FOREST ECOLOGY

Forest microclimate dynamics drive plant responses to warming

Florian Zellweger[1,2]*†, Pieter De Frenne[3]†, Jonathan Lenoir[4], Pieter Vangansbeke[3], Kris Verheyen[3], Markus Bernhardt-Römermann[5], Lander Baeten[3], Radim Hédl[6,7], Imre Berki[8], Jörg Brunet[9], Hans Van Calster[10], Markéta Chudomelová[6], Guillaume Decocq[4], Thomas Dirnböck[11], Tomasz Durak[12], Thilo Heinken[13], Bogdan Jaroszewicz[14], Martin Kopecký[15,16], František Máliš[17,18], Martin Macek[15], Marek Malicki[19], Tobias Naaf[20], Thomas A. Nagel[21], Adrienne Ortmann-Ajkai[22], Petr Petřík[15], Remigiusz Pielech[23], Kamila Reczyńska[19], Wolfgang Schmidt[24], Tibor Standovár[25], Krzysztof Świerkosz[26], Balázs Teleki[27], Ondřej Vild[6], Monika Wulf[20], David Coomes[1]*

Climate warming is causing a shift in biological communities in favor of warm-affinity species (i.e., thermophilization). Species responses often lag behind climate warming, but the reasons for such lags remain largely unknown. Here, we analyzed multidecadal understory microclimate dynamics in European forests and show that thermophilization and the climatic lag in forest plant communities are primarily controlled by microclimate. Increasing tree canopy cover reduces warming rates inside forests, but loss of canopy cover leads to increased local heat that exacerbates the disequilibrium between community responses and climate change. Reciprocal effects between plants and microclimates are key to understanding the response of forest biodiversity and functioning to climate and land-use changes.

Climate warming is having profound effects on ecological processes and biodiversity—and thus on ecosystem functioning and human well-being (*1*–*4*). Our knowledge and predictions about biotic responses to anthropogenic climate warming are largely based on air temperature data measured at official meteorological stations, which record free-air (macroclimate) temperature in open areas at 1.2 to 2 m above short grass (*5*, *6*). However, most organisms on Earth experience temperature conditions that differ from the macroclimate, mainly because the topography and vegetation create heterogeneous microclimates near the ground through interception of solar radiation, air mixing, and evapotranspiration (*7*, *8*). Local microclimates may explain why responses of biological communities and ecosystem processes are often partially uncoupled from macroclimate warming (*6*, *9*–*14*).

Range shifts toward higher latitudes and elevations are now commonly observed for many species and systems as organisms shift their geographical distributions to track their thermal requirements (*15*). With rising temperatures at a location, the presence or abundance of species adapted to higher temperatures is therefore expected to increase, whereas species adapted to lower temperatures may decline and eventually become excluded. Such directional shifts in community composition in favor of warm-affinity species are referred to as "thermophilization," a phenomenon that is increasingly documented in terrestrial and marine plants and animals (*12*–*14*, *16*, *17*). However, the thermophilization rate of many biological communities is not keeping pace with the velocity of contemporary macroclimate change (*18*, *19*), leading to a climatic lag or debt in community responses to macroclimate warming (*10*–*13*). Climatic debt effects may be the inevitable consequence of habitat fragmentation, slow dispersal, and long life spans (*20*), but the magnitude of the climatic debt may also be affected by different warming rates of localized microclimates. We know very little about how microclimates have changed over time, and it is unclear how any such change has modulated the temporal thermophilization rate and climatic debt observed in plant and animal communities (*12*–*14*, *17*). Effects of changes in vegetation cover on microclimates near the ground could have either accelerated or counteracted the effects of macroclimate warming on biological communities, but a long-term, large-scale, and multitaxa assessment of these effects is currently missing.

