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► **To cite this version:**

Pieter de Frenne, Florian Zellweger, Francisco Rodríguez-Sánchez, Brett Scheffers, Kristoffer Hylander, et al.. Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 2019, 3 (5), pp.744-749. 10.1038/s41559-019-0842-1 . hal-02352625

HAL Id: hal-02352625

<https://hal.science/hal-02352625>

Submitted on 13 Nov 2019

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Global buffering of temperatures under forest canopies

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24 **Abstract**

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

32 **Main text**

33 Biological impacts of macroclimate warming are increasingly evident across a wide array of
34 ecosystems¹⁻⁵. Many responses of biological communities and ecosystem processes, however, are
35 lagging behind warming of the macroclimate⁶⁻¹¹. Such time lags may be the inevitable consequence
36 of slow dispersal and demography^{3, 7, 8}, but may also be due to the buffering of localized
37 microclimates by vegetation and topography, such that organisms do not necessarily experience the
38 same degree of warming as measured at weather stations¹²⁻¹⁸. Biotic and abiotic features near the
39 ground create heterogeneous microclimates, mostly via effects on radiation, air mixing,
40 evapotranspiration and soil properties, all of which can influence biodiversity and ecosystem
41 functioning^{17, 18}.

42 To better predict the biotic consequences of climate change, we need to further our
43 understanding of how the local temperature experienced by living organisms (referred to as the
44 ‘microclimate’) changes in space and time. Macroclimates outside forests (sometimes referred to as
45 ‘free-air temperatures’ in the literature) are characterized by an extensive global network of weather
46 stations established in the well-mixed air of open areas (e.g. short grasslands) *c.* 2 m above the soil
47 surface^{19, 20} — habitat conditions that are not representative of the conditions experienced by the
48 majority of terrestrial species on Earth^{21, 22}. The study of microclimates is not new, since
49 microclimatological measurements began more than a century ago, but most climate-change studies
50 rely on weather station data that are specifically designed to correct for these microclimatic effects¹⁵⁻
51 ²⁰. Hence, future projections of climate change relying solely on macroclimate ignore the potential
52 impact of microclimates on biodiversity and ecosystem functioning^{1, 2, 5}.

53 Microclimates are particularly evident in forests, where the large majority of species live
54 underneath the canopy of trees that strongly influences local thermal conditions¹⁰⁻¹³. This is of major

55 concern for global-change science because forests cover one-quarter of the Earth's land surface and
56 harbor two-thirds of all terrestrial biodiversity²⁰⁻²³, and some studies have already shown that
57 microclimatic buffering can mediate the response of forest communities to climate change⁸⁻¹¹.

58 Here we report a systematic, global meta-analysis quantifying the thermal buffering capacity of
59 the Earth's dominant forested ecosystems (tropical to boreal forests) across five continents (Fig. 1).
60 Drawing on empirical studies with a strictly paired design (i.e. comparing microclimate with
61 macroclimate), we quantify the average temperature offset of forests and also how the magnitude of
62 such offsets depends on the macroclimatic context (i.e. outside forests). From a total of 98 sites and
63 74 studies, we retrieved paired temperature time series and/or summary statistics (i.e. minimum,
64 mean, or maximum temperatures) for exactly the same time period in (i) understory conditions in
65 forests (i.e. microclimate) and (ii) an adjacent open habitat without shade (i.e. macroclimate). Offset
66 values were always calculated as temperatures inside minus macroclimate temperatures outside
67 forests such that negative values reflect cooler forest temperatures.

68 In our global analysis of 714 paired temperature data, we found that tree canopies buffer
69 forest floors against both high and low macroclimatic temperatures. Mean and maximum understory
70 temperatures were, on average, cooler by 1.7 ± 0.3 and 4.1 ± 0.5 °C (mean \pm S.E., mixed-effects
71 models: both $P < 0.001$) than macroclimate temperatures, respectively. Conversely, minimum
72 temperatures of the forest understory were 1.1 ± 0.2 °C warmer than the macroclimate outside the
73 forest (mixed-effects model: $P < 0.001$; Fig. 1, Supplementary Figs. 1-2). Thus, forest understories
74 are not only cooler on average than nearby open habitats, but negative maximum temperature
75 offsets (cooler in forests) and positive minimum temperature offsets (warmer in forests) also
76 indicate lower temperature variation below the forest canopy.

77 Across the globe, the thermal offset of forests was negatively correlated with the macroclimate
78 temperature outside forests. Thermal offsets became more negative (i.e. lower temperatures in
79 forests) as macroclimate temperature increased, and more positive (i.e. higher temperatures in
80 forests) as macroclimate temperature decreased (Fig. 2a, Supplementary Figs. 3-4). The cooling of
81 mean and maximum temperatures was highest in tropical forests (probably partly as a result of the
82 latitudinal gradient in macroclimate temperatures; Fig. 2a) while minimum temperatures were highest
83 in boreal forests, relative to the macroclimate temperature (Fig. 2b). This means that the latitudinal
84 gradient of forest-floor temperatures is less steep than the latitudinal gradient in macroclimate
85 temperature and that the amplitude of change within a given microhabitat does not always equate to
86 the amplitude of macroclimate change¹¹.

87 To control for the effects of spatiotemporal changes in macroclimate temperatures (e.g.
88 sampling of tropical *vs.* boreal forests, low *vs.* high elevations or warm *vs.* cold years) on the
89 magnitude of the offset, we computed macroclimate temperature anomalies relative to the average
90 conditions over the period 1970-2000 for each of the 98 study sites, and subsequently used it as a
91 predictor variable instead of actual temperatures outside the forest reported in the original studies.
92 The results are in line with those using raw temperature values rather than anomalies: the cooling
93 effect on maximum and mean temperatures, as well as the warming effect on minimum
94 temperatures, are consistent along the gradient of temperature anomalies, with very similar slope
95 estimates compared to the models with actual macroclimate temperatures (Supplementary Fig. 5).

