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## Response to Comment by Schall & Heinrichs on “Forest microclimate dynamics drive plant responses to warming”

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## Abstract

Schall & Heinrichs question our interpretation that the climatic debt in understory plant communities is locally modulated by canopy buffering. However, our results clearly show that the discrepancy between microclimate warming rates and thermophilisation rates is highest in forests where canopy cover was reduced, suggesting that the pressures on communities to respond to warming is highest in those forests.

## Main text

Biological communities accumulate a climatic (thermal) debt when their response to warming does not keep up with the warming rate itself. Forest understory plant communities appear to respond particularly slowly to warming, and thus climatic debts are commonly observed in forest understory plant communities (1, 2). In line with conventional approaches used in the literature (e.g. (1, 2)), we define the climatic debt as the difference between the thermophilisation rate and the rate of climate warming, which are two independently calculated variables.

Schall & Heinrichs (3) question the validity of our climatic debt analysis because there is no 1:1 relationship between the floristic temperatures at one point in time used to quantify the thermophilisation rates, and the macro- and microclimate change rates. In this discussion, it is very important to keep in mind that the commonly applied approach to infer temperature conditions from plant species composition data (i.e., floristic temperatures) (4, 5) does not provide a metric that is designed to accurately reflect the actual temperatures at a particular time step across space, because these data are based on broad distribution ranges of individual species co-occurring in the community and are subject to considerable uncertainty, as outlined in detail by Rodríguez-Sánchez, P. De Frenne & A. Hampe (6). Thus, caution is needed when using such floristic temperatures to study *spatial* variation of community temperature preferences along a climatic gradient, as done by Schall & Heinrichs, especially when the studied macroclimatic gradient is relatively short, as it is the case in our study (the interquartile range of spatial macroclimate temperatures in the baseline and resurveys were only 2.4 and 2.2 °C, respectively). However, in our paper we study *temporal*, not spatial, changes in floristic temperatures *per unit time*, and for this purpose floristic temperatures have been shown to be very robust, providing a solid database for our thermophilisation and climatic debt analyses, exactly because they avoid the above mentioned uncertainties (6). Furthermore, our floristic temperatures per species are based on long-term macroclimate data during the vegetation period, whereas the macro- and microclimate change data were calculated independently based on summer maximum temperatures prevailing in the five preceding years of the respective field surveys. Schall & Heinrichs' finding that the floristic temperatures at one time step more closely follow the macroclimate than the microclimate temperatures is also very plausible and expected, exactly since the floristic temperatures were calculated from macroclimate data, not microclimate data, which are not yet available at such scales. The patterns shown in Schall & Heinrichs' Figs. 1B & C can thus be explained very well and provide no reason whatsoever to question the validity of our climate debt assessment. We would also like to point out that the mean thermophilisation rates we find in our study compare very well to the rates found in other lowland forests in Europe (1), as well as in forests in the Andes (2), and that the variation of our floristic temperatures for a given unit of spatial macroclimate change is similar to the respective variation found in these two

studies. Schall & Heinrichs' claim that the climatic debt seems to be a construct not supported by the floristic data does not hold.

Schall & Heinrichs further question our interpretation of the effect of canopy buffering on the climatic debt. As outlined in the introductory paragraph above, and in agreement with Schall & Heinrichs' concerns, it is obvious that microclimate warming and microclimatic debt are not independent from each other. In fact, given the frequently observed slow response of forest plant communities (1, 2), it can be expected that microclimate debts are more pronounced in areas with high rates of warming. We show that changes in temperature buffering due to dynamics in canopy cover are an important and integral component of forest microclimate warming. Indeed, canopy opening (e.g. due to clearcutting or tree mortality) is an important regulator of the forest-floor temperature which can act independent from macroclimate warming (7). It is thus reasonable to expect that changes in canopy-modulated temperature buffering are related to the microclimate debt, but not to macroclimate debt, which is independent from local canopy dynamics. What we show in Figure 3A in our report (7) is the contribution of the change in temperature buffering on the microclimatic debt. We argue that this is an interesting contribution because (i) it can be substantial but has been largely ignored in the literature, and (ii) it shows how the pressure on communities to respond to warming is locally modulated by canopy cover dynamics. We agree with Schall & Heinrichs' claim that the relationship between microclimate debt and canopy buffering does not provide evidence of a response of the understory community to climate change. Evidence of such a response is provided in Fig. 2 in our report (7). However, the said relationship provides insights into how the pressures for communities to respond to warming is locally modulated by canopy cover and associated changes in temperature buffering, and that is despite the non-independence between microclimate debt and microclimate warming. An ecologically realistic assessment of how much communities lag behind warming requires local temperature and microclimate warming data. In contrast to Schall & Heinrichs' critique and given our finding that thermophilisation is more related to microclimate warming than to macroclimate warming (Figure 2 in Zellweger *et al.* (7)), we indeed argued that microclimate warming, and not macroclimate warming, ultimately drives organismal responses to warming. These results also fully support our conclusion that a reduction in canopy cover and associated reduction in temperature buffering leads to higher rates of warming, thus seriously increasing the pressure for plant communities to respond to warming.