Microclimates are perhaps nowhere more evident than in forests, owing to their three-dimensional canopy structure that drives shading, air mixing, and evapotranspirative cooling (*7*, *21*). The tree canopy buffers forest floor temperatures against extreme heat (*9*), and this buffering capacity constantly changes with tree species, growth, and mortality, leading to highly dynamic microclimates across space and over time (*22*). Accounting for changes in canopy cover and the associated microclimate dynamics is therefore important to better understand the response of forest biodiversity to climate change. Here, we provide multidecadal evidence of forest subcanopy temperature changes, enabling the comparison between anthropogenic climate change, as measured by weather stations (macroclimate), and forest microclimate dynamics triggered by canopy cover changes over time. To this end, we combined subcanopy temperature measurements in 100 forest stands in temperate forest in Europe with 2955 permanent vegetation plots from 56 regions, where each plot has been resurveyed over a period of 12 to 66 years (*23*) (Fig. 1A and fig. S1). Using a continental-scale analysis of forest microclimates based on in situ empirical temperature and canopy cover data, we then predict changes in understory temperature during the growing season, building upon the relationship between canopy cover and the buffering of macroclimate temperatures (*21*) (Fig. 1, B and C).

We found that temporal changes in canopy cover varied greatly across the 56 European regions studied, ranging from –110% (significant canopy opening) to +113% (strong densification of the canopy) (1st and 99th percentile of distribution, respectively), with a mean canopy cover change not significantly different from zero (+2.6%; mixed-effects models P = 0.426; fig. S3). To predict how the microclimate in the understory of each plot had changed between the baseline survey and

[1]Forest Ecology and Conservation Group, Department of Plant Sciences, University of Cambridge, Cambridge CB23EA, UK. [2]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland. [3]Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, B-9090 Melle-Gontrode, Belgium. [4]UR "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, UMR 7058 CNRS-UPJV), Université de Picardie Jules Verne, 800037 Amiens Cedex 1, France. [5]Institute of Ecology and Evolution, Friedrich Schiller University Jena, D-07743 Jena, Germany. [6]Institute of Botany of the Czech Academy of Sciences, CZ-602 00 Brno, Czech Republic. [7]Department of Botany, Faculty of Science, Palacký University in Olomouc, CZ-78371 Olomouc, Czech Republic. [8]Institute of Environmental and Earth Sciences, University of Sopron, H-9400 Sopron, Hungary. [9]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, 230 53 Alnarp, Sweden. [10]Research Institute for Nature and Forest (INBO), B-1000 Brussels, Belgium. [11]Environment Agency Austria, A-1090 Vienna, Austria. [12]Department of Plant Physiology and Ecology, University of Rzeszów, PL-35-959 Rzeszów, Poland. [13]General Botany, Insitute of Biochemistry and Biology, University of Potsdam, 14469 Potsdam, Germany. [14]Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, 17-230 Białowieża, Poland. [15]Institute of Botany of the Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic. [16]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, CZ-165 21 Prague 6 - Suchdol, Czech Republic. [17]Faculty of Forestry, Technical University in Zvolen, SK-960 01 Zvolen, Slovakia. [18]National Forest Centre, SK-960 01 Zvolen, Slovakia. [19]Department of Botany, Institute of Environmental Biology, University of Wrocław, PL-50-328 50 Wrocław, Poland. [20]Leibniz Centre for Agricultural Landscape Research (ZALF), D-15374 Muencheberg, Germany. [21]Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Ljubljana 1000, Slovenia. [22]Department of Hydrobiology, Institute of Biology, University of Pécs, H-7624 Pécs, Hungary. [23]Department of Forest Biodiversity, Faculty of Forestry, University of Agriculture in Kraków, PL-32-425 Kraków, Poland. [24]Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, D-37077 Göttingen, Germany. [25]Department of Plant Systematics, Ecology and Theoretical Biology, Institute of Biology, L. Eötvös University, H-1117 Budapest, Hungary. [26]Museum of Natural History, University of Wrocław, PL-50-335 Wrocław. Poland. [27]MTA-DE Lendület Functional and Restoration Ecology Research Group, H-4032 Debrecen, Hungary.
***Corresponding author. Email: florian.zellweger@wsl.ch (F.Z.); dac18@cam.ac.uk (D.C.)** †These authors contributed equally to this work.

