rather than strong.

l. 411 – Macek et al. 2019 measured understory temperature at 2m height, which may be the possible cause for absence of effect of heat load on mean temperatures in contrast to this manuscript, as air in 2 m is likely less influenced by surface aspect.

l. 418 – statistically it was significant, but it accounted only for 0.8% of explained variability – this weakness of its effect should be outlined here.

l. 430 actually, the weak relation of CTI to microclimatic cooling is not surprising in the context of cited literature, considering that estimated effect size for CTI change for canopy cover between 79% and 100% using estimates from (De Frenne et al, 2013) is 0.00075 °C and observed effect size is -0.00822.

l. 477 – to what degree are mean and maximum temperatures correlated? I think that estimates for model using maximum temperatures should be provided at least as supplementary material. Maybe the difference between predictive power will be non-significant, but it is still testable.

Discussion – limited effect of canopy must be related to other mechanism than only to uncertainty in canopy cover estimation and limited canopy-cover induced temperature gradient (which should still result in about the same effect estimate, only with inflated standart error). Is it possible that the spatial mosaic of canopy is too fine (or too unstable in time) for plant communities to maintain stable populations of warm/cold adapted species in these microsites? Can you express the distance on which is canopy-induced microclimate autocorrelated in contrast to topoclimate to support such hypothesis?

l. 646 update reference (published version available):

Haesen S., Lenoir J., Gril E., De Frenne P., Lembrechts J.J., Kopecký M., Macek M., Man M., Wild J. & Van Meerbeek K. (2023) Microclimate reveals the true thermal niche of forest plant species. Ecology Letters 26: 2043–2055. https://doi.org/10.1111/ele.14312

Reviewed by anonymous reviewer 2, 29 July 2024

- **General comments**

The article investigates how topographic and forest-related factors influence forest microclimate and plant diversity and richness in temperate mountain forests. Specifically, it examines how variations in topoclimate and canopy cover affect understory temperatures and community composition, and deciphers the relative importance of one effect over another. The study finds that topographic features play a significant and major role in shaping microclimatic conditions, which in turn impacts plant diversity and composition. This research highlights the importance of considering both topographic and canopy factors in understanding forest microclimate dynamics. I found this article to be very interesting and well-executed.

My main comment regards the terms employed to refer to topographic and canopy-induced microclimatic conditions. The term ”topoclimate” is often used to describe the microclimatic conditions influenced by topographic features such as elevation, slope, and aspect. In contrast, ”microclimate” can refer to the local climatic conditions in a specific area, which may be influenced by both topographic and forest-related factors. But in the present manuscript, microclimate seems to refer only to forest-related factors. It would be beneficial to define these terms clearly at the outset and explain how they are used in the context of your study. For example, you might distinguish ”topoclimate” as the component of microclimate influenced by topography and ”forest-induced microclimate” or ”phytoclimate” as the component influenced by canopy cover.

The introduction should be longer, and more clearly articulate the contribution of the study to better emphasize the novelty and significance of the research. It should explicitly highlight the gap in current understanding that the study addresses by combining topographic and forest-related factors, which are often studied separately. Providing a more detailed rationale for why studying these factors conjointly is important would strengthen the introduction. Emphasizing how this integrated approach advances knowledge in the field and its implications for conservation and management could make the introduction more compelling.

Throughout the materials and methods sections, it would be beneficial to consistently remind readers of the research questions or hypotheses being addressed. This approach would help to maintain focus and context, making it clearer how each methodological choice contributes to answering the core research questions.

By addressing these points, the manuscript could more effectively convey its contributions and significance, improving its overall impact and clarity.

- **Title and abstract**

Does the title clearly reflect the content of the article?

