

Global buffering of temperatures under forest canopies

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Macroclimate warming is often assumed to occur within forests despite the potential for tree cover to modify microclimates. Here, using paired measurements, we compared the temperatures under the canopy versus in the open at 98 sites across 5 continents. We show that forests function as a thermal insulator, cooling the understory when ambient temperatures are hot and warming the understory when ambient temperatures are cold. The understory versus open temperature offset is magnified as temperatures become more extreme and is of greater magnitude than the warming of land temperatures over the past century. Tree canopies may thus reduce the severity of warming impacts on forest biodiversity and functioning.

The biological impacts of macroclimate warming are increasingly evident across a wide array of ecosystems^{1–5}. However, many responses of biological communities and ecosystem processes are lagging behind the warming of the macroclimate^{6–11}. Such time lags may be the inevitable consequence of slow dispersal and demography^{3,7,8}, but may also be due to the buffering of localized microclimates by vegetation and topography, such that organisms do not necessarily experience the same degree of warming measured at weather stations^{12–18}. Biotic and abiotic features near the ground create heterogeneous microclimates, mostly through effects on radiation, air mixing, evapotranspiration and soil properties—all of which can influence biodiversity and ecosystem functioning^{17,18}.

To better predict the biotic consequences of climate change, we need to enhance our understanding of how the local temperature experienced by living organisms (referred to as the microclimate) changes across space and time. Macroclimates outside forests (sometimes referred to as free-air temperatures in the literature) are characterized by an extensive global network of weather stations that are established in the well-mixed air of open areas (for example, short grasslands) around 2 m above the soil surface^{19,20}—habitat conditions that are not representative of the conditions experienced by the majority of terrestrial species on Earth^{21,22}. The study of microclimates is not new, as microclimatological measurements began more than a century ago; however, most climate change studies rely on weather-station data that are specifically designed to correct for these microclimatic effects^{15–20}. Therefore, future projections of climate change that rely solely on macroclimate data ignore

the potential impact of microclimates on biodiversity and ecosystem functioning^{1,2,5}.

Microclimates are particularly evident in forests, where the large majority of species live underneath a canopy of trees that strongly influences the local thermal conditions^{10–13}. This is of major concern for global-change science because forests cover one-quarter of the Earth's land surface and harbour two-thirds of all terrestrial biodiversity^{20–23}; some studies have already shown that microclimatic buffering can mediate the response of forest communities to climate change^{8–11}.

Here we report a systematic, global meta-analysis that quantifies the thermal buffering capacity of the Earth's dominant forested ecosystems (tropical to boreal forests) across five continents (Fig. 1). Drawing on empirical studies with a strictly paired design (that is, comparing microclimate with macroclimate), we quantify the average temperature offset of forests and how the magnitude of such offsets depends on the macroclimatic context (that is, outside forests). From a total of 98 sites and 74 studies, we retrieved paired temperature time series and/or summary statistics (that is, minimum, mean or maximum temperatures) for exactly the same time period in (1) understory conditions in forests (microclimate) and (2) an adjacent open habitat without shade (macroclimate). For all data, temperature offset values were calculated as the temperatures inside forests minus macroclimate temperatures outside forests; negative values reflect cooler forest temperatures.

In our global analysis of 714 paired temperature data points, we found that tree canopies buffer forest floors against both high and low macroclimatic temperatures. The mean and maximum understory temperatures were, on average, cooler than macroclimate temperatures by $1.7 \pm 0.3^\circ\text{C}$ and $4.1 \pm 0.5^\circ\text{C}$, respectively (mean \pm s.e.m., mixed-effects models: both $P < 0.001$). Conversely, the minimum temperatures of the forest understory were $1.1 \pm 0.2^\circ\text{C}$ warmer than the macroclimate outside the forest (mixed-effects model: $P < 0.001$; Fig. 1, Supplementary Figs. 1 and 2). Thus, forest understories are not only cooler on average than nearby open habitats, but negative maximum temperature offsets (cooler in forests) and positive minimum temperature offsets (warmer in forests) also indicate lower temperature variation below the forest canopy.

Across the globe, the temperature offset of forests was negatively correlated with the macroclimate temperature outside forests. Temperature offsets became more negative (that is, lower temper-