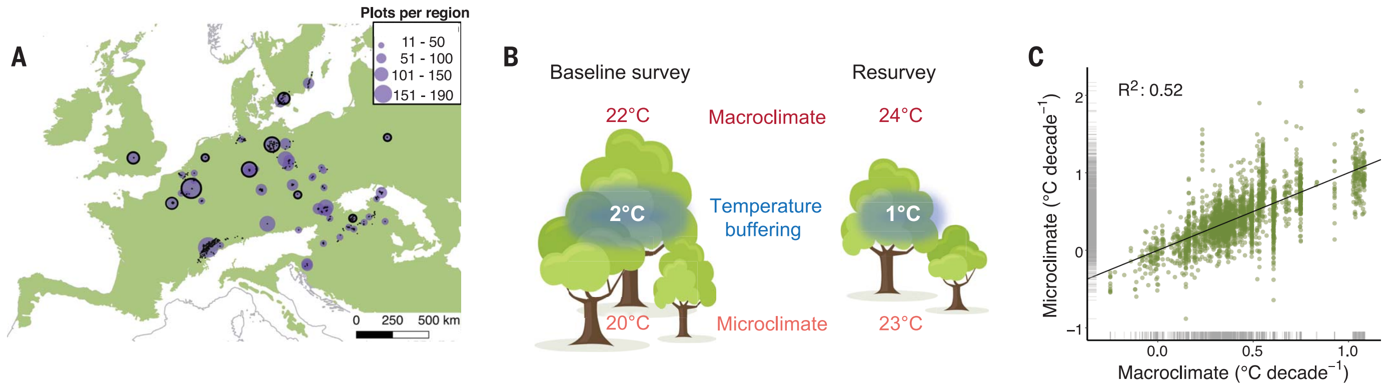


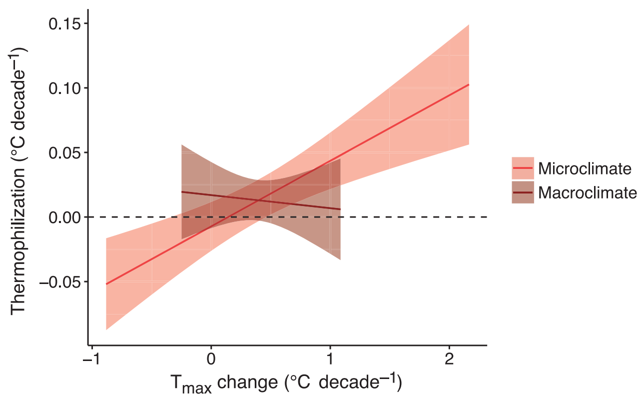
Fig. 1. Forest microclimate change after canopy cover changes over time is considerably more variable than macroclimate change. (**A**) Distribution of the 2955 resurveyed forest plots (black dots) in 56 regions (purple circles, scaled to the number of plots as indicated at the top right) across the temperate forest biome (green area) in Europe. We representatively sampled microclimate temperature in 100 forest stands, i.e., in 10 stands in each of 10 regions (black circles; effective n = 96) to estimate the maximum (macroclimate) temperature buffering during the growing season as a function of canopy cover (*23*) (fig. S2). (**B**) Schematic overview of the method used to approximate microclimate change in the forest understory. In this example, canopy cover at the time of the baseline survey was higher than that during the resurvey, resulting in a decrease in macroclimate temperature buffering from 2 to 1°C, which in turn led to a relatively larger increase in microclimate warming (20 to 23°C) compared with macroclimate warming (22 to 24°C). The relationship between canopy cover and the buffering of maximum macroclimate temperature was empirically assessed across the study area (fig. S2) (*21*). (**C**) Rate of macroclimate change plotted against the rate of microclimate change, with the black bisecting line representing the 1:1 relationship. Micro- and macroclimate have both significantly warmed (see text for statistical results). The distributions of values in the rates of micro- and macroclimate change are indicated by gray shading on each axis. Microclimate change rates are 45% more variable than macroclimate change rates, and macroclimate change rates only accounted for about half of the variation in microclimate change rates, as indicated by the marginal (conditional) R^2 value of 0.52 (0.69). All statistical results are based on mixed-effects models with region as a random-effect (intercept) term.

