

Microclimate moderates plant responses to macroclimate warming

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Edited by Harold A. Mooney, Stanford University, Stanford, CA, and approved September 24, 2013 (received for review June 13, 2013)

Recent global warming is acting across marine, freshwater, and terrestrial ecosystems to favor species adapted to warmer conditions and/or reduce the abundance of cold-adapted organisms (i.e., “thermophilization” of communities). Lack of community responses to increased temperature, however, has also been reported for several taxa and regions, suggesting that “climatic lags” may be frequent. Here we show that microclimatic effects brought about by forest canopy closure can buffer biotic responses to macroclimate warming, thus explaining an apparent climatic lag. Using data from 1,409 vegetation plots in European and North American temperate forests, each surveyed at least twice over an interval of 12–67 y, we document significant thermophilization of ground-layer plant communities. These changes reflect concurrent declines in species adapted to cooler conditions and increases in species adapted to warmer conditions. However, thermophilization, particularly the increase of warm-adapted species, is attenuated in forests whose canopies have become denser, probably reflecting cooler growing-season ground temperatures via increased shading. As standing stocks of trees have increased in many temperate forests in recent decades, local microclimatic effects may commonly be moderating the impacts of macroclimate warming on forest understories. Conversely, increases in harvesting woody biomass—e.g., for bioenergy—may open forest canopies and accelerate thermophilization of temperate forest biodiversity.

climate change | forest management | understory | climatic debt | range shifts

Biological signals of recent global warming are increasingly evident across a wide array of ecosystems (1–7). However, the temperature experienced by organisms at ground level (microclimate) can substantially differ from the atmospheric temperature due to local land cover and terrain variation in terms of vegetation structure, shading, topography, or slope orientation (8–15). The daytime or nighttime surface temperature in rough mountain terrain, for instance, can deviate by up to 9 °C from the air temperature (10). Likewise, forest structure creates substantial

temperature heterogeneity, with the interior daytime temperature in dense forests being commonly several degrees cooler than in more open habitats during the growing season (12–15). Spatial microclimatic temperature variation can thus be substantial relative to projected changes in average temperature over time, and biotic

Significance

Around the globe, climate warming is increasing the dominance of warm-adapted species—a process described as “thermophilization.” However, thermophilization often lags behind warming of the climate itself, with some recent studies showing no response at all. Using a unique database of more than 1,400 resurveyed vegetation plots in forests across Europe and North America, we document significant thermophilization of understory vegetation. However, the response to macroclimate warming was attenuated in forests whose canopies have become denser. This microclimatic effect likely reflects cooler forest-floor temperatures via increased shading during the growing season in denser forests. Because standing stocks of trees have increased in many temperate forests in recent decades, microclimate may commonly buffer understory plant responses to macroclimate warming.

Author contributions: P.D.F., F.R.-S., D.A.C., G.M.D., B.J.G., and K.V. designed research; P.D.F., F.R.-S., L.B., G.V., M.V., M.B.-R., C.D.B., J.B., J.C., G.M.D., H.D., O.E., F.S.G., R.H., T.H., M.H., P.H., M.A.J., D.L.K., K.J.K., F.J.G.M., T.N., M.N., G.P., P.P., J.S., G.S., H.V.C., D.M.W., G.-R.W., P.S.W., K.D.W., M.W., and K.V. performed research; P.D.F., F.R.-S., L.B., G.V., and K.V. analyzed data; and P.D.F., F.R.-S., D.A.C., L.B., M.V., M.B.-R., C.D.B., J.B., J.C., G.M.D., O.E., F.S.G., R.H., T.H., M.H., M.A.J., D.L.K., K.J.K., M.N., G.P., P.P., G.S., H.V.C., D.M.W., P.S.W., K.D.W., B.J.G., and K.V. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1311190110/-DCSupplemental.

preferences (26). Communities with many cold-adapted species will thus have a lower floristic temperature, and vice versa. To assess thermophilization over time, we compared the mean, fifth, and 95th percentiles of the temperature distribution for every plot at the old and recent survey, respectively (Fig. 1D). The shift of the mean of the distribution of floristic temperatures (in degrees Celsius per decade) then reflects the mean thermophilization. In contrast, shifts in the tails of the distribution of plot-level floristic temperatures (fifth and 95th percentiles) reflect changes in the occurrence of cold and warm-adapted species, respectively (Fig. 1D).