96 Together, these results suggest that the thermal offsetting capacity of forests across the globe
97 may translate into lower warming in the forest understory compared to warming trends using
98 weather-station data from non-forested areas. Forests across the globe are thus effectively serving as
99 a thermal insulator compared with open areas, with such a buffering effect potentially reducing the

100 severity of climate change impacts on forest ecosystems. The offset values we report here now have
101 to be compared to the thermal sensitivities of species and ecosystem processes to better predict
102 ecological responses to increasing temperatures.

103 In addition to spatiotemporal variability, we also tested for additional factors that might
104 explain some of the variation among studies in the magnitude of temperature offsets, such as forest
105 composition (evergreen, mixed or deciduous), tree height, topography, distance to the coast, or the
106 height of the temperature sensors (e.g. aboveground or belowground) (Supplementary Figs. 6-7;
107 Supplementary Table 5). Sensor height indeed impacted the magnitude of the offset: the buffering in
108 forests was strongest close to the ground while the difference in temperatures between forests and
109 open habitats disappeared higher up above-ground, both for minimum and maximum temperatures
110 (Supplementary Fig. 7). Contrary to what we expected based on the scientific literature²⁴, we did not
111 detect an effect of the type of dominant tree species (evergreen, deciduous or mixed), topography,
112 distance to the coast or forest height on the offset; more targeted studies will be needed to provide
113 stronger tests of such factors.

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

123 Our results underpin a neglected function of forests: an offset of within-forest temperatures
124 that is of greater magnitude than the global warming of land and ocean temperatures over the past
125 century (~0.85 °C, ref. 4) and also the warming of regional surface temperatures following
126 deforestation (usually < 1 °C, ref. 26). Forest canopies serve as thermal insulating layers, likely
127 offsetting the impacts of anthropogenic climate change in the understory, where a large share of
128 forest biodiversity resides and key ecosystem processes take place^{21,22}. It is thus essential to
129 incorporate microclimates into biodiversity and climate science as well as into forest management
130 and policy. As forest loss, degradation, and conversion to monoculture crops continues^{27,28}, human
131 land use might undermine ecosystems' natural ability to mediate climate warming (a positive
132 feedback). Such feedbacks to climate systems may be further exacerbated via effects of
133 microclimates on soil CO₂ and CH₄ fluxes and sub-canopy evapotranspiration rates²⁹.

134 Advances in studies of micro- vs. macroclimate change have thus far been limited by the
135 availability of suitable spatial data to model and map small-scale heterogeneity of microclimate
136 conditions^{10-17,24}. Our global analysis shows the importance of forests in moderating climate
137 warming, and the next step will be to incorporate fine-grained thermal variability into bioclimatic
138 modelling of future species demography and distributions¹⁴⁻¹⁷. Our findings indicate that well-
139 quantified microclimates are key to improving predictions of climate-change impacts and assisting
140 management decisions. Forest managers and policy makers alike can potentially exploit microclimate
141 buffering as a regulating service when developing mitigation and adaptation plans to safeguard forest
142 biodiversity and functioning as well as human well-being in a future, warmer world.

143 **Methods**

144 Literature search and data extraction

145 We performed a literature search on ISI Web of Science to compile suitable published studies
146 assessing the thermal offsetting capacity of forest ecosystems. This search was updated until 15 June
147 2017 and performed by each of three authors (PDF, FZ, JL) independently, using keywords such as
148 microclimat*, microrefug*, microhabitat*, forest*, temperature* and buffer*. The combined number
149 of potentially suitable papers found by these three independent searches was 706. We then screened
150 the titles and abstracts to find studies that potentially met our requirements for data extraction (see
151 the next paragraph). We considered forest microclimates to represent the suite of climatic conditions
152 measured in localized areas near the ground and within the forest understory (below tree canopies).
153 Microclimatic conditions include temperature, precipitation, wind and humidity, but the focus here
154 was on the temperature of the air layer below tree canopies and the temperature of the topsoil due
155 to their importance for the responses of forest organisms and ecosystem functioning to
156 macroclimate warming. The macroclimate was considered as the climate in free-air conditions,
157 representative of a large geographic region without direct canopy effects. This definition follows the
158 definition used by meteorologists who record synoptic or macroclimate conditions from
159 standardized weather stations¹⁹⁻²⁰.

160 Our criteria for study inclusion were the following: studies had to report temperature values
161 (time series or summary statistics such as minimum, mean or maximum values) according to a
162 strictly paired design comparing microclimate below trees (inside forests) with temperatures
163 recorded from a reference neighbouring site outside the forest without any influence of trees (i.e.
164 macroclimate conditions). Reference sites were either a nearby open site equipped with the same
165 type of (shielded) temperature loggers, a nearby weather station (as long as the distance did not
166 confound with the temperature offset of the canopy, e.g. due to significant topographic differences),

167 or a logger placed above the upper canopy surface. Constancy of the location of temperature sensors
168 within a pair of observations (e.g. forest soil temperatures were only compared with control soil
169 temperatures) was a requirement. Temperature data presented in tables or text were entered directly
170 into our database. Temperature data not available directly in the text, raw data or as tables but
171 presented in figures in the original papers (42.3 % of the total number of offset values) were
172 extracted using the digitalization software *WebPlotDigitizer*
173 (<https://automeris.io/WebPlotDigitizer/>). We did not set any limit on the study duration, i.e. we
174 extracted data from studies that quantified paired temperature time series during single days up to
175 several years. If studies were performed along an edge-to-core transect, we only considered the
176 measurements outside the forest farthest away from the edge versus the measurement closest to the
177 core of the forest (as far away from the edge as possible). We screened the titles and abstracts of all
178 above-mentioned 706 publications. In addition, we included a formal process of scanning references
179 lists of relevant papers and further added potentially relevant papers extracted from these reference
180 lists. In total, we identified 74 studies published between 1939 and 2017 that met our above-
181 mentioned requirements for data extraction. The majority of the studies were reported in peer
182 reviewed journal articles, but also 2 PhD theses, 1 book and 2 institutional reports were included.

