

Microclimate moderates plant responses to macroclimate warming

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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.

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responses to macroclimate warming may be buffered by microclimatic heterogeneity (9–11). It seems likely that microclimates can modulate the large-scale, multispecies, and long-term response of biota to macroclimate warming, but this is currently unverified. Testing this idea will permit incorporation of fine-grained thermal variability into bioclimatic modeling of future species distributions (11, 16), and is particularly relevant to forest understories, which play a key role in vital ecosystem services of forests such as tree regeneration, nutrient cycling, and pollination (17, 18). Additionally, microclimatic buffering might help to explain the lag of community responses to increased temperature that has been reported for several taxa and regions (3, 5, 7).

Temperate forests comprise 16% (5.3 million km²) of the world's forests (19), and understory plants represent on average more than 80% of temperate forest plant diversity (17). Temperate forests have recently experienced pronounced climate warming, but have also been heavily influenced by other environmental changes. Changing forest management regimes due to altered socioeconomic conditions, but also eutrophication, climate warming, and fire suppression, have resulted in increased tree growth, standing stocks, and densities in many temperate forests of the northern hemisphere (20–25). In Western Europe, for instance, logging and natural losses of tree biomass have been consistently lower than annual growth increments, resulting in an almost doubling of standing stocks of trees per hectare between 1950 and 2000 (21). Hence, forests' powerful influence on ter-

restrial microclimates raises the intriguing possibility that non-climatic drivers of global change, such as forest canopy closure, might have lowered ground-level temperatures via increased shading, thereby counteracting the effects of macroclimate warming on the forest understory.

Here we compiled plant occurrence data (1,032 species in total) from 1,409 resurveyed vegetation plots in temperate deciduous forests. The plots were distributed across 29 regions of temperate Europe and North America (Fig. 1A and B) with an average interval of 34.5 y (range: 12–67 y) between the original and repeated vegetation surveys (Table S1). From these plots, we tested for plant community responses to recent macroclimate warming and assessed the potential role of changes in forest canopy cover in modulating such responses. To quantify possible thermophilization of communities, we inferred the temperature preferences of species from distribution data by means of ecological niche modeling (16) (Fig. 1A–C). This method builds on previous use of species' temperature preferences to assess community-level climate-change impacts (3–6). We then calculated the floristic temperature for each plot by sampling from the temperature preference distributions of all species that were present at the time of the surveys. The probability of sampling a temperature for a particular species was determined by the shape of its thermal response curve as estimated by niche modeling. We repeated this resampling procedure 500 times to account for the variability and uncertainty in species' temperature