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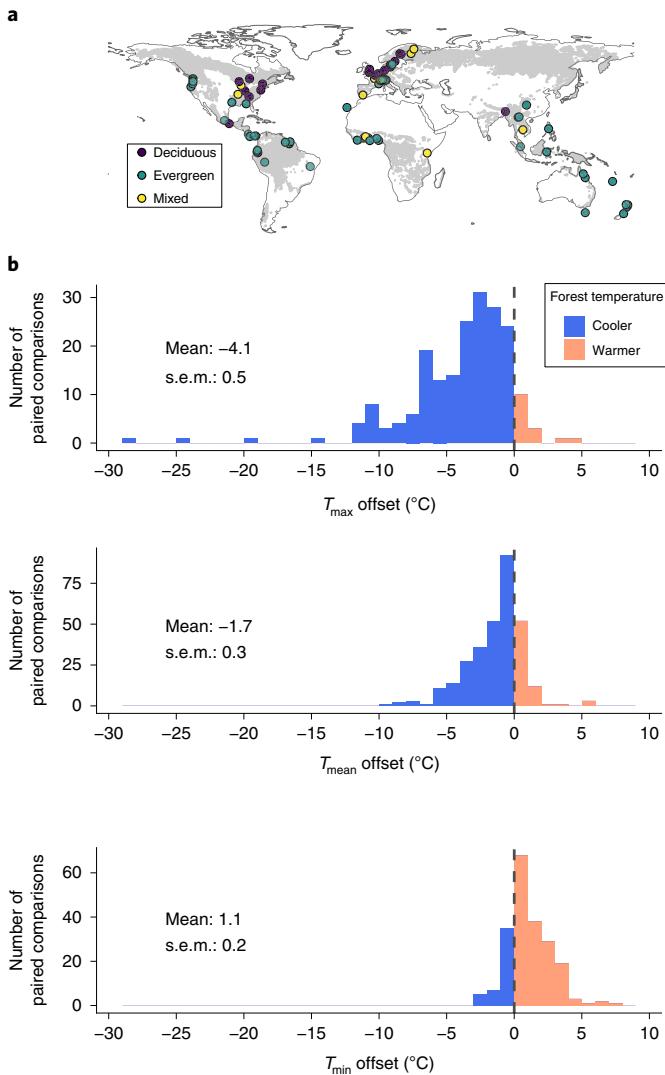


Fig. 1 | Forests buffer temperatures under canopies globally. **a,** Distribution of the 98 study sites and their vegetation types. **b,** Histograms display the 714 paired temperature offset values for maximum (T_{\max}), mean (T_{mean}) and minimum (T_{\min}) temperatures. Maximum and mean temperatures are consistently cooler, and minimum temperatures consistently warmer, within forests compared to macroclimate temperatures. Temperature offset means \pm s.e.m. are based on mixed-effects models with study as a random-effect term. Full statistical analyses, data and code are reported in the Supplementary Information and ref. ³⁷. Credit: The grey map background in **a** shows the global distribution of forests, from <https://www.unep-wcmc.org/resources-and-data/generalised-original-and-current-forest>; the world map is from <http://www.naturalearthdata.com/>.

tures in forests) as macroclimate temperature increased, and more positive (that is, higher temperatures in forests) as macroclimate temperature decreased (Fig. 2a, Supplementary Figs. 3 and 4). The cooling of mean and maximum temperatures was highest in tropical forests (probably partly due to the latitudinal gradient in macroclimate temperatures; Fig. 2a) whereas minimum temperatures were highest in boreal forests, relative to the macroclimate temperature (Fig. 2b). This means that the latitudinal gradient of forest-floor temperatures is less steep than the latitudinal gradient in macroclimate temperature, and that the amplitude of change within a given microhabitat does not always equate to the amplitude of macroclimate change¹¹.

To control for the effects of spatiotemporal changes in macroclimate temperatures (for example, sampling of tropical versus boreal forests, low versus high elevations or warm versus cold years) on the magnitude of the offset, we computed macroclimate temperature anomalies relative to the average conditions over the period 1970–2000 for each of the 98 study sites, and subsequently used these anomalies as a predictor variable instead of actual temperatures outside the forest that were reported in the original studies. The results are in line with those that use raw temperature values rather than anomalies; the cooling effect on maximum and mean temperatures—as well as the warming effect on minimum temperatures—is consistent along the gradient of temperature anomalies, with very similar slope estimates compared to the models with actual macroclimate temperatures (Supplementary Fig. 5).

Taken together, these results suggest that the temperature offsetting capacity of forests across the globe may translate into lower warming in the forest understory compared with warming trends using weather-station data from non-forested areas. Forests across the globe are thus effectively serving as a thermal insulator compared with open areas; such a buffering effect has the potential to reduce the severity of climate change impacts on forest ecosystems. The temperature offset values that we report here should be compared with the thermal sensitivities of species and ecosystem processes to better predict ecological responses to increasing temperatures.

We also tested for other factors that might explain some of the variation in the magnitude of temperature offsets among studies, such as forest composition, tree height, topography, distance to the coast or the height of the temperature sensors (for example, aboveground or belowground) (Supplementary Figs. 6 and 7, Supplementary Table 5). Sensor height was found to impact the magnitude of the offset; the buffering in forests was strongest close to the ground and the difference in temperatures between forests and open habitats disappeared higher above ground, both for minimum and maximum temperatures (Supplementary Fig. 7). Contrary to what we expected on the basis of the scientific literature²⁴, we did not detect an effect of the type of dominant tree species (evergreen, deciduous or mixed), topography, distance to the coast or forest height on the offset; more targeted studies will be needed to provide stronger tests of such factors.

Palaeoecological records show that temperature changes of greater magnitude and rate have stronger biological consequences^{5,25}. Here we have shown that microclimate buffering in forests has the potential to partly offset the warming experienced in the forest understory due to anthropogenic climate change, effectively reducing the severity of impacts from heating of the atmosphere. As such, closed forest canopies might provide a line of defence against the impacts of current and future warming on the ecological processes that influence forest ecosystems (for example, tree regeneration, demography and community reshuffling, litter decomposition, and soil water and nutrient cycling). As offsetting was strongest for maximum temperatures, we might expect extreme events such as heat waves to be more strongly attenuated than gradual temperature changes.