183 When raw temperature data were available, we computed three summary statistics: maximum,
184 mean and minimum temperatures across time. If available, we extracted temperatures outside and
185 inside the forest and then calculated the magnitude of the offset as understory temperature minus
186 temperature outside the forest; negative values thus reflect cooler temperatures below tree canopies
187 while positive values reflect warmer understory temperatures. A third of the studies (34 % of offset
188 values) only reported the macroclimate vs. understory temperature difference (and not the forest and
189 macroclimate temperatures separately). In these instances, only the offset value itself was directly
190 entered in our database. Replicate forest sites (at least several kilometers apart), seasons

191 (meteorological seasons, later aggregated to growing vs. non-growing season) and temperature
192 metrics (maximum, mean, minimum, air or soil temperatures) within the same study were entered on
193 different rows into the database. Temperature values of longer time series were always aggregated
194 per season and/or year.

195 All authors contributed to the data extraction from the original papers. After the first data
196 extraction, however, all entries into the database were thoroughly double-checked by four authors
197 (PDF, FZ, FRS, JL), working together closely to resolve any discrepancies or ambiguities and to
198 ensure a standardized protocol across all papers. We used the following R packages for data
199 management, cleaning and visualization: readxl³⁰, dplyr³¹, CoordinateCleaner³², knitr³³, rmarkdown³⁴,
200 ggplot2³⁵, and cowplot³⁶, as well as custom R code³⁷.

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

204

205 Predictor variables

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

- 208 • *Location*: Latitude, longitude and elevation (meters above sea level).
- 209 • *Biome*: Based on the geographical coordinates, we classified each site into one of the
210 following three biomes: tropical (latitude was between 23.5°S and 23.5°N); temperate
211 (latitude was between 23.5° and 55°); or boreal (latitude was higher than 55°).

- 212
- *Vegetation type*: Based on the original source article, or, if needed, additional sources (e.g. 213 other papers from the same study site and/or authors), the forest type was classified into 214 each of three categories: deciduous (if dominant tree species was deciduous; 1 in dataset via 215 ref. 37); evergreen (if dominant tree species was evergreen; 2); or mixed (3).
 - *Study length*: number of days during which temperatures were measured, ranging from 1 day 216 to 10 years. 217
 - *Forest density*: We extracted for each study site, if available, any of the following variables 218 relating to forest density: canopy cover (%); tree basal area ($\text{m}^2 \text{ha}^{-1}$); tree density (number ha^{-1}); 219 and leaf area index (LAI). Each of the above-described variables was available for a 220 minority of offset values: 16 % for canopy cover, 23 % for basal area, 7 % for tree density 221 and 8 % for LAI. For reasons of paucity of these data, we do not consider these variables 222 further in our analyses, but the raw data are available in ref. 37. 223
 - *Forest height*: We extracted for each study site, if available (39 % of offset values), the height 224 of the dominant tree individuals (in meters). 225
 - *Topographic heterogeneity and distance to the coast*: because of known effects of topography²⁴ on 226 microclimates, we also extracted topographic heterogeneity using raster layers derived from 227 the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) at 250 m 228 resolution³⁸. We here focused on two variables that capture topographic heterogeneity within 229 a 1 km^2 pixel around each pair of measurements (forest and macroclimate outside forest): (i) 230 the standard deviation of elevation values aggregated per 1 km^2 (further referred to as 231 ‘elevational variation’), and (ii) the median of the topographic position index (TPI) values at 232 1 km resolution. The TPI is the difference between the elevation of a focal cell and the mean 233 of its eight surrounding cells. Positive and negative values correspond to ridges and valleys, 234 respectively, while zero values correspond to flat areas³⁸. Finally, we also extracted the 235

236 distance from each pair of measurements (forest and macroclimate outside forest) to the
237 nearest coastline.

- 238 • *Season of sampling*: Temperature measurements were classified as having taken place during
239 the growing season, the non-growing season, or whether the whole year was sampled
240 (annual). This was aggregated based on reported meteorological seasons and/or climate
241 information in the original study. The dry and winter season were classified as the non-
242 growing season in tropical and temperate biomes, respectively.
- 243 • *Height of the sensor* (continuous variable, in meters above or below the soil surface): positive
244 for aboveground, negative for belowground sensors. While soil temperatures obviously do
245 not reflect macroclimate temperatures, they still allow for a comparison of forests' thermal
246 buffering capacity on soil organisms and processes. The effects of macroclimate
247 temperatures on the offset were similar when only considering sensors placed > 0 cm above
248 the soil surface.
- 249 • *Macroclimate temperature anomalies*: We calculated the difference between each macroclimate
250 temperature and the long-term average temperature for a given site. This was done in order
251 to test if the increase in temperature offset with warmer macroclimate temperatures was due
252 in part to temporal variation in macroclimate, rather than only spatial variation.
253 Macroclimate temperatures are thus compared to a common baseline. Using these
254 temperature anomalies, we asked how the magnitude of the thermal offset capacity of forests
255 varies along a gradient of deviations from long-term temperature averages, analogous to
256 IPCC definitions of climate change⁴. We used 1970-2000 as reference period to compare our
257 macroclimate temperatures outside forests against a common base period. Location-specific
258 long-term averages (1970-2000) of mean annual temperatures were extracted from

259 WorldClim version 2 at 30 arc-second spatial resolution (approximately equivalent to 0.86
260 km² at the equator) for each study site³⁹.

