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

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Zellweger *et al.* (Reports, 15 May 2020, p. 772) claimed that forest plant communities' response to global warming is primarily controlled by microclimate dynamics. We show that community thermophilization is poorly explained by the underlying components of microclimate, and that global warming primarily controls the climatic lag of plant communities. Deconstructing the underlying components of microclimate provides insights for managers.

The debate about the efficiency of canopy cover in mitigating or amplifying the effect of global warming on forest plant communities has important implications for forest and environmental management (1–3). Zellweger *et al.* (4) tested the relationship between reshuffling in plant communities and changes in subcanopy microclimate conditions statistically inferred from canopy cover trends over the past few decades. They concluded that microclimate dynamics are pertinent in understanding the responses of forest plant communities to global warming. Although we agree that microclimate is an important driver, we stress that the claim that “thermophilization and the climatic lag in forest plant communities are primarily controlled by microclimate” simplifies a more complex regulation of plant communities by global warming. Microclimate stems from global climatic trends [macroclimate in (4)] and local habitat characteristics [canopy cover in (4)] that buffer or amplify the effect of macroclimate. Because these two components act simultaneously, their relative influence on biodiversity needs to be assessed explicitly (2). By not doing so, Zellweger *et al.* underestimated the effect of macroclimate on biodiversity. The explicit consideration of these two components provides crucial information to managers and policymakers on which component (local and/or global) to focus management efforts for effective mitigation of global change impacts on biodiversity. Here, we provide an alternative statistical approach that explicitly tests for the relative effects of each component of microclimate on forest plant communities. Beyond an alternative interpretation of Zellweger *et al.*'s dataset, we hope to contribute to a consensus on how to assess the effects of the underlying components of microclimate on biodiversity.

Our alternative analytical approach aims at comparing and assessing the relative effects of local and global drivers of microclimate explicitly (2). This comparison is necessary to interpret the effect of microclimate change on plant communities, as the latter can be largely driven by global warming. On the basis of the same linear mixed-effect models framework as Zellweger *et al.*, we propose the following model: thermophilization or microdebt = macroTC + ΔT_{buff} + macroTC* ΔT_{buff} + (1|region), where macroTC and ΔT_{buff} are the global and local components of microclimate, respectively, and macroTC* ΔT_{buff} is their interaction (5). This model assumes that change in macroclimate temperature (macroTC), change in temperature buffering (ΔT_{buff}), and the two-term interaction likely explain the microclimatic debt (microdebt) or the community thermophilization.

First, Zellweger *et al.* showed that thermophilization of plant communities (i.e., changes in communities toward more warm-affinity species assemblages) increased with microclimate warming (4). This is correct, but we wish to point out that microclimate explained only 1.1% of thermophilization. Our analysis further showed that canopy closure had cooled local climate conditions within forest stands and mitigated the thermophilization of plant communities as macroclimate warmed (Table 1). Although significant, change in temperature buffering due to canopy openness and closure and its interplay with global warming explained only 0.5% and 0.2% of the community thermophilization, respectively. Therefore, we cautiously conclude that community thermophilization is not primarily explained by microclimate change and these underlying local or global drivers. Instead, the reshuffling of plant communities might be the result of species persistence (through

adaptive and nonadaptive evolutionary pathways), species dispersal, species interaction, and other components of global change (2, 6–9), likely explaining why community thermophilization does not strictly follow microclimate change.

Second, we showed that underlying local and global drivers of microclimate explained 77.1% of the microclimatic debt (i.e., the difference between the thermophilization rate of plant communities and actual changes in microclimate conditions, which quantifies the lag in plant community responses to warming; Table 1). Change in macroclimate explained a much greater portion of the variance in microclimatic debt than did change in temperature buffering (44.6% versus 31.1%; Fig. 1A). Global warming also amplified the microclimatic debt to a higher degree than change in temperature buffering (mean effect of macroTC = 0.252 versus mean effect of ΔT_{buff} = -0.210; Table 1). Moreover, the effect of ΔT_{buff} on microclimatic debt was modulated by the magnitude of global warming (mean effect of the interaction term = -0.05; Table 1). This showed that the amplifying effect of global warming on microclimatic debt increased as the temperature buffering decreased as a result of canopy openness, with an effect of global warming that was greater by a factor of ~6.5 when canopy opened rather than closed over time (Fig. 1B). The amplifying effect of global warming on microclimatic debt was significant even when the temperature buffering effect was maximal (mean effect of macroTC = 0.073 when ΔT_{buff} = 2.8°C; $P < 0.001$), which suggests a consistent influence of global warming on plant communities, regardless of the change in canopy cover.