Our results underpin a neglected function of forests—an offset of within-forest temperatures that is of greater magnitude than the global warming of land and ocean temperatures over the past century ($\sim 0.85^{\circ}\text{C}$; ref. ⁴), and greater than the warming of regional surface temperatures following deforestation (usually $<1^{\circ}\text{C}$; ref. ²⁶). Forest canopies serve as thermal insulating layers, probably offsetting the impacts of anthropogenic climate change in the understory, where a large share of forest biodiversity resides and key ecosystem processes take place^{21,22}. It is thus essential to incorporate microclimates into biodiversity and climate science, and forest management and policy. As forest loss, degradation and conversion to monoculture crops continues^{27,28}, human land use might undermine the natural ability of ecosystems to mediate climate warming (a positive

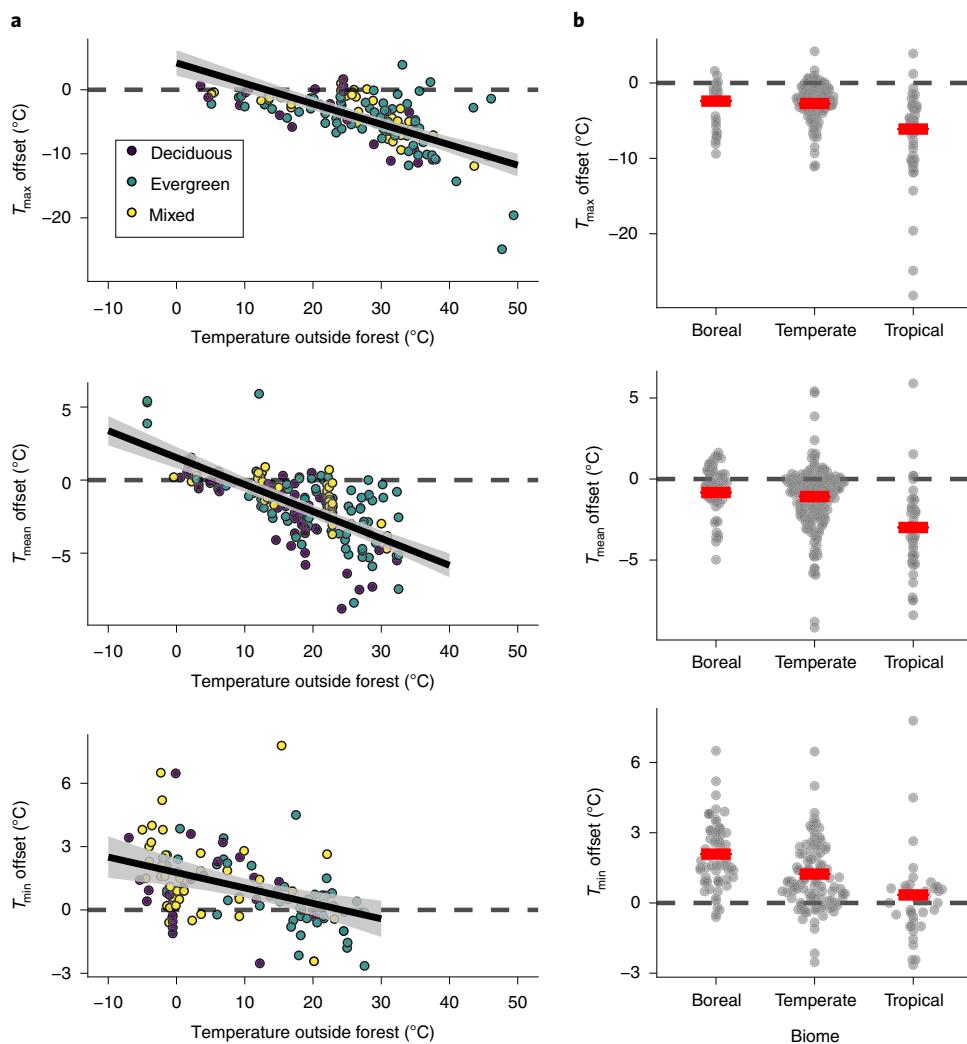


Fig. 2 | Forest temperature offsets under canopies are negatively related to warming air temperatures and dependent on the biome. **a**, The magnitude of the temperature offset within forests depends on ambient macroclimate temperature; the higher the warming, the higher the temperature offset (T_{\max} and T_{mean}). For minimum temperatures, positive offsets increase with colder temperatures. **b**, Study sites were classified into boreal, temperate or tropical, based on their latitude. Regression slopes (black lines), 95% confidence intervals (grey shading) and offset means (red lines) are based on mixed-effects models with study as a random-effect term. Full statistical analyses, data and code are reported in the Supplementary Information and ref. ³⁷.

feedback). Such feedback effects to climate systems may be further exacerbated through effects of microclimates on soil CO₂ and CH₄ fluxes and subcanopy evapotranspiration rates²⁹.

Advances in studies of microclimate versus macroclimate change have thus far been limited by the availability of suitable spatial data to model and map small-scale heterogeneity of microclimate conditions^{10–17,24}. Our global analysis shows the importance of forests in moderating climate warming, and the next step will be to incorporate fine-grained thermal variability into bioclimatic modelling of future species demography and distributions^{14–17}. Our findings indicate that well-quantified microclimates are key to improving predictions of climate change impacts and assisting management decisions. Forest managers and policymakers alike can potentially exploit microclimate buffering as a regulating service when developing mitigation and adaptation plans to safeguard forest biodiversity and functioning as well as human well-being in a future, warmer world.