No. The current title, 'Topoclimate Buffers Floristic Diversity from Macroclimate in Temperate Mountain Forests,' might suggest that the study investigates a buffering effect between macroclimate and forest microclimate through the lens of topographic forcing factors, which is not the primary focus of your research. The research does not focus on macroclimate directly. Instead, it compares how various microclimatic conditions, influenced by topographic positioning and forest cover, affect understory temperature and plant diversity and decipher the role of each of those forcing factors. The study primarily examines how topoclimate and canopy cover influence understory temperature and community composition within mountain forests. To better reflect the study's content and focus, consider revising the title to emphasize the role of topoclimate in shaping forest microclimate and biodiversity.

Does the abstract present the main findings of the study?

Yes.

- **Introduction**

Are the research questions/hypotheses/predictions clearly presented?

Yes, the introduction provides a comprehensive overview of the influences of topography and forest canopy on microclimate and understory vegetation. However, it could benefit from a clearer articulation of the unique value and necessity of studying these factors conjointly. While the separate effects of topographic and forest-related factors on microclimate are well documented, the introduction should emphasize the gap in understanding how these factors interact and jointly influence plant communities, but also how current research tends to study one aspect in isolation, and addressing this oversight could significantly advance our knowledge in this field.

Does the introduction build on relevant research in the field?

Yes, but the only area I would suggest strengthening is making the significance and implications of this research a bit more explicit. For example, you could emphasize how identifying climate refugia is crucial for conservation and even maybe management in the face of rapid warming. Or you could highlight how better understanding these microclimate dynamics could improve the accuracy of species distribution models that you mentioned in L59. Adding that extra layer of context would help further motivate the study.

L61-62: You seem to make a distinction between topoclimate and microclimate here. To enhance clarity, consider using the term 'phytoclimate' to refer specifically to the microclimate shaped by the forest canopy and 'topoclimate' to describe the microclimate influenced by topography.

L65: Could you clarify what you mean by 'climate stability' in this context? Are you referring to the attenuation/buffering of the macroclimate? Or are you suggesting an increased buffering effect, leading to a decoupling effect and greater spatiotemporal stability as warming continues?

L73: A clear definition of decoupling is missing.

L74: Please delete the "." after the citation.

L82: You mention that the relative importance of canopy vs. topography is "less known" and that there is no consensus, but what are the key gaps in understanding? What hypotheses or predictions can you make based on the existing evidence?

L91: Please add references here.

L94-95: Maybe rephrase to make it clearer that this is one of your hypotheses.

L96: You can add a sentence emphasizing the novelty of this research, combining topographic and forest effects on microclimate and plant communities. I would consider adding a bit more context or justification for each one. For example, why is it important to understand the relative influence of topography vs. canopy cover on understory temperatures? What are the broader implications of determining how microclimate shapes community composition and species' thermal affinities?

- **Materials and methods**

Are the methods and analyses sufficiently detailed to allow replication by other researchers?

Yes

Are the methods and statistical analyses appropriate and well described?

Yes. However, it would be very helpful to consistently remind the reader of the research question driving each investigation to provide context and enhance the clarity of the analysis, improving the overall flow.

Figure 1: You could add the name of the Thur River directly to the map. In the caption, please add the

reference for the 25m-DEM.

L128: "25-meter resolution digital elevation modelS": did you use multiple DEMs?

L129: Why did you specifically choose those topographic variables (proxies of specific processes you aim to uncover, i.e. cold air pooling ...)? Maybe add a brief justification with corresponding references for each variable.

L134: While the Heat Load Index (HLI) accounts for slope orientation and shading from nearby topographic features, it is not a direct measure of incoming solar radiation. Instead, it provides a relative estimate of the warmth of a location based on these factors. Please clarify accordingly. Besides, why not directly compute a solar radiation variable (using GIS for example)?

L130-133: I would recommend putting all package information in a separate paragraph to increase fluidity.

L143: Explicitly explain why you correlated it with field measurements (I expect this is to validate the satellite data as a reliable proxy for actual canopy conditions).

L147: It may be good to specify that non-forested areas were excluded because the study's main focus is on understory temperatures. Clarifying this will help remind readers of the study's primary objective.