261

262 Data analyses

263 To report summary statistics of the thermal offset capacity of forests globally (Supplementary Table
264 1), two contrasting approaches were adopted. First, the raw mean, median and quantiles were
265 calculated. Then, we carried out a multilevel modeling framework using intercept-only linear mixed-
266 effects models (LMMs) without fixed predictor variables but with ‘*study*’ as a random intercept term
267 to account for pseudo-replication in some of the 74 selected studies. The intercept of intercept-only
268 models represents the average magnitude of the thermal offset of forests while accounting for the
269 non-independence among replicates from the same study. When fitting our intercept-only LMMs,
270 we used the restricted maximum likelihood method in the *lmer* function from the *lme4*-package⁴⁰ as
271 recommended by Zuur et al.⁴¹.

272 Applying a conventional meta-analytical model *sensu stricto* with weighting of different
273 observations by means of variance estimates⁴² was not possible here: an estimate of uncertainty
274 (standard error, deviation, coefficient of variation or confidence intervals) of the offset values was
275 reported for only a small minority (13.6 %) of offset values included in our database.

276 Next, we assessed how macroclimate temperatures and macroclimate temperature anomalies
277 predicted variation in the temperature offset of forests globally. As above, we fitted LMMs with
278 macroclimate temperatures and macroclimate temperature anomalies as fixed effects and ‘*study*’ as a
279 random effect using restricted maximum likelihood in the *lmer* function from the *lme4*-package⁴⁰. We
280 also performed χ^2 -tests by comparing the univariate LMM including a single predictor with the

281 baseline intercept-only model⁴¹. Goodness-of-fit was determined by calculating marginal and
282 conditional R² values following ref. 43 using the *r.squaredGLMM* function in the *MuMIn*-package⁴⁴.

283 We also determined how variables such as absolute latitude, biome, elevation, vegetation type,
284 distance to the coast, the elevational variation and topographic position, season, and sensor height
285 influenced variation in the offset of forests, and how they interacted with macroclimate
286 temperatures. We first ran seven separate univariate LMMs, one per predictor variable as a fixed
287 effect in our LMMs. As earlier, we again fitted LMMs with a random effect term ‘*study*’ using
288 restricted maximum likelihood in the *lmer* function from the *lme4*-package⁴⁰. In order to test
289 interactions, we finally also ran LMMs with two predictor variables each: the macroclimate
290 temperature and each of these seven other predictors (i.e. one-by-one of these seven variables *
291 macroclimate temperature); for the sake of simplicity, higher level interactions were not considered
292 (Supplementary Table 6).

293 Finally, the linearity of the relationship between the temperature offset and macroclimate
294 temperatures was tested with General Additive Mixed Models with the *gamm*-function in the *mgcv*-
295 package⁴⁵ and again *study* was added as random term (Supplementary Fig. 4). Our main findings were
296 robust to the decisions to (i) analyze understory temperatures as the response variable against
297 macroclimate temperature as a fixed effect in LMMs, instead of intercept-only LMMs based on
298 offset values (Supplementary Fig. 3), and (ii) add random intercepts into LMMs, instead of random
299 slopes (Supplementary Table 7). Omitting a few outlier values from a single study¹²⁰ from the
300 analyses also did not affect our conclusions (Supplementary Table 8).

301 All analyses were performed in R version 3.4.4 (ref. 46) and all retained papers are in the
302 reference list⁴⁷⁻¹²⁰. All raw data and code are available in ref. 37. Full results of the statistical analyses
303 are reported in Supplementary Tables 1-8. We followed best practices for reporting meta-analyses

304 recommended by the PRISMA guidelines¹²¹ and included a flow diagram summarising the search
305 criteria in Supplementary Fig. 8.

306 **Acknowledgements**

307 PDF received funding from the European Research Council (ERC) under the European Union's
308 Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833), KV
309 through ERC Consolidator Grant PASTFORWARD 614839, FRS by a postdoctoral fellowship
310 from the Spanish Ministry of Economy and Competitiveness (FPD-2013-16756), FZ by the Swiss
311 National Science Foundation (project 172198) and MV by the Natural Sciences and Engineering
312 Research Council, Canada.

313 **Author contributions**

314 PDF, FZ and JL conceived and designed research. PDF, FZ, JL and FRS assembled and revised the
315 database, and analyzed the data. All authors compiled data and wrote the manuscript.