Methods

Literature search and data extraction. We performed a literature search on ISI Web of Science to compile suitable published studies assessing the temperature

offsetting capacity of forest ecosystems. This search was updated until 15 June 2017 and performed by each of three authors (P.D.F., F.Z. and J.L.) independently, using keywords such as microclimat*, microrefug*, microhabitat*, forest*, temperature* and buffer*. The combined number of potentially suitable papers found by these three independent searches was 706. We then screened the titles and abstracts to find studies that potentially met our requirements for data extraction (see below). We considered forest microclimates to represent the suite of climatic conditions measured in localized areas near the ground and within the forest understory (below tree canopies). Microclimatic conditions include temperature, precipitation, wind and humidity; however, the focus here was on the temperature of the air layer below tree canopies and the temperature of the topsoil, owing to their importance for the responses of forest organisms and ecosystem functioning to macroclimate warming. The macroclimate was considered to be the climate in free-air conditions—representative of a large geographical region without direct canopy effects. This definition follows that used by meteorologists who record synoptic or macroclimate conditions from standardized weather stations^{19,20}.

Our criteria for study inclusion were the following: studies had to report temperature values (time series or summary statistics such as minimum, mean or maximum values) according to a strictly paired design that compared the microclimate below trees (inside forests) with temperatures recorded from a neighbouring reference site outside the forest without any influence of trees. Reference sites were a nearby open site equipped with the same type of (shielded) temperature loggers, a nearby weather station (provided the distance did not conflict with the temperature offset of the canopy, for example, due to significant

topographic differences) or a logger placed above the upper canopy surface. Consistency between the locations of temperature sensors within a pair of observations (for example, forest soil temperatures were only compared with control soil temperatures) was a requirement. Temperature data presented in tables or text were entered directly into our database. Temperature data not available directly in the text, raw data or as tables but presented in figures in the original papers (42.3% of the total number of offset values) were extracted using the digitalization software WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>). We did not set any limit on the study duration, that is, we extracted data from studies that quantified paired temperature time series during single days up to several years. If studies were performed along an edge-to-core transect, we considered only the measurements outside the forest farthest away from the edge versus the measurement closest to the core of the forest (as far away from the edge as possible). We screened the titles and abstracts of all 706 of the above-mentioned publications. We also included a formal process of scanning the reference lists of relevant papers and extracting more potentially relevant papers from these reference lists. In total, we identified 74 studies—published between 1939 and 2017—that met our above-mentioned requirements for data extraction. The majority of the studies were reported in peer-reviewed journal articles, although two PhD theses, one book and two institutional reports were also included.

When raw temperature data were available, we computed three summary statistics: maximum, mean and minimum temperatures through time. If available, we extracted temperatures outside and inside the forest, and then calculated the magnitude of temperature offset as the understory temperature minus the temperature outside the forest; negative values thus reflect cooler temperatures below tree canopies while positive values reflect warmer understory temperatures. A third of the studies (34% of offset values) reported only the macroclimate versus understory temperature difference (and not the forest and macroclimate temperatures separately). In these instances, only the offset value itself was directly entered in our database. Replicate forest sites (at least several kilometres apart), seasons (meteorological seasons, later aggregated to growing versus non-growing season) and temperature metrics (maximum, mean, minimum, air or soil temperatures) within the same study were entered into different rows of the database. Temperature values of longer time series were always aggregated per season and/or year.

All authors contributed to the data extraction from the original papers. After the first data extraction, however, all entries into the database were thoroughly double-checked by four authors (P.D.F., F.Z., F.R.S. and J.L.), working together closely to resolve any discrepancies or ambiguities and to ensure a standardized protocol was used across all papers. We used the following R packages for data management, cleaning and visualization: `readxl`³⁰, `dplyr`³¹, `CoordinateCleaner`³², `knitr`³³, `rmarkdown`³⁴, `ggplot2`³⁵ and `cowplot`³⁶, as well as custom R code³⁷.

In total, our final database consisted of 714 paired temperature offset data points from 74 independent studies spread across 5 continents. Our full database with all variables used in the analyses, as well as all source code, is available in ref. ³⁷.

Predictor variables. Apart from the temperature variables, we also extracted the following attributes for each offset value and/or study, if they were available in the original source article:

- Location. Latitude, longitude and elevation (metres above sea level).
- Biome. We classified each site into one of the following three biomes on the basis of the geographical coordinates: tropical (23.5°S–23.5°N), temperate (23.5°N–55°N, or 23.5°S–55°S) or boreal (>55°N or >55°S).
- Vegetation type. Forest type was classified into each of three categories on the basis of the original source article, or additional sources if necessary (for example, other papers from the same study site and/or authors): deciduous (if the dominant tree species was deciduous; indicated as 1 in the dataset³⁷), evergreen (if the dominant tree species was evergreen; indicated as 2 in the dataset) or mixed (indicated as 3 in the dataset).
- Study length. The number of days during which temperatures were measured, ranging from 1 d to 10 yr.
- Forest density. We extracted any of the following variables that are related to forest density for each study site, if available: percentage of canopy cover, tree basal area ($\text{m}^2 \text{ ha}^{-1}$), tree density (number of trees per ha) and leaf area index. Each of the above-described variables was available for a minority of offset values: 16% for canopy cover, 23% for basal area, 7% for tree density and 8% for leaf area index. Owing to the paucity of these data, we do not consider these variables further in our analyses, but the raw data are available³⁷.
- Forest height. We extracted for each study site, if available (39% of offset values), the height of the dominant tree individuals (in metres).
- Topographic heterogeneity and distance to the coast. Owing to the known effects of topography²⁴ on microclimates, we also extracted topographic heterogeneity using raster layers derived from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) dataset at 250 m resolution³⁸. Here we focused on two variables that capture topographic heterogeneity within a 1 km² pixel around each pair of measurements (forest and macroclimate outside forest): (1) the s.d. of elevation values aggregated per 1 km² (further referred to as elevational variation), and (2) the median of the topographic

position index values at 1 km resolution. The topographic position index is the difference between the elevation of a focal cell and the mean of its eight surrounding cells. Positive and negative values correspond to ridges and valleys, respectively, while zero values correspond to flat areas³⁸. We also extracted the distance from each pair of measurements (forest and macroclimate outside forest) to the nearest coastline.

- Season of sampling. Temperature measurements were classified as having taken place during the growing season, the non-growing season or whether the whole year was sampled (annual). This was aggregated on the basis of reported meteorological seasons and/or climate information in the original study. The dry and winter season were classified as the non-growing season in tropical and temperate biomes, respectively.
- Height of the sensor (continuous variable, in metres above or below the soil surface). Data were positive for aboveground and negative for belowground sensors. Although soil temperatures do not reflect macroclimate temperatures, they still allow for a comparison of forests' thermal buffering capacity on soil organisms and processes. The effects of macroclimate temperatures on the temperature offset were similar when only considering sensors placed >0 cm above the soil surface.
- Macroclimate temperature anomalies. We calculated the difference between each macroclimate temperature and the long-term average temperature for a given site. This was done to test whether the increase in temperature offset with warmer macroclimate temperatures was due in part to temporal variation in macroclimate, rather than only spatial variation. Macroclimate temperatures were thus compared to a common baseline, using 1970–2000 as a reference period. Using these temperature anomalies, we asked how the magnitude of the temperature offset capacity of forests varies along a gradient of deviations from long-term temperature averages, analogous to IPCC definitions of climate change⁴. Location-specific long-term averages (1970–2000) of mean annual temperatures were extracted from WorldClim v.2 at 30-arcsec spatial resolution (approximately equivalent to 0.86 km² at the Equator) for each study site³⁹.

Data analyses. To report summary statistics of the temperature offset capacity of forests globally (Supplementary Table 1), two contrasting approaches were adopted. First, the raw mean, median and quantiles were calculated. Then we carried out a multilevel-modelling framework using intercept-only linear mixed-effects models (LMMs) without fixed predictor variables but using 'study' as a random intercept term to account for pseudoreplication in some of the 74 selected studies. The intercept of intercept-only models represents the average magnitude of the temperature offset of forests while accounting for the non-independence among replicates from the same study. When fitting our intercept-only LMMs, we used the restricted maximum likelihood method in the `lmer` function from the `lme4` package⁴⁰ as recommended by Zuur et al.⁴¹

Applying a conventional meta-analytical model sensu stricto with the weighting of different observations by means of variance estimates⁴² was not possible here; an estimate of uncertainty (s.e.m., s.d., coefficient of variation or confidence intervals) of the offset values was reported for only a small minority (13.6%) of offset values included in our database.

Next, we assessed how macroclimate temperatures and macroclimate temperature anomalies predicted variation in the temperature offset of forests globally. As above, we fitted LMMs with macroclimate temperatures, macroclimate temperature anomalies as fixed effects and 'study' as a random effect using restricted maximum likelihood in the `lmer` function from the `lme4` package⁴⁰. We also performed χ^2 tests by comparing the univariate LMM including a single predictor with the baseline intercept-only model⁴¹. Goodness-of-fit was determined by calculating the marginal and conditional coefficient of determination (R^2) as previously reported⁴³ using the `r.squaredGLMM` function in the `MuMin` package⁴⁴.

We also determined how variables such as absolute latitude, biome, elevation, vegetation type, distance to the coast, elevational variation and topographic position, season and sensor height influenced variation in the offset of forests, and how they interacted with macroclimate temperatures. We first ran seven separate univariate LMMs, one per predictor variable as a fixed effect. As above, we fitted LMMs with a random effect term 'study' using restricted maximum likelihood in the `lmer` function from the `lme4` package⁴⁰. To test interactions, we also ran LMMs with two predictor variables each: the macroclimate temperature and each of the seven other predictors individually; for the sake of simplicity, higher-level interactions were not considered (Supplementary Table 6).

Finally, the linearity of the relationship between the temperature offset and macroclimate temperatures was tested with general additive mixed models using the `gamm` function in the `mgcv` package⁴⁵ and again 'study' was added as a random term (Supplementary Fig. 4). Our main findings were robust to the decisions to (1) analyse understory temperatures as the response variable against macroclimate temperature as a fixed effect in LMMs, instead of intercept-only LMMs on the basis of offset values (Supplementary Fig. 3), and (2) add random intercepts into LMMs, instead of random slopes (Supplementary Table 7). Omitting a few outlier values from a single study⁴⁶ from the analyses also did not affect our conclusions (Supplementary Table 8).