FIG. 1B DESIGNED BY FREEPICK.COM

resurvey, we applied a previously published statistical model to estimate temperature buffering as a function of canopy cover (*21*, *23*) (fig. S2). The predicted maximum temperatures in the forest understories have significantly increased over the past decades, with mean (±SEM) rates of 0.40 ± 0.04 and 0.38 ± 0.03°C per decade for micro- and macroclimate warming, respectively (both estimates of warming rates are based on mixed-effects models: $P < 0.001$). However, the rate of microclimate change was 45% more variable (1st and 99th percentiles: –0.32 to 1.36°C per decade) than the rate of macroclimate change (1st and 99th percentiles: –0.08 to 1.08°C per decade) (fig. S4). The rate of macroclimate change was significantly ($P < 0.001$) related to the rate of microclimate change but left 48% of the total variation in microclimate change unexplained (slope: 1.05, R^2 = 0.52, $P < 0.001$) (Fig. 1C).

To quantify the thermophilization, we inferred the thermal affinity for each vascular plant species present in our dataset from its current distribution ranges. Using these species-specific temperature affinity values, we calculated the rate of change in the community-based maximum temperature affinity values between the resurvey and baseline survey (*14*, *23*) (fig. S6). We expected changes in maximum temperature affinity values to be most closely related to changes in micro- and macroclimate maximum temperatures during the growing season (*23*). This biotic reconstruction of temperature changes based on the observed changes in the composition of species assemblages has been widely used to assess community-level climate change impacts in a variety of terrestrial and marine taxa (*12*–*14*, *16*). The resulting thermophilization rates across the 2955 permanent plots ranged from –0.84 to 1.05°C per decade, with a mean (±SEM) of 0.01 ± 0.01°C [which was not significantly different from zero (P = 0.09) (*23*)]. The thermophilization rate of forest understory vegetation was positively linked to the rate of microclimate warming [scaled slope estimate: 0.02, 95th confidence interval (CI): 0.01 to 0.03, P < 0.001] but not to macroclimate warming (scaled slope estimate: –0.002, CI: –0.01 to 0.01, P = 0.70) (Fig. 2).

Fig. 2. Thermophilization in forest understory plant communities is related to microclimate change, not to macroclimate change. Thermophilization rates increase with increasing microclimate warming of maximum temperatures during the growing season (T_{max}), as shown by the regression slope and 95% CIs for microclimate. The thermophilization rate was not statistically related to the rate of macroclimate warming (see text for statistical results).



To quantify how forest microclimate affected the observed climatic debt accumulated by a plant community in a given plot, we subtracted the thermophilization rate (ΔT_{plant}) per unit of time (Δt) from the rate of microclimate change (ΔT_{micro}) per unit of time [i.e., microclimate debt: $(\Delta T_{micro}/\Delta t)$ – $(\Delta T_{plant}/\Delta t)$] and from macroclimate change (ΔT_{macro}) per unit of time [i.e., macroclimate debt: $(\Delta T_{macro}/\Delta t)$ – $(\Delta T_{plant}/\Delta t)$] in each focal plot. Despite very similar means (±SEM) for the microclimatic debt (0.38 ± 0.04°C per decade) and macroclimatic debt (0.37 ± 0.04°C per decade), the climatic debts calculated using macroclimate data underrepresent the variability in microclimatic debt (fig. S7). We found