316 **Competing interests**

317 The authors declare no competing interests.

318 **Materials and Correspondence**

319 Correspondence and requests for materials should be addressed to P.D.F.

320 **Data availability**

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

- 324 1. Willis, K.J. & Bhagwat S.A. Biodiversity and climate change. *Science* **326**, 806-807 (2009).
- 325 2. Scheffers, B.R. et al. The broad footprint of climate change from genes to biomes to people.
- 326 *Science* **354**, aaf7671 (2016).
- 327 3. Lenoir, J. & Svenning, J.C. Climate-related range shifts – a global multidimensional synthesis
- 328 and new research directions. *Ecography* **38**, 15-28 (2015).
- 329 4. IPCC. *Climate Change 2013: The Physical Science Basis* (Cambridge University Press, Cambridge,
- 330 2013).
- 331 5. Moritz, C. & Agudo, R. The future of species under climate change: resilience or decline?
- 332 *Science* **341**, 504-508 (2013).
- 333 6. Devictor, V. et al. Differences in the climatic debts of birds and butterflies at a continental
- 334 scale. *Nat. Clim. Change* **2**, 121-124 (2012).
- 335 7. Dullinger, S. et al. Extinction debt of high-mountain plants under twenty-first-century
- 336 climate change. *Nat. Clim. Change* **2**, 619-622 (2012).
- 337 8. Bertrand, R. et al. Changes in plant community composition lag behind climate warming in
- 338 lowland forests. *Nature* **479**, 517-520 (2011).
- 339 9. Ash, J.D., Givnish, T.J. & Waller, D.M. Tracking lags in historical plant species' shifts in
- 340 relation to regional climate change. *Glob. Change Biol.* **23**, 1305-1315 (2017).
- 341 10. De Frenne, P. et al. Microclimate moderates plant responses to macroclimate warming. *Proc.*
- 342 *Natl. Acad. Sci. U.S.A.* **110**, 18561-18565 (2013).
- 343 11. Scheffers, B.R. et al. Microhabitats reduce animal's exposure to climate extremes. *Glob.*
- 344 *Change Biol.* **20**, 495–503 (2013).
- 345 12. Senior R.A. et al. Tropical forests are thermally buffered despite intensive selective logging.
- 346 *Glob. Change Biol.* **24**, 1267-1278 (2018).
- 347 13. Frey, S.J.K. et al. Spatial models reveal the microclimatic buffering capacity of old-growth
- 348 forests. *Science Adv.* **2**, e1501392 (2016).
- 349 14. Dobrowski, S.Z. A climatic basis for microrefugia: the influence of terrain on climate. *Glob.*
- 350 *Change Biol.* **17**, 1022-1035 (2011).
- 351 15. Potter, K.A., Arthur, W.H. & Pincebourde, S. Microclimatic challenges in global change
- 352 biology. *Glob. Change Biol.* **19**, 2932-2939 (2013).
- 353 16. Lenoir, J., Hattab, T. & Pierre, G. Climatic microrefugia under anthropogenic climate
- 354 change: implications for species redistribution. *Ecography* **40**, 253-266 (2017).
- 355 17. Bramer, I. et al. “Advances in Monitoring and Modelling Climate at Ecologically Relevant
- 356 Scales” in *Adv. Ecol. Res.*, Bohan, D.A. et al., Eds. (Elsevier, 2018), vol. 58, pp. 101-161.
- 357 18. Geiger, R. Aron, R.H. & Todhunter, P. *The climate near the ground* (Rowman & Littlefield,
- 358 Plymouth, ed. 7, 2009).
- 359 19. World Meteorological Organization. *Guide to Meteorological Instruments and Methods of Observation*
- 360 (WMO-No. 8, Geneva, 2008).
- 361 20. De Frenne, P. & Verheyen, K. Weather stations lack forest data. *Science* **351**, 234-234 (2016).
- 362 21. Jenkins, C.N., Pimm, S.L. & Joppa, L.N. Global patterns of terrestrial vertebrate diversity
- 363 and conservation. *Proc. Natl. Acad. Sci. U.S.A.* **110**, E2602-E2610 (2013).
- 364 22. Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Biodiversity Synthesis*
- 365 (World Resources Institute, Washington, DC, 2005).

- 366 23. Food and Agriculture Organization of the United Nations. *Global Forest Resources Assessment*
367 (FAO, Rome, 2015).
- 368 24. Jucker, T. et al. Canopy structure and topography jointly constrain the microclimate of
369 human-modified tropical landscapes. *Global Change Biol.* **24**, 5243-5258 (2018).
- 370 25. Mayhew, P.J., Jenkins, G.B. & Benton, T.G. A long-term association between global
371 temperature and biodiversity, origination and extinction in the fossil record. *Proc. Roy. Soc.*
372 *Lond. B.: Bio.* **275**, 47-53 (2008).
- 373 26. Lejeune, Q. et al. Historical deforestation locally increased the intensity of hot days in
374 northern mid-latitudes. *Nat. Clim. Change* **8**, 386-390 (2018).
- 375 27. Hansen, M.C. et al. High-resolution global maps of 21st-century forest cover change. *Science*
376 **342**, 850-853 (2013).
- 377 28. Watson, J.E.M. et al. The exceptional value of intact forest ecosystems. *Nat. Ecol. Evol.* **2**,
378 599-610 (2018).
- 379 29. Good, S.P., Noone, D. & Bowen, G. Hydrologic connectivity constrains partitioning of
380 global terrestrial water fluxes. *Science* **349**, 175-177 (2015).
- 381 30. Wickham, H. & Bryan, J. *Readxl: Read Excel Files* (2017; [https://CRAN.R-](https://CRAN.R-project.org/package=readxl)
382 [project.org/package=readxl](https://CRAN.R-project.org/package=readxl)).
- 383 31. Wickham, H. et al. *Dplyr: A Grammar of Data Manipulation* (2017; [https://CRAN.R-](https://CRAN.R-project.org/package=dplyr)
384 [project.org/package=dplyr](https://CRAN.R-project.org/package=dplyr)).
- 385 32. Zizka, A. *CoordinateCleaner: Automated Cleaning of Occurrence Records from Biological Collections*
386 (2018; <https://CRAN.R-project.org/package=CoordinateCleaner>).
- 387 33. Xie, Y. *Knitr: A General-Purpose Package for Dynamic Report Generation in R* (2018;
388 <https://yihui.name/knitr/>).
- 389 34. Allaire, J.J. et al. *Rmarkdown: Dynamic Documents for R* (2018; [https://CRAN.R-](https://CRAN.R-project.org/package=rmarkdown)
390 [project.org/package=rmarkdown](https://CRAN.R-project.org/package=rmarkdown)).
- 391 35. H. Wickham, *Ggplot2: Elegant Graphics for Data Analysis* (Springer-Verlag, New York, 2009;
392 <http://ggplot2.org>).
- 393 36. Wilke, C. *Cowplot: Streamlined Plot Theme and Plot Annotations for 'Ggplot2'* (2017;
394 <https://CRAN.R-project.org/package=cowplot>).
- 395 37. De Frenne, P., Lenoir, J. & Rodríguez-Sánchez, F. Global buffering of temperatures under
396 forest canopies Data and Code. *FigsShare* [https://doi.org/ 10.6084/m9.figshare.7604849](https://doi.org/10.6084/m9.figshare.7604849)
397 (2019).
- 398 38. Amatulli, G. et al. A suite of global, cross-scale topographic variables for environmental and
399 biodiversity modelling. *Scientific Data* **5**, 180040 (2018).
- 400 39. Fick, S.E. & Hijmans, R.J. Worldclim 2: New 1-km spatial resolution climate surfaces for
401 global land areas. *Int. J. Clim.* **37**, 4302-4315 (2017)
- 402 40. Bates, D. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **67**, 1-48 (2015).
- 403 41. Zuur, A.F. et al. *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York,
404 2009).
- 405 42. Gurevitch, J. et al. Meta-analysis and the science of research synthesis. *Nature* **555**, 175
406 (2018).
- 407 43. Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R² from
408 generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133-142 (2013).