L151-154: Consider rephrasing for clarity

L156: The choice of a 0.75 threshold for the Heat Load Index to distinguish between north and south-facing slopes is intriguing. Could you provide more detail on how this threshold was determined? Was it based on specific characteristics of the study area, a natural break in the distribution of HLI values, or other considerations?

L162: To further emphasize the robustness of your experimental design, consider explicitly stating its thoroughness throughout this paragraph: you could highlight how the systematic inclusion of various elevation strata, canopy covers, slope orientations, and topographic positions ensures a wide range of microclimatic conditions are captured.

L172: It would be beneficial to define canopy closure and canopy cover to clarify the distinction between these two measurements and why those variables are relevant to answer your questions.

L179: If "Glama" canopy cover estimates were not used in the analysis, their inclusion in the methods section might be redundant. Also, why do you think you found a poor correlation between those measures and the remotely sensed tree density?

L180: So, you computed a percentage of canopy cover and canopy closure by visual observation and also using hemispherical pictures analyzed with "Glama." In the end, you used the visual estimation of canopy cover in your analysis, not the one computed with "Glama." As for canopy closure, you used the Glama estimation to fix your threshold of low vs. high canopy cover. Is that correct? If so, it might be beneficial to explicitly state this rationale to clarify why different methods were employed for different purposes within your study.

L209: You can briefly reintroduce your question that leads to the use of thermal optimum species' value, as well as briefly explain what they are (units ...).

L211: Do you mean that out of the 348 unique recorded species, thermal optimum values were available for 30 species in the ClimPlant database, covering 90.0% of the occurrences of the whole floristic dataset?

L214: You specify that the CTI is calculated without weighting for abundance. It might be beneficial to briefly explain why this approach was chosen and how it aligns with the study's objectives (avoiding potential biases from dominant species? Or something else?).

L220: You can add a justification of why including a pH optimum value here, how does it help you answer your questions?

L236: You computed the daily maximum temperature instead of using the 95th percentile of maximum temperatures, which is more commonly used in the literature. Given that you already removed values lower than the 5th centile and higher than the 95th centile to avoid biases, could you explain the rationale behind choosing daily maximum temperature over the "remaining" 95th percentile of maximum temperatures? What benefits did you see in this approach for your specific study objectives?

L236: Could you clarify why you chose to compute a single mean and maximum daily temperature for the entire growing season per plot?

L238: Clearly state the question you aim to answer in doing such models.

L240: Given that your temperature measurements come from multiple loggers within the study region, why did you not consider including random effects in your models to account for potential spatial variability?

L243: Mentioning the additional models with field-measured canopy closure here interrupts the main discussion. It might be clearer to address these alternative methods in a separate section to keep the focus on your primary analysis.

Table S3: Verify the content of the caption so that it accurately reflects what is included in the table: if the visual canopy cover estimation is not part of the table, omit this detail or correct the caption accordingly.

L246: It would be helpful to elaborate a little bit more on the rationale for examining the interaction between HLI and canopy cover and clearly state your hypothesis (impact of HLI on temperature can be moderated or amplified by the presence or absence of canopy cover?).

L250: The current paragraph blends results with methods. Consider revising it to clearly describe how the model results can be used to map each factor's contribution. For example, mention that a high R^2 value supports the reliable mapping of different variables and saves detailed results or reference to the figure for the results section.

L256: The extrapolation for pixels with lower canopy closure is likely a method to ensure that the model's outputs cover the entire study area, even if those predictions come with increased uncertainty due to limited data in those specific conditions. Can you clarify the basis for this approach in the main text?

L261: It would be helpful to briefly elaborate on why soil pH was modeled separately and its impact on species richness and CTI. Additionally, can you clarify the significance of the R^2 values (32.6% for richness and 21.5% for CTI) and the rationale behind using residuals to correct for soil pH? This would enhance understanding of the correction method and its implications.

