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

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Abstract: In our study about forest plant community responses to microclimate warming we define forest microclimate warming as the combination of macroclimate warming and the modulating temperature buffering effect generated by the canopy layer. Bertrand *et al.* suggests to analyse the effects of macroclimate warming and temperature buffering on understory plant community responses separately, but this reveals no new insights and does not affect our interpretations and conclusions.

Main Text

Considering that canopy structure and composition are important determinants of spatial and temporal variation in forest microclimate (1, 2), we inferred the microclimate from macroclimate data and the modulating effect of the canopy layer (Fig 1B) (3). Bertrand *et al.* used our data to separately analyse the effects of macroclimate warming and temperature buffering on community thermophilisation and its associated microclimatic debt (i.e. the difference between the rate of forest microclimate warming and the rate of community thermophilisation). We argue that it is ecologically more meaningful to analyse community responses to global warming based on the warming rates that the forest understory organisms actually experience, i.e. the microclimate warming rates. 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 is not suited to provide 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, potentially generating misleading guidelines for forest and environmental management”. This would imply a shortcoming of our paper which is not supported by their additional analysis. In fact, macroclimate warming is an integrative part of microclimate warming and microclimate warming happens 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. 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 Fig. 3A (3), temporal changes in canopy cover can mitigate or amplify the microclimatic debt of forest plant communities, a finding that is of interest to foresters and policy makers engaged in forest biodiversity conservation. This finding is further supported by Fig S5 (3), where we show the relationship between microclimate warming and canopy cover changes over time. It is not readily clear what “crucial information to managers and policy makers” Bertrand *et al.*'s additional analysis actually provides. 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 regards to Bertrand *et al.*'s comments on our thermophilisation analysis, we stress that we studied directional shifts in species composition as a result of temperature changes by analysing community thermophilisation. This allowed us to focus explicitly on warming effects on plant communities. Our results show that the thermophilisation rate in forest plant communities are more related to microclimate warming than to macroclimate warming, because microclimate data include both the temperature buffering information as well as macroclimate data. We acknowledge the large variation and high degree of stochasticity in the thermophilisation rates in the main text of our paper, and we are most certainly aware that other drivers of community turnover, such as drought, changes in soil acidity and nutrients, or the colonisation of invasive species – all mentioned in the supplementary material – may also affect community turnover. However, in the context of warming temperatures, we are confident that our interpretation that thermophilisation in forest plant communities are primarily controlled by microclimate warming, and not macroclimate warming, is sound and supported by our analysis and results (Fig 2) (3). We also fully agree that macroclimate warming can contribute to community thermophilisation, as other studies have found (e.g., 4, 5), 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 Fig. 1C and Fig. 2).

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 (less predictor variables than in Bertrand *et al.*) to analyse the effect of microclimate warming on the microclimatic debt can therefore be formulated as follows: microclimatic debt \sim microclimate warming. The resulting marginal R-squared 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. So, why would we need a more complex model when an ecologically more meaningful and simpler one can explain more variation in our data? These model evaluations show that our interpretation and conclusion that the climatic debt in forest plant communities is primarily controlled by microclimate is sound and supported by our analysis and results. While we agree with Bertrand *et al.*'s that global 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 our paper in Fig. 1C (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. Bertrand *et al.* conclude that their approach provides “a complete and mechanistic understanding of the role of microclimate on plant biodiversity response to global change”. We disagree with this conclusion as it is hardly possible to shed light into the actual mechanisms without (experimental) data on factors such as species-level ecophysiology, demography or trophic interactions, all of which are not contained in our large-scale observational dataset. We also cannot see how a model that is further from ecological reality should improve mechanistic understanding.

Finally, we agree with Bertrand *et al.*'s general statement that preserving forest biodiversity requires controlling global warming. However, the critical focus with regards to our report is how and at what scale global warming needs 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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