Results and Discussion

Significant community turnover took place over time in the temperate forests we sampled: on average, one-third of the species present in the old surveys has been replaced by other species today; the mean Lennon dissimilarity index (*SI Materials and Methods*) across all plots was 0.69 (95% bootstrapping confidence interval: [0.68, 0.70]), both in Europe (dissimilarity was 0.70 [0.69, 0.71]) and North America (0.65 [0.62, 0.68]). This floristic turnover partly arose from the nonrandom replacement of species in terms of their temperature preferences, illustrated by significant thermophilization both in European and eastern North American forests (Fig. 2A). On average, the estimated thermophilization rate was $0.041^{\circ}\text{C}\cdot\text{decade}^{-1}$ (the range across 10 different modeling methods was $0.027\text{--}0.056^{\circ}\text{C}\cdot\text{decade}^{-1}$; *Table S4*). Significant interregional variation was present, with thermophilization rates ranging from $+0.83^{\circ}\text{C}\cdot\text{decade}^{-1}$ (Great Smoky Mountains) to $-0.64^{\circ}\text{C}\cdot\text{decade}^{-1}$ (Ireland). Thermophilization was significantly positive in 20 of 29 regions, sig-

nificantly negative in eight study regions, and unchanged in one region (Fig. 2B).

The overall thermophilization of understory plant communities has been driven by concurrent gains of relatively warm-adapted species and loss of cold-adapted taxa, as revealed by the shifts in the cold (fifth percentile) and warm (95th percentile) ends of the floristic temperature distribution (Fig. 2C). In the eastern North American forest plots, however, both warm-adapted and cold-tolerant species have increased (Fig. 2C) due to continuous immigration of new species (i.e., overall increase in species richness), which does not occur in the European plots (*SI Results*). The mean thermophilization of understory plant communities that we observe across temperate deciduous forests in two continents expands on earlier findings that mountain vegetation communities are showing increases of lower-altitude species at higher altitudes, leading to novel species assemblages (3, 4, 27). The thermophilization of vegetation is consistent with the warming climate observed across the regions: the mean rise in April-to-September temperatures between the old and recent survey was $0.28^{\circ}\text{C}\cdot\text{decade}^{-1}$ (*Table S1*). We found a positive relationship between the thermophilization and the region-specific April-to-September temperature change, indicating higher thermophilization in areas with higher rates of warming (mean slope 0.07 , $P < 0.001$; *SI Results*). European and North American temperate deciduous forest vegetation is thus changing as expected by macroclimate warming, but thermophilization lags behind rising temperatures.

We found that local changes in forest canopy cover modulate the thermophilization of vegetation; thermophilization was lowest in forests that became denser, and highest in forests that