All analyses were performed in R⁴⁷ v.3.4.4 and all retained papers are in the reference list^[3,4,6,48–119]. All raw data and code can be found in ref.³⁷. Full results of the statistical analyses are reported in Supplementary Tables 1–8. We followed best practices for reporting meta-analyses recommended by the PRISMA guidelines²⁰ and included a flow diagram summarizing the search criteria in Supplementary Fig. 8.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The datasets and code generated and analysed during the current study are available in the figshare repository³⁷, with the identifier 10.6084/m9.figshare.7604849.

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References

- Willis, K. J. & Bhagwat, S. A. *Science* **326**, 806–807 (2009).
- Scheffers, B. R. et al. *Science* **354**, aaf7671 (2016).
- Lenoir, J. & Svenning, J. C. *Ecography* **38**, 15–28 (2015).
- IPCC Climate Change 2013: *The Physical Science Basis* (eds Stocker, T. F. et al.) (Cambridge Univ. Press, 2013).
- Moritz, C. & Agudo, R. *Science* **341**, 504–508 (2013).
- Devictor, V. et al. *Nat. Clim. Change* **2**, 121–124 (2012).
- Dullinger, S. et al. *Nat. Clim. Change* **2**, 619–622 (2012).
- Bertrand, R. et al. *Nature* **479**, 517–520 (2011).
- Ash, J. D., Givnish, T. J. & Waller, D. M. *Glob. Change Biol.* **23**, 1305–1315 (2017).
- De Frenne, P. et al. *Proc. Natl Acad. Sci. USA* **110**, 18561–18565 (2013).
- Scheffers, B. R. et al. *Glob. Change Biol.* **20**, 495–503 (2013).
- Senior, R. A. et al. *Glob. Change Biol.* **24**, 1267–1278 (2018).
- Frey, S. J. K. et al. *Sci. Adv.* **2**, e1501392 (2016).
- Dobrowski, S. Z. *Glob. Change Biol.* **17**, 1022–1035 (2011).
- Potter, K. A., Arthur, W. H. & Pincebourde, S. *Glob. Change Biol.* **19**, 2932–2939 (2013).
- Lenoir, J., Hattab, T. & Pierre, G. *Ecography* **40**, 253–266 (2017).
- Bramer, I. et al. in *Advances in Ecological Research* Vol. 58 (eds Bohan, D. A. et al.) 101–161 (Elsevier, 2018).
- Geiger, R., Aron, R. H. & Todhunter, P. *The Climate Near the Ground* 7th edn (Rowman & Littlefield, 2009).
- Guide to Meteorological Instruments and Methods of Observation WMO report No. 8 (World Meteorological Organization, 2008).
- De Frenne, P. & Verheyen, K. *Science* **351**, 234 (2016).
- Jenkins, C. N., Pimm, S. L. & Joppa, L. N. *Proc. Natl Acad. Sci. USA* **110**, E2602–E2610 (2013).
- Millennium Ecosystem Assessment *Ecosystems and Human Well-being: Biodiversity Synthesis* (World Resources Institute, 2005).
- Global Forest Resources Assessment (FAO, 2015).
- Jucker, T. et al. *Glob. Change Biol.* **24**, 5243–5258 (2018).
- Mayhew, P. J., Jenkins, G. B. & Benton, T. G. *Proc. R. Soc. B.* **275**, 47–53 (2008).
- Lejeune, Q. et al. *Nat. Clim. Change* **8**, 386–390 (2018).
- Hansen, M. C. et al. *Science* **342**, 850–853 (2013).
- Watson, J. E. M. et al. *Nat. Ecol. Evol.* **2**, 599–610 (2018).
- Good, S. P., Noone, D. & Bowen, G. *Science* **349**, 175–177 (2015).
- Wickham, H. & Bryan, J. *Readxl: read excel files*. R package v1.0.0. <https://CRAN.R-project.org/package=readxl> (2017).
- Wickham, H. et al. *Dplyr: a grammar of data manipulation*. R package v0.7.4. <https://CRAN.R-project.org/package=dplyr> (2017).
- Zizka, A. *CoordinateCleaner: automated cleaning of occurrence records from biological collections*. R package v1.0.7. <https://CRAN.R-project.org/package=CoordinateCleaner> (2018).
- Xie, Y. *Knitr: a general-purpose package for dynamic report generation in R*. R package v1.2.0. <https://yihui.name/knitr/> (2018).
- Allaire, J. J. et al. *Rmarkdown: dynamic documents for R*. R package v1.9. <https://CRAN.R-project.org/package=rmarkdown> (2018).
- Wickham, H. *Ggplot2: Elegant Graphics for Data Analysis* (Springer, 2009).
- Wilke, C. *Cowplot: streamlined plot theme and plot annotations for 'Ggplot2'*. R package v0.9.2. <https://CRAN.R-project.org/package=cowplot> (2017).
- De Frenne, P., Lenoir, J. & Rodríguez-Sánchez, F. Global buffering of temperatures under forest canopies data and code. *Figshare* <https://doi.org/10.6084/m9.figshare.7604849> (2019).
- Amatulli, G. et al. *Sci. Data* **5**, 180040 (2018).
- Fick, S. E. & Hijmans, R. J. *Int. J. Clim.* **37**, 4302–4315 (2017).
- Bates, D. *J. Stat. Softw.* **67**, 1–48 (2015).
- Zuur, A. F. et al. *Mixed Effects Models and Extensions in Ecology with R* (Springer, 2009).