- 409 44. Barton, K. *MuMIn: Multi-Model Inference*. R package version 1.40.4 (2018; [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
410 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)).
- 411 45. Wood, S.N. *Generalized Additive Models: An Introduction with R* (Chapman and Hall/CRC, ed. 2,
412 2017).
- 413 46. R Core Team. *R: A language and environment for statistical computing* (R Foundation for Statistical
414 Computing, Vienna, Austria, 2018; <https://www.R-project.org/>).
- 415 47. André, M. F. et al. Contrasting weathering and climate regimes in forested and cleared
416 sandstone temples of the Angkor region. *Earth Surf. Process. Landforms* **37**, 519–532 (2012).
- 417 48. Arunachalam, A. & Arunachalam, K. Influence of gap size and soil properties on microbial
418 biomass in a subtropical humid forest of north-east India. *Plant Soil* **223**, 187–195 (2000).
- 419 49. Asbjornsen, H., Ashton, M. S., Vogt, D. J. & Palacios, S. Effects of habitat fragmentation on
420 the buffering capacity of edge environments in a seasonally dry tropical oak forest ecosystem
421 in Oaxaca, Mexico. *Agric. Ecosyst. Environ.* **103**, 481–495 (2004).
- 422 50. Barg, A. K. & Edmonds, R. L. Influence of partial cutting on site microclimate, soil nitrogen
423 dynamics, and microbial biomass in Douglas-fir stands in western Washington. *Can. J. For.*
424 *Res.* **29**, 705–713 (1999).
- 425 51. Belsky, A. J. et al. The Effects of Trees on Their Physical, Chemical and Biological
426 Environments in a Semi-Arid Savanna in Kenya. *J. Appl. Ecol.* **26**, 1005 (1989).
- 427 52. Blennow, K. Modelling minimum air temperature in partially and clear felled forests. *Agric.*
428 *For. Meteorol.* **91**, 223–235 (1998).
- 429 53. Brower, L. P. et al. Oyamel fir forest trunks provide thermal advantages for overwintering
430 monarch butterflies in Mexico. *Insect Conserv. Divers.* **2**, 163–175 (2009).
- 431 54. Cachan, P. Signification écologique des variations microclimatiques verticales dans la forêt
432 sempervirente de basse Côte d'Ivoire. *Ann. Fac. Sci. Dakar* **8**, 89–155 (1963).
- 433 55. Carlson, D. W. & Groot, A. Microclimate of clear-cut, forest interior, and small openings in
434 trembling aspen forest. *Agric. For. Meteorol.* **87**, 313–329 (1997).
- 435 56. Chen, J., Franklin, J. F. & Spies, T. A. Contrasting microclimates among clearcut, edge, and
436 interior of old-growth Douglas-fir forest. *Agric. For. Meteorol.* **63**, 219–237 (1993).
- 437 57. Chen, J. et al. Microclimate in forest ecosystem and landscape ecology. *Bioscience* **49**, 288–297
438 (1999).
- 439 58. Childs, S. W. & Flint, L. E. Effect of shadeboards, shelterwoods, and clearcuts on temperature
440 and moisture environments. *For. Ecol. Manage.* **18**, 205–217 (1987).
- 441 59. Currylow, A. F., MacGowan, B. J. & Williams, R. N. Short-term forest management effects
442 on a long-lived ectotherm. *PLoS One* **7**, (2012).
- 443 60. Daily, G. C. & Ehrlich, P. R. Nocturnality and species survival. *Proc. Natl. Acad. Sci.* **93**,
444 11709–11712 (1996).
- 445 61. Davies-Colley, R. J., Payne, G. W. & van Elswijk, M. Microforest gradients across a forest
446 edge. *N. Z. J. Ecol.* **24**, 111–121 (2000).
- 447 62. Denslow, J. S. Gap partitioning among tropical rainforest trees. *Biotropica* **12**, 47–55 (1980).
- 448 63. Didham, R. K. & Ewers, R. M. Edge effects disrupt vertical stratification of microclimate in
449 a temperate forest canopy. *Pacific Sci.* **68**, 493–508 (2014).
- 450 64. Dovčiak, M. & Brown, J. Secondary edge effects in regenerating forest landscapes:
451 Vegetation and microclimate patterns and their implications for management and
452 conservation. *New For.* **45**, 733–744 (2014).