We agree with Schall & Heinrichs' conclusion that understory plant communities have responded only weakly to warming temperatures. That is actually the crucial point, because at the same time the temperatures themselves have warmed markedly, causing a climatic debt. It may indeed be that the microclimate temperature variation observed within our studied forests were within the thermal tolerances of most species, but given the slow response of these species, the currently observed climate warming rates continue to erode their thermal safety margins, especially at their equatorward range boundaries. This has serious implications for future forest diversity and function (8) and will likely be felt first and strongest in forests subject to relatively high local warming rates due to a reduction in canopy buffering. We argue that this is an important finding, which should be taken into consideration in the discussion about the future and management of forest biodiversity in a warming world.

5 Finally, we fully and evidently agree that deep shade is not beneficial for many species,  
and we have never claimed otherwise. Instead, we make the point that it is important to consider  
the effects of different forest management practices on local microclimates in any endeavor to  
safeguard forest biodiversity in a warming world. Forest ecologists are very much aware that  
10 many species benefit from canopy openings, and many of us have extensively worked on this  
topic (9–11). We also fully agree that, at a landscape scale, biodiversity is enhanced by forest  
patches with deep shade and more open patches or edge habitat, as shown by many studies,  
including our own work (12, 13). Environmental change affects forest understory plant  
communities in many ways, and we agree with the general remarks in Schall & Heinrichs  
15 concluding paragraphs. However, in terms of recent warming effects on forest biodiversity, we  
argue that microclimate warming and its local drivers deserve increased attention.

## References

1. R. Bertrand et al., Changes in plant community composition lag behind climate warming  
15 in lowland forests. *Nature*. **479**, 517–520 (2011).
2. B. Fadrique et al., Widespread but heterogeneous responses of Andean forests to climate  
change. *Nature*. **564**, 207–212 (2018).
3. P. Schall, S. Heinrichs, Comment on “Forest microclimate dynamics drive plant responses  
to warming.” *Science*. (2020).
- 20 4. P. De Frenne et al., Microclimate moderates plant responses to macroclimate warming.  
*Proc. Natl. Acad. Sci.* **110**, 18561–18565 (2013).
5. V. Devictor et al., Differences in the climatic debts of birds and butterflies at a continental  
scale. *Nat. Clim. Chang.* **2**, 121–124 (2012).
6. F. Rodríguez-Sánchez, P. De Frenne, A. Hampe, Uncertainty in thermal tolerances and  
25 climatic debt. *Nat. Clim. Chang.* **2** (2012), doi:10.1038/.
7. F. Zellweger et al., Forest microclimate dynamics drive plant responses to warming.  
*Science*. **369**, 772–775 (2020).
8. D. Landuyt et al., The functional role of temperate forest understorey vegetation in a  
changing world. *Glob. Chang. Biol.* **25**, 3625–3641 (2019).
- 30 9. O. Vild, J. Roleček, R. Hédli, M. Kopecký, D. Utinek, Experimental restoration of  
coppice-with-standards: Response of understorey vegetation from the conservation  
perspective. *For. Ecol. Manage.* **310**, 234–241 (2013).
10. H. Van Calster et al., Diverging effects of overstorey conversion scenarios on the  
understorey vegetation in a former coppice-with-standards forest. *For. Ecol. Manage.* **256**,  
35 519–528 (2008).
11. K. Verheyen, I. Fastenaekels, M. Vellend, L. De Keersmaeker, M. Hermy, Landscape  
factors and regional differences in recovery rates of herb layer richness in Flanders  
(Belgium). *Landsc. Ecol.* **21**, 1109–1118 (2006).
- 40 12. A. Valdés et al., High ecosystem service delivery potential of small woodlands in  
agricultural landscapes. *J. Appl. Ecol.* **57**, 4–16 (2020).
13. S. Govaert et al., Edge effects on understorey plant communities in European forests

depend on management. *J. Veg. Sci.* **31**, 281–292 (2020).