Response to Comment on “Forest microclimate dynamics drive plant responses to warming”

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Schall and 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 thermophilization rates is highest in forests where canopy cover was reduced, which suggests that the need for communities to respond to warming is highest in those forests.

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 cited literature [e.g., (1, 2)], we define the climatic debt as the difference between the thermophilization rate and the rate of climate warming, which are two independently calculated variables. Schall and Heinrichs (3) question the validity of our climatic debt analysis because there is no 1:1 relationship between the floristic temperatures and the macro- and microclimate temperatures at one point in time. In this discussion, it is important to keep in mind that the commonly applied approach to inferring temperature conditions from plant species composition data (i.e., floristic temperatures) (4, 5) is not 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 RodríguezSánchez et al. (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 and Heinrichs, especially when the studied macroclimatic gradient is relatively short, as is the case in our study (the interquartile ranges of spatial macroclimate temperatures in the baseline and resurveys were only 2.4° and 2.2°C, respectively). However, in our paper we studied temporal, not spatial, changes in floristic temperatures per unit time, and for this purpose floristic temperatures have been shown to be unbiased and robust, providing a solid database for our thermophilization and climatic debt analyses (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 on the basis of summer maximum temperatures prevailing in the 5 preceding years of the respective field surveys. Schall and 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 because the floristic temperatures were calculated from macroclimate data, not microclimate data, which are not yet available at such scales. The patterns shown in Schall and Heinrichs' figure 1, B and C, can thus be explained very well and provide no reason to question the validity of our climate debt assessment. We also note that the mean thermophilization rates we found in our study compare 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 and Heinrichs' claim that the climatic debt seems to be a construct not supported by the floristic data does not hold.

Schall and Heinrichs further question our interpretation of the effect of canopy buffering on climatic debt. As outlined above, and in agreement with Schall and 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. Regulating effects of canopy opening (e.g., due to clearcutting or tree mortality) on forest-floor temperature can act independently 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. What we show in figure 3A of (7) is the contribution of the change in temperature buffering to 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 need for communities to respond to warming is locally modulated by canopy cover dynamics. We agree with Schall and 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 figure 2 of (7). However, the said relationship shows how the need for communities to respond to warming is locally modulated by canopy buffering, despite the non-independence between microclimate debt and microclimate warming. An ecologically realistic assessment of how much communities lag behind warming requires data about microclimate warming. In contrast to Schall and Heinrichs' critique and given our finding that thermophilization is more related to microclimate warming than to macroclimate warming [figure 2 of (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 buffering leads to higher rates of warming, thus seriously increasing the pressure for plant communities to respond to warming.

We agree with Schall and 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 variations observed within our studied forests were within the thermal tolerances of most species, but given their slow response, 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 most strongly in forests subject to relatively high local warming rates due to a reduction in canopy buffering.

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 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 and Heinrichs' concluding paragraphs. However, in terms of recent warming effects on forest biodiversity, we argue that microclimate warming and its local drivers deserve increased attention

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