L264: Add references. I would also put the bioindicated pH per plot method (L220-222) here instead.

L273: Can you elaborate a bit more concerning the discretizing of the surveys into 'cold,' 'intermediate,' and 'warm' classes? How does this classification enhance the interpretation of species richness and CTI differences?

L278: It may be useful for the readers to clarify at the beginning of the paragraph the purpose of this approach.

- **Results**

Are the results described and interpreted correctly?

Yes

L285: The growing season temperature of 2022 was above average. While the historical context is useful, it might be more impactful to directly put this observation into the Materials and Methods section.

L290: Maybe line wrap after "the lowest elevation plots".

L291: You can add that your model revealed that …

L295: When saying that topographic position has a lesser effect on temperature, it kind of minimizes it, but 0.56°C is significant. Consider rephrasing to acknowledge its importance.

L305: Precise here that it is in similar models when the percentage of canopy closure estimated through remote sensing was replaced by the visual estimation of canopy cover.

Figure 2: It might be useful to add a title for each panel or make the legend title more explicit.

L348: Add the subsection number of your methods.

L351: You refer here to the microclimate as being only linked to the canopy cooling effect on understory temperature, but as said earlier in the introduction, forcing factors of microclimate include both topographic and forest-related features. Microclimatic cooling can be induced by topography and/or forest features.

- **Discussion**

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument?

Yes, the authors have appropriately emphasized the strengths and limitations of their study. However, I would encourage them to highlight more explicitly the novelty of their research. Specifically, they should emphasize how their study uniquely combines both topographic and forest-related features to analyze their combined impact on forest microclimate and the communities they support. This approach is a significant contribution because, in the current literature, these aspects are often studied separately.

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? Yes

L404: Again here, why make such a distinction between topoclimate and microclimate, instead of topoclimate and forest-induced microclimate, or phytoclimate?

L406: Instead of topoclimate, I would enumerate the topographic variables here.

L421: forest-related factors

L430: You could also discuss the tree type, whether deciduous or coniferous, which may or may not contrast with other studies on forest microclimate. Including insights on how the type of trees in your study area might have influenced your results would provide valuable context and strengthen your discussion.

L459: You can elaborate a bit more on this significant interaction. Moreover, could it be linked to the fact that your sampling strategy wasn't able to capture unusuak valley bottoms of high elevations?

L461: Then what would be your recommendation in terms of methodologies to study canopy cover/closure?

L464-465: Can you be more precise here?

L468: Add references that may support this statement.

L471: Mean temperature, or topoclimate?

L504-507: But decoupling is not what you studied here. Still, as you found that the main driver of microclimate and community assemblage is related to topoclimate, it raises a great perspective not discussed here. It's worth noting that if decoupling from climate change depends solely on forest-related features (like canopy cover or closure), the impacts of climate change on forest cover could reduce this buffering effect, adversely affecting the understory. In contrast, if mountain forests benefit from decoupling due to topographic features, this could help preserve the buffering effects of the canopy and, consequently, the species it supports in the understory. This highlights the importance of considering both topoclimatic and forest-related factors in conservation strategies to mitigate climate change impacts.

Reviewed by anonymous reviewer 1, 15 July 2024

cf. pdf attached

I answered the provided questions below but answering by Yes or No to these questions is a bit rough so see my comments for more details

Title and abstract

Does the title clearly reflect the content of the article? Yes
Does the abstract present the main findings of the study? Yes

Introduction

Are the research questions/hypotheses/predictions clearly presented? Yes
Does the introduction build on relevant research in the field? Yes

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? Yes
Are the methods and statistical analyses appropriate and well described? Yes, few details could be explained instead of citing R functions (cf. comments)

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? NA
Are the results described and interpreted correctly? Yes

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? Yes, few more details on possible limitis could be included (cf. comments)
Are the conclusions adequately supported by the results (without overstating the implications of the findings)? Yes

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