- 453 65. Evans, G. C. Ecological studies on the rain forest of southern Nigeria. II. The atmospheric
454 environmental conditions. *J. Ecol.* **27**, 437–482 (1939).
- 455 66. Fetcher, N., Oberbauer, S. F. & Strain, B. R. Vegetation effects on microclimate in lowland
456 tropical forest in Costa Rica. *Int. J. Biometeorol.* **29**, 145–155 (1985).
- 457 67. Frey, S. J. K. et al. Spatial models reveal the microclimatic buffering capacity of old-growth
458 forests. *Sci. Adv.* **2**, (2016).
- 459 68. Fridley, J. D. Downscaling climate over complex terrain: High finescale (<1000 m) spatial
460 variation of near-ground temperatures in a montane forested landscape (Great Smoky
461 Mountains). *J. Appl. Meteorol. Climatol.* **48**, 1033–1049 (2009).
- 462 69. Gaudio, N., Gendre, X., Saudreau, M., Seigner, V. & Balandier, P. Impact of tree canopy on
463 thermal and radiative microclimates in a mixed temperate forest: A new statistical method to
464 analyse hourly temporal dynamics. *Agric. For. Meteorol.* **237–238**, 71–79 (2017).
- 465 70. Ghuman, B. S. & Lal, R. Effects of partial clearing on microclimate in a humid tropical
466 forest. *Agri* **40**, 17–29 (1987).
- 467 71. Graae, B. J. et al. On the use of weather data in ecological studies along altitudinal and
468 latitudinal gradients. *Oikos* **121**, 3–19 (2012).
- 469 72. Granberg, H. B., Ottosson-Löfvenius, M. & Odin, H. Radiative and aerodynamic effects of
470 an open pine shelterwood on calm, clear nights. *Agric. For. Meteorol.* **63**, 171–188 (1993).
- 471 73. Groot, A. & Carlson, D. W. Influence of shelter on night temperatures, frost damage, and
472 bud break of white spruce seedlings. *Can. J. For. Res.* **26**, 1531–1538 (1996).
- 473 74. Grubb, P. J. & Whitmore, T. C. A comparison of montane and lowland rain forest in
474 Ecuador : II. The climate and its effects on the distribution and physiognomy of the forests.
475 *J. Ecol.* **54**, 303–333 (1966).
- 476 75. Heithecker, T. D. & Halpern, C. B. Edge-related gradients in microclimate in forest
477 aggregates following structural retention harvests in western Washington. *For. Ecol. Manage.*
478 **248**, 163–173 (2007).
- 479 76. Holl, K. D. Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain,
480 seed germination, microclimate and soil. *Biotropica* **31**, 229–242 (1999).
- 481 77. Honnay, O., Verheyen, K. & Hermy, M. Permeability of ancient forest edges for weedy plant
482 species invasion. *For. Ecol. Manage.* **161**, 109–122 (2002).
- 483 78. Hopkins, B. Vegetation of the Olokemeji Forest Reserve, Nigeria: III. The Microclimates
484 with Special Reference to their Seasonal Changes. *J. Ecol.* **53**, 125–138 (1965).
- 485 79. Ibanez, T., Hély, C. & Gaucherel, C. Sharp transitions in microclimatic conditions between
486 savanna and forest in New Caledonia: Insights into the vulnerability of forest edges to fire.
487 *Austral Ecol.* **38**, 680–687 (2013).
- 488 80. Jiménez, C., Tejedor, M. & Rodríguez, M. Influence of land use changes on the soil
489 temperature regime of Andosols on Tenerife, Canary Islands, Spain. *Eur. J. Soil Sci.* **58**, 445–
490 449 (2007).
- 491 81. Johansson, D. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr Suec.*
492 **59**, 1–136 (1974).
- 493 82. Joly, D. Etude comparative de la température en forêt et en espace ouvert dans le parc
494 naturel régional du haut-jura. *Climatologie* **11**, 19–33 (2014).
- 495 83. Karki, U. & Goodman, M. S. Microclimatic differences between mature loblolly-pine
496 silvopasture and open-pasture. *Agrofor. Syst.* **89**, 319–325 (2015).

- 497 84. Korb, J. & Linsenmair, K. E. The effects of temperature on the architecture and distribution
498 of *Macrotermes bellicosus* (isoptera, macrotermitinae) mounds in different habitats of a
499 West African Guinea savanna. *Insectes Soc.* **45**, 51–65 (1998).
- 500 85. Kubin, E. & Kempainen, L. Effect of clearcutting of boreal spruce forest on air and soil
501 temperature conditions. *Acta For. Fenn.* **225**, (1991).
- 502 86. Lal, R. & Cummings, D. J. Clearing a tropical forest I. Effects on soil and micro-climate. *F.*
503 *Crop. Res.* **2**, 91–107 (1979).
- 504 87. Langvall, O. & Ottosson Löfvenius, M. Effect of shelterwood density on nocturnal near-
505 ground temperature, frost injury risk and budburst date of Norway spruce. *For. Ecol. Manage.*
506 **168**, 149–161 (2002).
- 507 88. Latimer, C. E. & Zuckerberg, B. Forest fragmentation alters winter microclimates and
508 microrefugia in human-modified landscapes. *Ecography (Cop.)*. **40**, 158–170 (2017).
- 509 89. Lawson, G. W., Armstrong-Mensah, K. O. & Hall, J. B. A Catena in Tropical Moist Semi-
510 Deciduous Forest Near Kade, Ghana. *J. Ecol.* **58**, 371–398 (1970).
- 511 90. Locosselli, G. M., Cardim, R. H. & Ceccantini, G. Rock outcrops reduce temperature-
512 induced stress for tropical conifer by decoupling regional climate in the semiarid
513 environment. *Int. J. Biometeorol.* **60**, 639–649 (2016).
- 514 91. Lofvenius, M. O. Temperature and radiation regimes in pine shelterwood and clear-cut area.
515 (1993).
- 516 92. Lüdi, W. & Zoller, H. Über den Einfluss der Waldnähe auf das Lokalklima : Untersuchungen
517 im Gebiete des Hardwaldes bei Muttenz (Base) (in German). *Bericht über das Geobot.*
518 *Forschungsinstitut Rübel Zürich* (2018).
- 519 93. Luskin, M. S. & Potts, M. D. Microclimate and habitat heterogeneity through the oil palm
520 lifecycle. *Basic Appl. Ecol.* **12**, 540–551 (2011).
- 521 94. Matlack, G. R. Microenvironment variation within and among forest edge sites in the
522 Eastern United States. **66**, 185–194 (1993).
- 523 95. Meleason, M. A. & Quinn, J. M. Influence of riparian buffer width on air temperature at
524 Whangapoua Forest, Coromandel Peninsula, New Zealand. *For. Ecol. Manage.* **191**, 365–371
525 (2004).
- 526 96. Morecroft, M. D., Taylor, M. E. & Oliver, H. R. Air and soil microclimates of deciduous
527 woodland compared to an open site. *Agric. For. Meteorol.* **90**, 141–156 (1998).
- 528 97. Nunez, M. & Bowman, D. M. J. S. Nocturnal cooling in a high altitude stand of *Eucalyptus*
529 *delegatensis* as related to stand density. *Aust. For. Res.* **16**, 185–197 (1986).
- 530 98. Odin, H., Magnusson, B. & Bäckström, P.-O. Effect of low shelterwood on minimum
531 temperature near the ground. in *Ecology and Management of Forest Biomass Production Systems* (ed.
532 Perttu, K.) 77–99 (Swedish University of Agricultural Sciences, Department of Ecology and
533 Environmental Research, Report 15, 1984).
- 534 99. Porté, A., Huard, F. & Dreyfus, P. Microclimate beneath pine plantation, semi-mature pine
535 plantation and mixed broadleaved-pine forest. *Agric. For. Meteorol.* **126**, 175–182 (2004).
- 536 100. Potter, B. E., Teclaw, R. M. & Zasada, J. C. The impact of forest structure on near-
537 ground temperatures during two years of contrasting temperature extremes. *Agric. For.*
538 *Meteorol.* **106**, 331–336 (2001).
- 539 101. Renaud, V., Innes, J. L., Dobbertin, M. & Rebetez, M. Comparison between open-
540 site and below-canopy climatic conditions in Switzerland for different types of forests over