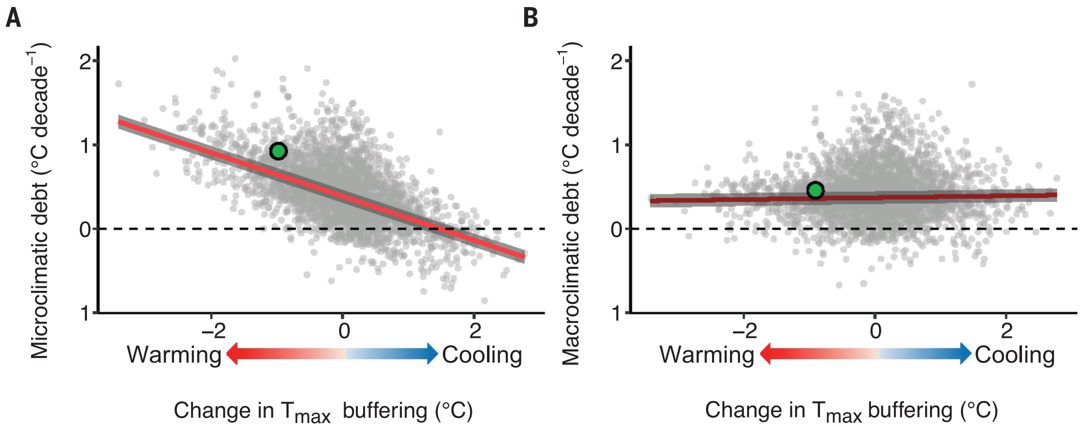


Fig. 3. Temperature buffering by canopy cover explains the climatic debt in forest plant communities. (**A**) Climatic debt calculated based on microclimate temperature change (i.e., microclimatic debt) increases with decreasing maximum temperature (T_{max}) buffering after a reduction of canopy cover [slope: –1.88, marginal (conditional) R^2 = 0.51 (0.75), P < 0.001]. Negative values on the *x*-axis represent a warming effect (reduced canopy cover and thus less T_{max} buffering); positive values represent a cooling effect (increased canopy cover and thus more T_{max} buffering). (**B**) Climatic debts calculated using macroclimate temperature change (i.e., macroclimate debt) are only weakly related to differences in temperature buffering [slope: 0.13, marginal (conditional) R^2 = 0 (0.25), P = 0.06]. The linear regression lines are plotted including the 95% CIs (gray bands). The green dots indicate exemplified micro- and macroclimate debts after the change (reduction) in T_{max} buffering illustrated in Fig. 1B.

the greatest microclimate warming in areas where canopy cover and thus the temperature buffering declined, and these were also areas where the microclimatic debt was greatest (Fig. 3A). Despite higher thermophilization rates with increasing microclimate warming (Fig. 2), locally increased heat caused by a reduction of canopy cover impedes the ability of understory plant communities to respond to such high rates of warming. On the contrary, we found lower microclimatic debts in sites with increased canopy cover; there, temperature buffering led to a cooling effect during the growing season. These patterns remain hidden when analyzing climatic debts based on macroclimate data (Fig. 3B). Realistic assessments of the current pressures on communities caused by climate warming thus require long-term data on microclimate change.

Canopy cover dynamics have triggered microclimate changes over time in forest interiors that can differ considerably from macroclimate changes outside forests. This has important implications for predicting biodiversity responses to climate and land use (e.g., forest management) change, which interactively drive the emergence of new thermal environments. With the predicted increase of heat waves (*4*), many species and communities may suffer greatly from loss of canopy cover, e.g., after tree harvesting or dieback (*24*). The resulting impacts are serious because forests harbor most of the terrestrial biodiversity and many ecosystem services and livelihoods critically depend on forest biodiversity (*1*, *25*). Forest managers and policy-makers should therefore consider the effects of different forest management practices on local microclimates in their endeavors to safeguard forest biodiversity in a warming world.

Our results support the hypothesis that the thermophilization rate in forest understory plant communities is primarily driven by the rate of subcanopy microclimate change (*10*, *12*) and not by the rate of macroclimate change. This finding provides empirical evidence that microclimate change ultimately drives organismal responses to climate change, a frequently ignored fact when using macroclimate data to study biotic responses to climate change (*8*, *26*, *27*).

Increasing climatic debts in community responses to climate change mean that a growing number of species are occurring in suboptimal climatic conditions, potentially accelerating the loss of biodiversity. Our results suggest that microclimates can amplify as well as decrease the disequilibrium between community responses and macroclimate change, suggesting that climatic debts based on macroclimate data (*13*, *20*) should be revisited and interpreted with caution. Microclimate data, therefore, considerably improve the local relevance of the climatic debt concept for climate change impact assessments on biodiversity, a field that will benefit from emerging datasets and methods to quantify microclimatic variability in space and over time (*28*, *29*). In fact, high rates of microclimate warming can greatly exceed the capacity of understory plant species to spatially track their thermal niche, suggesting that other factors limiting species establishment, such as plant–water relations (*30*), habitat fragmentation, and dispersal limitation, may impede or severely delay community responses (*11*). Such effects may outweigh remedial effects of microclimate variability to reduce the pressures of climate change on biological communities, e.g., by providing thermal refuges and facilitating short-distance thermal niche tracking (*27*, *31*, *32*).

