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Response to Comment on "Forest microclimate dynamics drive plant responses to warming"

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Bertrand *et al*. question our interpretation about warming effects on the thermophilization in forest plant communities and propose an alternative way to analyze climatic debt. We show that microclimate warming is a better predictor than macroclimate warming for studying forest plant community responses to warming. Their additional analyses do not affect or change our interpretations and conclusions.

Canopy structure and composition are important determinants of spatial and temporal variation in forest microclimate (*1*, *2*). Accordingly, we inferred the microclimate from macroclimate data and the modulating effect of the canopy layer [figure 1B in Zellweger *et al.* (*3*)]. Bertrand *et al.* (*4*) used our data to separately analyze the effects of macroclimate warming and temperature buffering on community thermophilization and its associated microclimatic debt (i.e., the difference between the rate of forest microclimate warming and the rate of community thermophilization). We argue that it is ecologically more meaningful to analyze community responses to global warming based on the warming rates that the forest understory organisms actually experience—that is, the microclimate warming rates—applying a "plant's-eye view" approach on biodiversity responses to climate change (*5*, *6*). For that specific reason, in our report (*3*), we directly incorporated the widely acknowledged temperature buffering effect that canopy cover has on macroclimate to assess the rate of microclimate warming, which we subsequently related to community thermophilization. We therefore believe that Bertrand *et al.*'s slightly different model to deconstruct the microclimate warming rate experienced by forest-dwelling organisms into macroclimate warming and temperature buffering hardly provides additional insights into the effects of microclimate dynamics on forest understory plant responses to warming.

Because we did not separate macroclimate warming from temperature buffering, Bertrand *et al.* claim that we "underestimated the effect of macroclimate on biodiversity." This would imply a shortcoming of our paper that is not supported by their additional analysis. In fact, macroclimate warming is an integral part of microclimate warming, and microclimate warming happens in part because of macroclimate warming. The main point drawn from our study is that the rate of forest microclimate warming is simply a better and more natural predictor variable for studying forest understory plant community responses to climate change than the rate of macroclimate warming. Arguably, from a forest floor organism's view, the microclimate is more relevant than the macroclimate. Microclimate change rates should therefore be preferred over macroclimate data in future assessments of biodiversity responses to climate change.

As discussed in our paper, our results indeed have implications for forest management and biodiversity conservation. For example, as shown in figure 3A of (*3*), temporal changes in canopy cover can mitigate or amplify the need for forest plant communities to respond to warming, a finding that is of interest to foresters and policymakers engaged in forest biodiversity conservation. This finding is further supported by figure S5 of (*3*), where we show the relationship between microclimate warming and canopy cover changes over time. We therefore disagree with Bertrand *et al.*'s claim that removing macroclimate change from calculations of microclimate change provides crucial information to managers and policymakers. However, we entirely agree with Bertrand *et al.* that a sole focus on canopy cover management does not represent a sustainable long-term solution to counteract the pressures imposed on forest biodiversity by global warming, and we have never argued otherwise.

With regard to Bertrand *et al.*'s comments on our thermophilization analysis, we stress that we studied directional shifts in species composition as a result of temperature changes by analyzing community thermophilization. This allowed us to focus explicitly on warming effects on plant communities. Our results show that the thermophilization rates in forest plant communities are more related to microclimate warming than to macroclimate warming, because microclimate data integrate the temperature buffering information as well as macroclimate data. Bertrand *et al.*'s reanalysis actually supports this finding, but it is noteworthy that neither the microclimate warming rates nor the macroclimate warming rates were strongly related to the thermophilization rates. In the main text of our paper, we acknowledge the large variation and high degree of stochasticity in the thermophilization rates overserved in our continental dataset reaching back to 1934, and we are most certainly aware that other drivers—such as drought, changes in soil acidity and nutrients, or the colonization of invasive species—may also affect community turnover. We clearly refer to these factors in the supplementary materials and study these other drivers extensively in other work. However, in the context of warming temperatures, we are confident that our interpretation that thermophilization in forest plant communities is primarily controlled by microclimate warming, and not macroclimate warming, is sound and supported by our analyses (*3*). We also fully agree that macroclimate warming can contribute to community thermophilization, as other studies have found [e.g., (*7*, *8*)], and we reference these studies in our paper without contradicting them. However, in our dataset this relationship was statistically not significant. Please note that Bertrand *et al.*'s claim that their "analysis further showed that canopy closure had cooled local climate conditions within forest stands and mitigated the thermophilization of plant communities as macroclimate warmed" does not represent an additional finding, as we have already shown this in our paper [see figure 1C and figure 2 of (*3*)].

As outlined above, the two main explanatory variables in Bertrand *et al.*'s model (i.e., macroclimate warming and changes in temperature buffering) represent our definition of forest microclimate warming in this study. Following Occam's razor principle, a more parsimonious statistical model (fewer predictor variables than in Bertrand *et al.*) to analyze the effect of microclimate warming on the microclimatic debt can therefore be formulated as follows: microclimatic debt ~ microclimate warming. The resulting marginal R^2 and AIC values for this model are 79.1% and −2463. The respective values for Bertrand *et al.*'s model with our data, which includes a much more complex formula with two predictor variables and their interaction effect, are 77.1% and −2257. These model evaluations show that our conclusion that the climatic debt in forest plant communities is primarily controlled by microclimate is sound and supported by our analyses and results. However, it is important to note that microclimate debt and microclimate warming are not independent of each other, because the latter was used to calculate the former. Although we agree with Bertrand *et al.* that macroclimate warming can affect the microclimatic debt, we would like to point out that this is not surprising given the strong correlation between macroclimate warming and microclimate warming, as shown in figure 1C of (*3*). Our understanding of the relative importance of micro- and macroclimate change for driving community responses to climate change is still far from complete and warrants further research.

Finally, we agree with Bertrand *et al.*'s universal statement that preserving forest biodiversity requires controlling global warming. The critical focus with regard to our report is how, and at what scale, warming temperatures need to be quantified in order to better understand the response of forest biodiversity to climate change. In this regard, forest microclimate ecology has a lot to teach us.

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