- Gurevitch, J. et al. *Nature* **555**, 175–182 (2018).
- Nakagawa, S. & Schielzeth, H. *Methods Ecol. Evol.* **4**, 133–142 (2013).
- Barton, K. *MuMin: Multi-Model Inference*. R package v1.40.4. <https://CRAN.R-project.org/package=MuMin> (2018).
- Wood, S. N. *Generalized Additive Models: An Introduction with R* 2nd edn (Chapman and Hall/CRC, 2017).
- Zhu, H., Xu, Z. F., Wang, H. & Li, B. G. *Biodivers. Conserv.* **13**, 1355–1372 (2004).
- R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2017); <http://www.R-project.org/>
- André, M. F. et al. *Earth Surf. Process. Landf.* **37**, 519–532 (2012).
- Arunachalam, A. & Arunachalam, K. *Plant Soil* **223**, 187–195 (2000).
- Asbjørnsen, H., Ashton, M. S., Vogt, D. J. & Palacios, S. *Agric. Ecosyst. Environ.* **103**, 481–495 (2004).
- Barg, A. K. & Edmonds, R. L. *Can. J. For. Res.* **29**, 705–713 (1999).
- Belsky, A. J. et al. *J. Appl. Ecol.* **26**, 1005–1024 (1989).
- Blennow, K. *Agric. For. Meteorol.* **91**, 223–235 (1998).
- Brower, L. P. et al. *Insect Conserv. Divers.* **2**, 163–175 (2009).
- Cachan, P. *Ann. Fac. Sci. Dakar* **8**, 89–155 (1963).
- Carlson, D. W. & Groot, A. *Agric. For. Meteorol.* **87**, 313–329 (1997).
- Chen, J., Franklin, J. F. & Spies, T. A. *Agric. For. Meteorol.* **63**, 219–237 (1993).
- Chen, J. et al. *Bioscience* **49**, 288–297 (1999).
- Childs, S. W. & Flint, L. E. *For. Ecol. Manage.* **18**, 205–217 (1987).
- Currylow, A. F., MacGowan, B. J. & Williams, R. N. *PLoS ONE* **7**, e40473 (2012).
- Daily, G. C. & Ehrlich, P. R. *Proc. Natl Acad. Sci. USA* **93**, 11709–11712 (1996).
- Davies-Colley, R. J., Payne, G. W. & van Elswijk, M. N. Z. *J. Ecol.* **24**, 111–121 (2000).
- Denslow, J. S. *Biotropica* **12**, 47–55 (1980).
- Didham, R. K. & Ewers, R. M. *Pac. Sci.* **68**, 493–508 (2014).
- Dovčiak, M. & Brown, J. *New For.* **45**, 733–744 (2014).
- Evans, G. C. *J. Ecol.* **27**, 436–482 (1939).
- Fletcher, N., Oberbauer, S. F. & Strain, B. R. *Int. J. Biometeorol.* **29**, 145–155 (1985).
- Fridley, J. D. *J. Appl. Meteorol. Climatol.* **48**, 1033–1049 (2009).
- Gaudio, N., Gendre, X., Saudreau, M., Seigner, V. & Balandier, P. *Agric. For. Meteorol.* **237–238**, 71–79 (2017).
- Ghuman, B. S. & Lal, R. *Agric. For. Meteorol.* **40**, 17–29 (1987).
- Graae, B. J. et al. *Oikos* **121**, 3–19 (2012).
- Granberg, H. B., Ottosson-Löfvenius, M. & Odin, H. *Agric. For. Meteorol.* **63**, 171–188 (1993).
- Groot, A. & Carlson, D. W. *Can. J. For. Res.* **26**, 1531–1538 (1996).
- Grubb, P. J. & Whitmore, T. C. *J. Ecol.* **54**, 303–333 (1966).
- Heithecker, T. D. & Halpern, C. B. *For. Ecol. Manage.* **248**, 163–173 (2007).
- Holl, K. D. *Biotropica* **31**, 229–242 (1999).
- Honnay, O., Verheyen, K. & Hermy, M. *For. Ecol. Manage.* **161**, 109–122 (2002).
- Hopkins, B. *J. Ecol.* **53**, 125–138 (1965).
- Ibanez, T., Hély, C. & Gaucherel, C. *Austral. Ecol.* **38**, 680–687 (2013).
- Jiménez, C., Tejedor, M. & Rodríguez, M. *Eur. J. Soil Sci.* **58**, 445–449 (2007).
- Johansson, D. *Acta Phytogeogr. Suec.* **59**, 1–136 (1974).
- Joly, D. *Climatologie* **11**, 19–33 (2014).
- Karki, U. & Goodman, M. S. *Agrofor. Syst.* **89**, 319–325 (2015).
- Korb, J. & Linsenmair, K. E. *Insectes Soc.* **45**, 51–65 (1998).
- Kubin, E. & Kempainen, L. *Acta For. Fenn.* **225**, (1991).
- Lal, R. & Cummings, D. J. F. *Crop. Res.* **2**, 91–107 (1979).
- Langvall, O. & Ottosson Löfvenius, M. *For. Ecol. Manage.* **168**, 149–161 (2002).
- Latimer, C. E. & Zuckerberg, B. *Ecography* **40**, 158–170 (2017).
- Lawson, G. W., Armstrong-Mensah, K. O. & Hall, J. B. *J. Ecol.* **58**, 371–398 (1970).
- Locosselli, G. M., Cardim, R. H. & Ceccantini, G. *Int. J. Biometeorol.* **60**, 639–649 (2016).
- Lofvenius, M. O. Temperature and radiation regimes in pine shelterwood and clear-cut area. PhD thesis, Swedish University of Agricultural Sciences (1993).
- Lüdi, W. & Zoller, H. *Über den Einfluss der Waldnähe auf das Lokalklima: Untersuchungen im Gebiete des Hardwaldes bei Muttenz (Base)* (in German) (Geobotanisches Forschungsinstitut Rübel Zürich, 2018).
- Luskin, M. S. & Potts, M. D. *Basic Appl. Ecol.* **12**, 540–551 (2011).
- Matlack, G. R. *Biol. Conserv.* **66**, 185–194 (1993).
- Meleason, M. A. & Quinn, J. M. *For. Ecol. Manage.* **191**, 365–371 (2004).
- Morecroft, M. D., Taylor, M. E. & Oliver, H. R. *Agric. For. Meteorol.* **90**, 141–156 (1998).