In this study, we have provided evidence that forest community responses to climate change are most closely related to microclimate change and not to macroclimate change. Despite widespread evidence for thermophilization trends in plant communities (*14*, *17*), many community responses are strongly lagging behind warming, thereby accumulating a climatic debt (*10*). Growing pressures from woody biomass extraction and the increasing vulnerability of forests to climate change will lead to frequent canopy cover disturbance and tree dieback (*33*). This will severely intensify the emergence of adverse thermal habitat conditions for many species, impeding the ability of communities to keep track with anthropogenic environmental changes. Our findings also show that climate change impacts on forest plant communities have been reduced by higher standing stocks and associated cooling after increases in thermal buffering (*34*). Accounting for the microclimate in assessments of the impact of global change on forest biodiversity and functioning is crucial if we are to better understand and counteract the increasing pressures imposed on forests.

REFERENCES AND NOTES

1. G. T. Pecl *et al.*, *Science* **355**, eaai9214 (2017).
2. B. R. Scheffers *et al.*, *Science* **354**, aaf7671 (2016).
3. C. Parmesan, *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).
4. Intergovernmental Panel on Climate Change, *AR5 Climate Change 2014: Impacts, Adaptation, and Vulnerability* (2014); https://www.ipcc.ch/report/ar5/wg2/.
5. World Meteorological Organization, *Guide to Meteorological Instruments and Methods of Observation* (2008); https://www.weather.gov/media/epz/mesonet/CWOP-WMO8.pdf.
6. C. Moritz, R. Agudo, *Science* **341**, 504–508 (2013).
7. R. Geiger, R. H. Aron, P. Todhunter, *The Climate Near the Ground* (Rowman and Littlefield, 2003).
8. K. A. Potter, H. Arthur Woods, S. Pincebourde, *Glob. Chang. Biol.* **19**, 2932–2939 (2013).
9. P. De Frenne *et al.*, *Nat. Ecol. Evol.* **3**, 744–749 (2019).
10. R. Bertrand *et al.*, *Nature* **479**, 517–520 (2011).
11. J. M. Alexander *et al.*, *Glob. Change Biol.* **24**, 563–579 (2018).
12. B. Fadrique *et al.*, *Nature* **564**, 207–212 (2018).
13. V. Devictor *et al.*, *Nat. Clim. Chang.* **2**, 121–124 (2012).
14. P. De Frenne *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 18561–18565 (2013).
15. J. Lenoir, J. C. Svenning, *Ecography* **38**, 15–28 (2015).
16. R. D. Stuart-Smith, G. J. Edgar, N. S. Barrett, S. J. Kininmonth, A. E. Bates, *Nature* **528**, 88–92 (2015).
17. M. Gottfried *et al.*, *Nat. Clim. Chang.* **2**, 111–115 (2012).
18. S. R. Loarie *et al.*, *Nature* **462**, 1052–1055 (2009).
19. M. T. Burrows *et al.*, *Science* **334**, 652–655 (2011).
20. R. Bertrand *et al.*, *Nat. Commun.* **7**, 12643 (2016).
21. F. Zellweger *et al.*, *Glob. Ecol. Biogeogr.* **28**, 1774–1786 (2019).
22. T. Jucker *et al.*, *Glob. Chang. Biol.* **24**, 5243–5258 (2018).
23. Materials and methods are available as supplementary materials.
24. A. J. Nowakowski *et al.*, *Ecol. Lett.* **21**, 345–355 (2018).