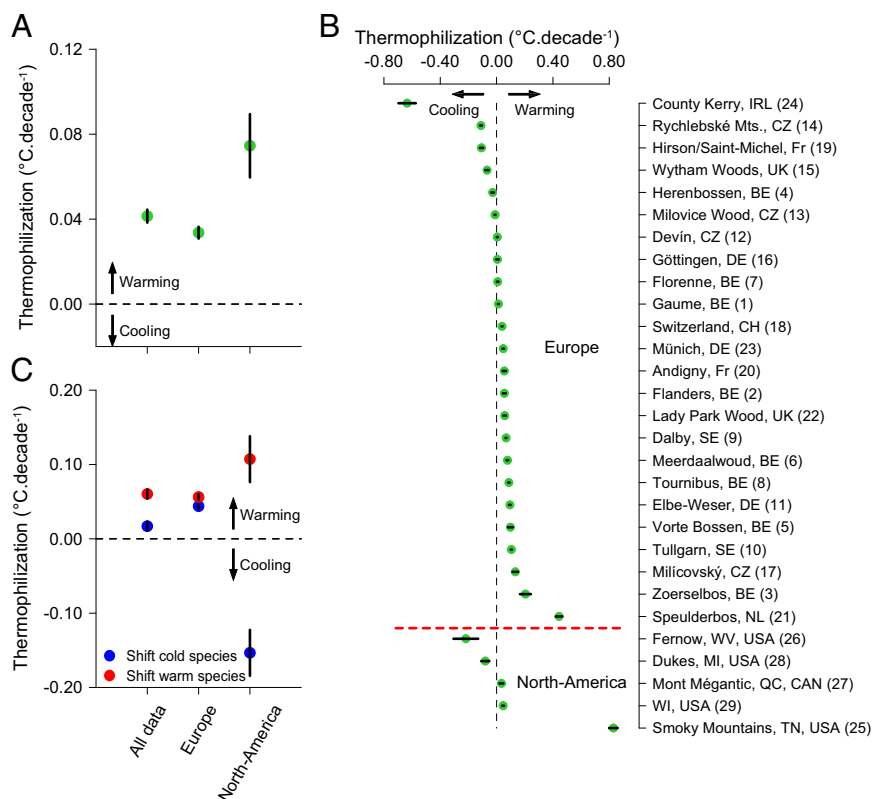


Fig. 2. Thermophilization of temperate forest understories across Europe and North America. (A and B) Mean thermophilization (positive values denote increases over time) for all data and in European and American forests (A) and for the individual regions (B). The numbers between brackets refer to the sites in Fig. 1. (C) Mean shifts in relatively cold-adapted (blue) and warm-adapted species (red) for all plots, and in Europe and North America. Positive values reflect positive shifts of the left and right tail, i.e., decreases of cold-adapted and increases of warm-adapted taxa, respectively. Error bars denote the 95% confidence intervals based on 500 resampled species' temperature preferences.

Calculation of Thermophilization. We calculated the thermophilization for each plot by sampling from the inferred temperature preference distributions of the species present (Fig. 1). The long-term mean temperature and precipitation in the growing season (April to September; Fig. S2) were used to estimate species' thermal response curves by means of ecological niche modeling (16). To account for variability and uncertainty in species' thermal preferences and niche widths (26), the distribution of plot-level floristic temperatures at each survey was constructed by resampling 500 times from species' thermal response curves. The mean thermophilization per plot was quantified as the difference between the mean floristic temperature (in degrees Celsius) between the recent and original survey, divided by the time interval (in decades) between the two surveys. In addition, we determined the contribution of the loss of cold-adapted and the gain of warm-adapted species to the thermophilization patterns by quantifying the shifts in the left and right tails (fifth and 95th percentiles, respectively) of the plot-level distribution of floristic temperatures (Fig. 1D and Figs. S3 and S4).

Forest Cover and Temperature Change vs. Thermophilization. The relationships between forest canopy cover and temperature changes on the one hand,

and thermophilization on the other hand (shifts in the mean, fifth, and 95th percentiles of the distribution of floristic temperatures over time) were assessed using mixed-effect models with "study region" as a random-effect term for each of the 500 resampled species' temperature preferences. Sensitivity analyses revealed that excluding precipitation, applying various climatic periods, study area extents, and modeling approaches, and randomly removing subsets of species resulted in consistent results (see *SI Materials and Methods* for a detailed account of the methods and *SI Results* for supporting results).

ACKNOWLEDGMENTS. We thank J. Kartesz and M. Nishino for the American species distribution maps, two anonymous reviewers for valuable comments, and the Research Foundation–Flanders (FWO) for funding the scientific research network FLEUR. Support for this work was provided by FWO Postdoctoral Fellowships (to P.D.F. and L.B.), European Union Seventh Framework Programme FP7/2007–2013 Grant 275094 (to F.R.-S.), the Natural Sciences and Engineering Research Council of Canada (M.V. and C.D.B.), and long-term research development project RVO 67985939 (to R.H. and P.P.).

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