97. Nunez, M. & Bowman, D. M. J. S. *Aust. For. Res.* **16**, 185–197 (1986).
98. Odin, H., Magnusson, B. & Bäckström, P.-O. Effect of low shelterwood on minimum temperature near the ground. In *Ecology and Management of Forest Biomass Production Systems* (Perttu, K. ed.) 77–99 (Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Report 15, 1984).
99. Porté, A., Huard, F. & Dreyfus, P. *Agric. For. Meteorol.* **126**, 175–182 (2004).
100. Potter, B. E., Teclaw, R. M. & Zasada, J. C. *Agric. For. Meteorol.* **106**, 331–336 (2001).
101. Renaud, V., Innes, J. L., Dobbertin, M. & Rebetez, M. *Theor. Appl. Climatol.* **105**, 119–127 (2011).
102. Rodríguez-Sánchez, F., Pérez-Barrales, R., Ojeda, F., Vargas, P. & Arroyo, J. *Quat. Sci. Rev.* **27**, 2100–2117 (2008).
103. Scheffers, B. R. et al. *Proc. R. Soc. B Biol. Sci.* **280**, 20131581 (2013).
104. Schulz, J. P. *Meded. Bot. Museum en Herb. R.U.U.* **163**, 1–267 (1960).
105. Seebacher, F. & Alfrod, R. A. J. *Herpetol.* **36**, 95–98 (2002).
106. Shanks, R. E. & Norris, F. H. *Ecology* **31**, 532–539 (1950).
107. Shoo, L. P., Storlie, C., Williams, Y. M. & Williams, S. E. *Int. J. Biometeorol.* **54**, 475–478 (2010).
108. Sporn, S. G., Bos, M. M., Kessler, M. & Gradstein, S. R. *Biodivers. Conserv.* **19**, 745–760 (2010).
109. Suggitt, A. J. et al. *Oikos* **120**, 1–8 (2011).
110. Vajda, A. & Venäläinen, A. *Boreal Environ. Res.* **10**, 299–314 (2005).
111. Valigura, R. A. J. *Environ. Manage.* **40**, 283–295 (1994).
112. van Dam, O. *Forest filled with gaps: Effects of gap size on water and nutrient cycling in tropical rain forest*. PhD thesis, Utrecht University, 2001.
113. Varner, J. & Dearing, M. D. *PLoS One* **9**, e104648 (2014).
114. Vitt, L. & Avila-Pires, T. *Conserv. Biol.* **12**, 654–664 (1998).
115. Williams-Linera, G. *J. Ecol.* **78**, 356–373 (1990).
116. Xu, M., Qi, Y., Chen, J. & Song, B. *Plant Ecol.* **173**, 39–57 (2004).
117. Yan, M., Zhong, Z. & Liu, J. *Front. Biol. China* **2**, 62–68 (2007).
118. Yanoviak, S. P. *Selbyana* **20**, 106–115 (1999).
119. Young, A. & Mitchell, N. *67*, 63–72 (1994).
120. Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G. & The PRISMA Group *PLoS Med.* **6**, e1000097 (2009).

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Author contributions

P.D.F., F.Z. and J.L. conceived and designed the research. P.D.F., F.Z., J.L. and F.R.-S. assembled and revised the database and analysed the data. All authors compiled data and wrote the manuscript.

Competing interests

The authors declare no competing interests.

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Sampling strategy	Literature search
Data collection	Literature search
Timing and spatial scale	Spatial: global Temporal: all literature published till June 2017 is included.
Data exclusions	No data that met our criteria were excluded
Reproducibility	Our literature search as well as all analyses are fully reproducible (meta-analysis of only published sources, open data and code)
Randomization	Not relevant (meta-analysis)
Blinding	Not relevant (meta-analysis)

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