25. Millennium Ecosystem Assessment, *Ecosystems and Human Well-Being: Biodiversity Synthesis* (World Resource Institute, 2005); https://www.millenniumassessment.org/documents/document.354.aspx.pdf.
26. I. Bramer *et al*., *Adv. Ecol. Res.* **58**, 101–161 (2018).
27. J. Lenoir, T. Hattab, G. Pierre, *Ecography* **40**, 253–266 (2017).
28. F. Zellweger, P. De Frenne, J. Lenoir, D. Rocchini, D. Coomes, *Trends Ecol. Evol.* **34**, 327–341 (2019).
29. M. R. Kearney, P. K. Gillingham, I. Bramer, J. P. Duffy, I. M. D. Maclean, *Methods Ecol. Evol.* (2019).
30. C. P. Reyer *et al*., *Glob. Chang. Biol.* **19**, 75–89 (2013).
31. A. J. Suggitt *et al*., *Nat. Clim. Chang.* **8**, 713–717 (2018).
32. D. Scherrer, C. Körner, *J. Biogeogr.* **38**, 406–416 (2011).
33. M. Lindner *et al*., *For. Ecol. Manage.* **259**, 698–709 (2010).
34. S. Gold, A. Korotkov, V. Sasse, *For. Policy Econ.* **8**, 183–192 (2006).
35. F. Zellweger *et al*., Data and code for: Forest microclimate dynamics drive plant responses to warming, Dryad (2020); https://doi.org/10.5061/dryad.r7sqv9s83.

ACKNOWLEDGMENTS

We thank P. Hommel, D. Closset-Kopp, M. Diekmann, K. Kirby, and G.-R. Walther for providing data. **Funding:** F.Z. received funding from the Swiss National Science Foundation (project 172198) and the Isaac Newton Trust, P.D.F. and P.V. from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (ERC Starting Grant FORMICA 757833), and K.V. from ERC Consolidator Grant PASTFORWARD (614839). The Czech Science Foundation and Czech Academy of Sciences funded M.C., O.V., and R.H. (17-09283S, RVO 67985939); M. Macek and M.K. (17-13998S, RVO 67985939); and P.P. (RVO 67985939). M. Malicki received funding from the Czech Science Foundation (project GACR 20-28119S). T.N. received funding from the Slovenian Research Agency (J4-1765). B.T. received funding from the Ministry for Innovation and Technology in Hungary. I.B. received funding from Agrárklíma II (VKSZ_12-1-2013-0034). R.P. received funding from the Polish Ministry of Science and Higher Education (DS-3421). F.M. received funding from the Slovak Research and Development Agency (APVV-15-0270). **Author contributions:** F.Z., P.D.F., and D.C. conceived and designed research. F.Z. analyzed the data with help from P.D.F. P.V. and P.D.F. calculated the thermal response curves. J.L. contributed data and valuable methodological comments. All other authors contributed data. F.Z. wrote the manuscript together with P.D.F. and D.C. All other authors commented, edited, and approved the manuscript. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Data and code used in this study are available on Dryad (*35*).

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/368/6492/772/suppl/DC1
Materials and Methods
Figs. S1 to S10
References (*36*–*60*)

8 January 2020; accepted 12 March 2020
10.1126/science.aba6880

Science

Forest microclimate dynamics drive plant responses to warming

Florian Zellweger, Pieter De Frenne, Jonathan Lenoir, Pieter Vangansbeke, Kris Verheyen, Markus Bernhardt-Römermann, Lander Baeten, Radim Hédl, Imre Berki, Jörg Brunet, Hans Van Calster, Markéta Chudomelová, Guillaume Decocq, Thomas Dirnböck, Tomasz Durak, Thilo Heinken, Bogdan Jaroszewicz, Martin Kopecký, Frantisek Mális, Martin Macek, Marek Malicki, Tobias Naaf, Thomas A. Nagel, Adrienne Ortmann-Ajkai, Petr Petrík, Remigiusz Pielech, Kamila Reczynska, Wolfgang Schmidt, Tibor Standovár, Krzysztof Swierkosz, Balázs Teleki, Ondrej Vild, Monika Wulf and David Coomes

Science **368** (6492), 772-775.
DOI: 10.1126/science.aba6880

Local factors restrain forest warming

Microclimates are key to understanding how organisms and ecosystems respond to macroclimate change, yet they are frequently neglected when studying biotic responses to global change. Zellweger *et al.* provide a long-term, continental-scale assessment of the effects of micro- and macroclimate on the community composition of European forests (see the Perspective by Lembrechts and Nijs). They show that changes in forest canopy cover are fundamentally important for driving community responses to climate change. Closed canopies buffer against the effects of macroclimatic change through their cooling effect, slowing shifts in community composition, whereas open canopies tend to accelerate community change through local heating effects.

Science, this issue p. 772; see also p. 711

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.