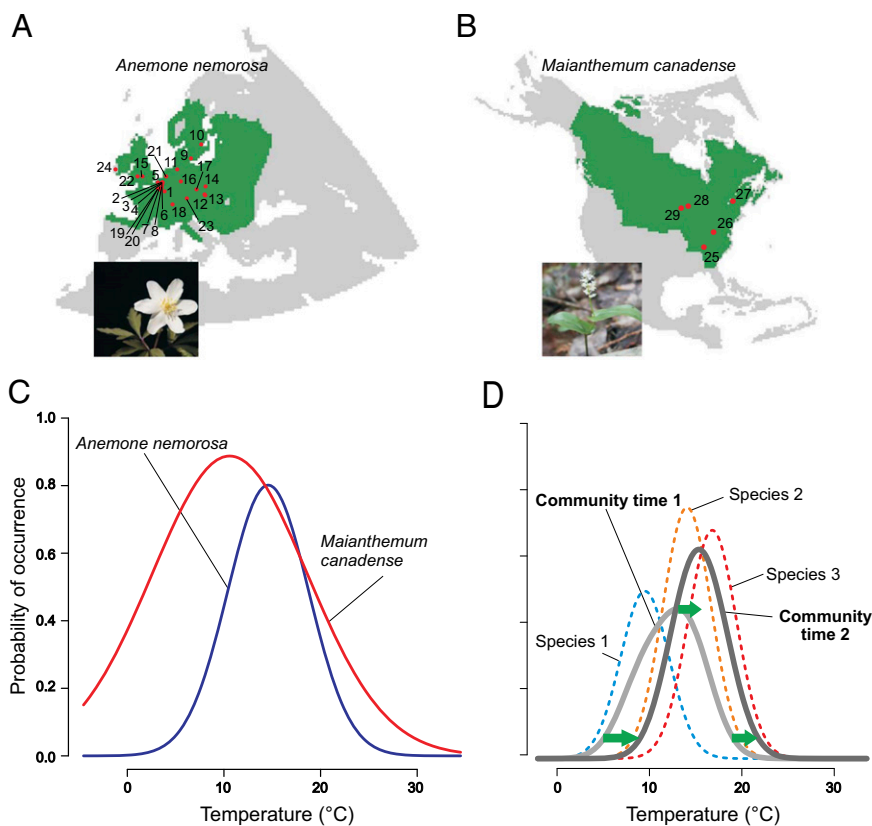


Fig. 1. Estimation of plant thermal response curves and temporal community-level responses to warming. (A–C) Thermal response curves were estimated from species' current distribution ranges (green areas in maps). The two most frequent understory species in the database are shown as an example: *Anemone nemorosa* from Europe (A) and *Maianthemum canadense* from North America (B) (Tables S2 and S3). The red dots indicate the locations of the 29 study regions and numbers refer to site descriptions in Table S1. (D) Hypothetical community response to warming: the community consists of species 1 and 2 at time 1 and species 2 and 3 at time 2, which results in thermophilization between time 1 and 2 because the more cold-adapted species 1 is lost from the community, and the more warm-adapted species 3 is gained. The green arrows represent the temporal shift of the mean, left tail (fifth percentile) and right tail (95th percentile) of the distribution of floristic temperatures and reflect the degree to which the mean thermophilization increases, cold-adapted species decrease, and warm-adapted species increase, respectively.

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 $0.041\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$ (the range across 10 different modeling methods was $0.027\text{--}0.056\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$; *Table S4*). Significant interregional variation was present, with thermophilization rates ranging from $+0.83\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$ (Great Smoky Mountains) to $-0.64\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$ (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 $0.28\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$ (*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

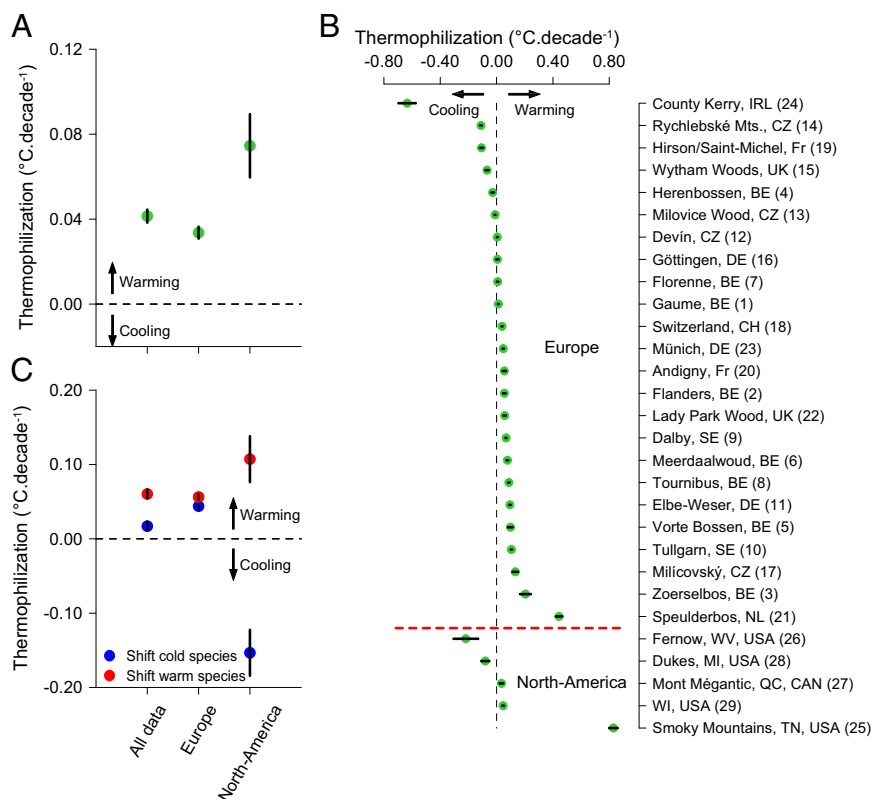


Fig. 2. Thermophilization of temperate forest understories across Europe and North America. (A and B) Mean thermophilization (positive values denote increases over time) for all data and in European and American forests (A) and for the individual regions (B). The numbers between brackets refer to the 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.

became more open over time (Fig. 3A). The relationship between forest canopy cover changes and the mean thermophilization was significantly negative (mean slope = -0.0073 , $P < 0.001$, range of slopes across 10 different modeling methods -0.0392 to -0.0015 ; Table S5). Moreover, the increase of warm-adapted species was consistently lower in plots that increased in canopy cover compared with plots that became more open over time, which experienced stronger thermophilization (mean slope = -0.0170 , $P < 0.001$, range across 10 different modeling methods -0.0463 to -0.0099). For cold-adapted species, the effects of canopy cover changes were lower and more variable (mean slope = -0.0071 , $P < 0.05$, range across 10 different modeling methods -0.0584 to $+0.0083$). Thus, cold-adapted taxa responded to a lesser extent to changes in forest canopy cover (Fig. 3B). Taken together, these results suggest that recent forest canopy closure in northern-hemispheric temperate forests has buffered the impacts of macroclimate warming on ground-layer plant communities, thus slowing changes in community composition.