Our reanalysis provides a more precise understanding of the role of microclimate dynamics in plant biodiversity response to climate change by highlighting the interplay between the local and global components of microclimate. Deconstructing the underlying components of microclimate change is required to formulate appropriate management avenues and to mitigate the effect of climate change on forest biodiversity. The reshuffling of understory plant communities toward warm-affinity assemblages is therefore not primarily controlled by microclimate change per se. The climatic lag observed in forest plant communities is mostly driven by a synergetic effect between global warming and changes in temperature buffering due to local habitat change (3), with a global warming effect persisting irrespective of the magnitude of canopy closure. If our results confirm that forest management should limit canopy openness (10), we stress that relying solely on canopy cover management to mitigate the effect of global warming on plants, and more broadly on forest ecosystems biodiversity, is not a long-term solution. Global warming is expected to increase tree mortality in the foreseeable future (11, 12), with the ef-

fect of opening up forest canopies over vast parts of the planet (13). To preserve forest biodiversity, one must first control global warming.

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Table 1. Summary statistics for the models explaining variation of thermophilization and microclimatic debt observed in forest plant communities ($n = 2943$ observations). Means and 95% confidence intervals of estimates, as well as the significance term for each fixed effect, were computed from 10,000 bootstrapped models. Boldface P values highlight significant effect (considering a threshold $\alpha < 0.05$).

Fixed effect	Variable	Thermophilization			Microclimatic debt		
		Mean	95% CI	P	Mean	95% CI	P
	Intercept	0.012	[-0.004; 0.027]	0.066	0.43	[0.409; 0.451]	<0.001
	MacroTC	-0.002	[-0.015; 0.011]	0.372	0.252	[0.237; 0.267]	<0.001
	ΔT_{buff}	-0.012	[-0.018; -0.005]	<0.001	-0.21	[-0.217; -0.203]	<0.001
	MacroTC \times ΔT_{buff}	-0.007	[-0.014; 0]	0.025	-0.05	[-0.057; -0.043]	<0.001
Variation explained	Marginal R^2	0.008	[0.002; 0.018]		0.771	[0.749; 0.79]	
	Conditional R^2	0.105	[0.066; 0.149]		0.812	[0.797; 0.825]	

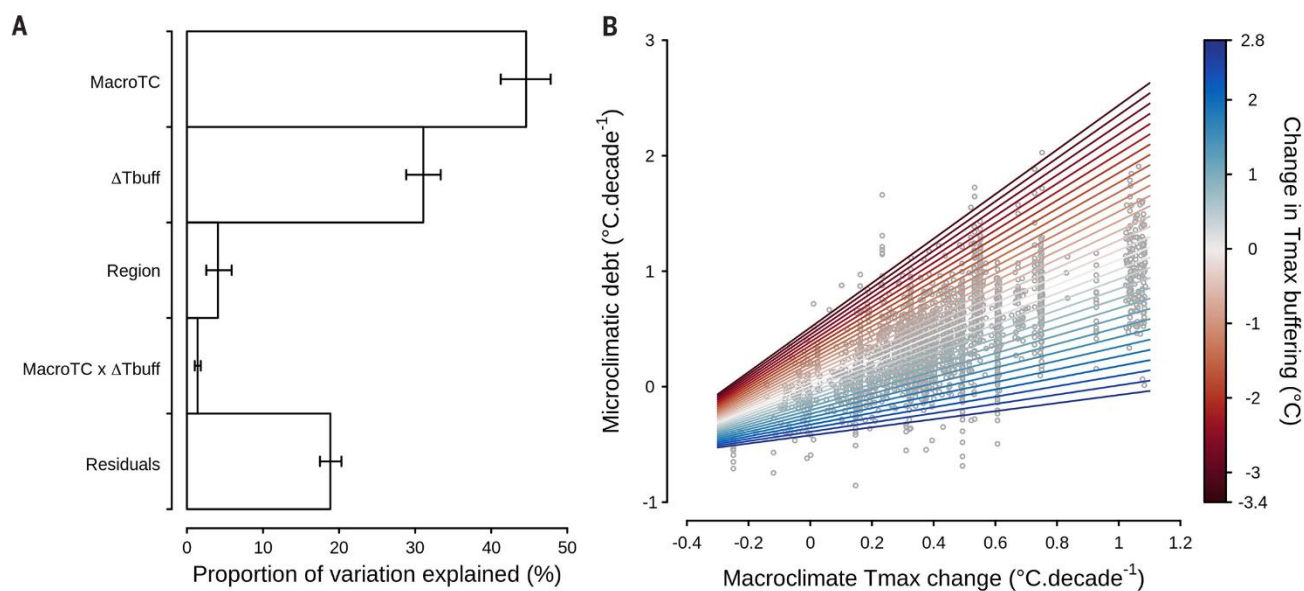


Fig. 1. Changes in macroclimate temperature (MacroTC) and in temperature buffering by canopy closure and openness (ΔT_{buff}) both explain the microclimatic debt in forest plant communities. (A) Proportion of the microclimatic debt variation explained by fixed effects (MacroTC and ΔT_{buff}), by random intercept (Region), and unexplained (Residuals). Error bars represent 95% confidence intervals computed from 10,000 bootstrap iterations. (B) The microclimatic debt rises as global warming increases and temperature buffering decreases as a result of canopy opening. Negative values on the x axis represent macroclimate cooling; positive values represent macroclimate warming. Dots are observations ($n = 2943$).

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