Forest canopy closure modulates macroclimatic trends through the effects on local microclimates. Dense tree canopies not only lower ground-layer temperatures but also increase relative air humidity and shade in the understory (12–15). Hence, the reported decrease in light-demanding understory plants in Europe (28) is also congruent with the local environmental effects caused by forest canopy closure. Higher relative humidity in dense forests can also protect forest herbs and tree seedlings from summer drought, decreasing mortality and thus buffering the impacts of large-scale climate change (15, 29). Furthermore, many forest herbs are known to be slow-colonizing species (30). Given the high degree of habitat fragmentation in contemporary landscapes, microclimatic buffering in dense forests may be a critical mechanism to ensure the future conservation of temperate forest plant diversity.

If forest canopy closure attenuates warming in the understory, atmospheric temperatures provide an unrealistic benchmark against which to compare floristic temperatures. Hence, land-use changes such as forest canopy closure could partially explain the lag observed between, for instance, lowland forest plant community composition (3) and temperature trends as measured

in weather stations (i.e., above dwarf vegetation in open areas). Instead of accumulating climatic lags, these understory communities could be mostly exploiting the buffering microclimatic effects brought about by canopy closure. Therefore, measuring climate change in the field and identifying the actual climatic lags of biota is crucial to further our understanding of community reordering and future biodiversity conservation in the face of climate change.

In sum, we observed increasing dominance of warm-adapted understory plants across more than 1,400 plots and 29 regions in European and North American temperate deciduous forests. Additionally, our most striking finding is the temporal buffering of the continent-wide response of understory vegetation to macroclimate warming by forest canopy closure. The importance of increased canopy cover in influencing understory biodiversity is particularly relevant in an era when forest management worldwide is confronted with increasing demands for woody biomass, not least as an alternative source of renewable energy (31, 32). In addition, current conservation actions in European forests are regularly directed toward restoring traditional management (e.g., coppicing in ancient forests), resulting in canopy opening. Such actions could not only result in soil nutrient depletion, lower biomass pools, and enhanced soil nitrogen release (28, 31), but also, depending on the silvicultural system applied, increase temperatures at the forest floor (12–15). Large-scale reopening of the canopy for woody biomass harvesting may thus hasten thermophilization of understory plant communities of temperate forests.

Materials and Methods

Understory Resurveys. We compiled complete species lists of 1,409 rigorously selected (*SI Materials and Methods*) resurveyed vegetation plots in European and North American ancient deciduous forests, and determined forest canopy cover changes (sum of the tree and shrub species' canopy cover) for 854 of the plots (19 regions; Table S1 and Fig. S1). Plots were either permanently marked or semipermanent (i.e., with known coordinates; *SI Materials and Methods*), and plot sizes ranged between 1 and 1,000 m² (Table S1). Plot-level changes in canopy cover between the old and recent surveys were quantified as response ratios $\log(\text{cover}_{\text{recent}}/\text{cover}_{\text{old}})$.

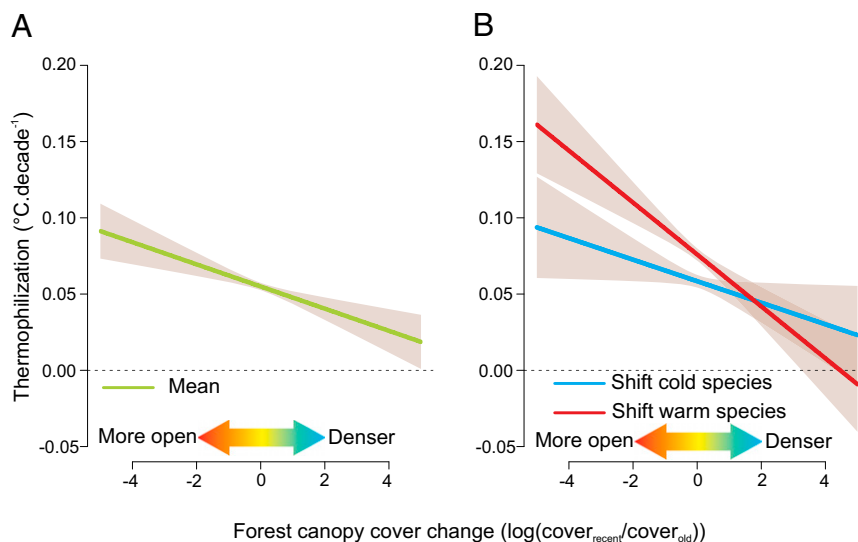


Fig. 3. Forest canopy closure modulates understory thermophilization. (A) Relationship between forest canopy cover change and mean thermophilization of understory plant communities in temperate European and North American forests. (B) Relationship between forest canopy cover change and decreases of cold-adapted species (expressed by the shift of the left tail of the plot-level distribution of floristic temperatures, blue) and increases of warm-adapted species (expressed by the shift of the right tail of the plot-level distribution of floristic temperatures, red). Relationships result from mixed-effect models for each of 500 samples; shaded areas denote 95% confidence intervals based on those samples. These results are mainly based on the European data (Table S1).

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).

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