- 541 10 years (1998-2007). *Theor. Appl. Climatol.* **105**, 119–127 (2011).
- 542 102. Rodríguez-Sánchez, F., Pérez-Barrales, R., Ojeda, F., Vargas, P. & Arroyo, J. The
543 Strait of Gibraltar as a melting pot for plant biodiversity. *Quat. Sci. Rev.* **27**, 2100–2117
544 (2008).
- 545 103. Scheffers, B. R. et al. Increasing arboreality with altitude: a novel biogeographic
546 dimension. *Proc. R. Soc. B Biol. Sci.* **280**, 20131581–20131581 (2013).
- 547 104. Schulz, J. P. Ecological studies on Rain Forest in Northern Suriname. *Meded. Bot.*
548 *Museum en Herb. R.U.U.* **163**, 1–267 (1960).
- 549 105. Seebacher, F. & Alford, R. A. Color pattern asymmetry as a correlated of habitat
550 disturbance in spotted salamanders (*Ambystoma maculatum*). *J. Herpetol.* **36**, 95–98 (2002).
- 551 106. Shanks, R. E. & Norris, F. H. Microclimatic variation in a small valley in eastern
552 Tennessee. *Ecology* **31**, 532–539 (1950).
- 553 107. Shoo, L. P., Storlie, C., Williams, Y. M. & Williams, S. E. Potential for mountaintop
554 boulder fields to buffer species against extreme heat stress under climate change. *Int. J.*
555 *Biometeorol.* **54**, 475–478 (2010).
- 556 108. Sporn, S. G., Bos, M. M., Kessler, M. & Gradstein, S. R. Vertical distribution of
557 epiphytic bryophytes in an Indonesian rainforest. *Biodivers. Conserv.* **19**, 745–760 (2010).
- 558 109. Suggitt, A. J. et al. Habitat microclimates drive fine-scale variation in extreme
559 temperatures. *Oikos* **120**, 1–8 (2011).
- 560 110. Vajda, A. & Venäläinen, A. Feedback processes between climate, surface and
561 vegetation at the northern climatological tree-line (Finnish Lapland). *Boreal Environ. Res.* **10**,
562 299–314 (2005).
- 563 111. Valigura, R. A. Modification of Texas clear-cut environments with Loblolly pine
564 shelterwoods. *J. Environ. Manage.* **40**, 283–295 (1994).
- 565 112. van Dam, O. Forest filled with gaps: Effects of gap size on water and nutrient
566 cycling in tropical rain forest. (PhD thesis. Utrecht University, Utrecht, 2001).
- 567 113. Varner, J. & Dearing, M. D. The importance of biologically relevant microclimates in
568 habitat suitability assessments. *PLoS One* **9**, e104648 (2014).
- 569 114. Vitt, L. & Avila-Pires, T. The impact of individual tree harvesting on thermal
570 environments of lizards in Amazonian rain forest. *Conserv. Biol.* **12**, 654–664 (1998).
- 571 115. Williams-Linera, G. Vegetation structure and environmental conditions of forest
572 edges in panama. *J. Ecol.* **78**, 356–373 (1990).
- 573 116. Xu, M., Qi, Y., Chen, J. & Song, B. Scale-dependent relationships between landscape
574 structure and microclimate. *Plant Ecol.* **173**, 39–57 (2004).
- 575 117. Yan, M., Zhong, Z. & Liu, J. Habitat fragmentation impacts on biodiversity of
576 evergreen broadleaved forests in Jinyun Mountains, China. *Front. Biol. China* **2**, 62–68 (2007).
- 577 118. Yanoviak, S. P. Community structure in water-filled tree holes of panama: Effects of
578 hole height and size. *Selbyana* **20**, 106–115 (1999).
- 579 119. Young, A. & Mitchell, N. Microclimate and vegetation edge effects in a fragmented
580 podocarp-broadleaf forest in New Zealand. **67**, 63–72 (1994).
- 581 120. Zhu, H., Xu, Z. F., Wang, H. & Li, B. G. Tropical rain forest fragmentation and its
582 ecological and species diversity changes in southern Yunnan. *Biodivers. Conserv.* **13**, 1355–1372
583 (2004).
- 584 121. Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G. & The PRISMA Group. Preferred

585 reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Med.*
586 **6**, e1000097 (2009).
587
588

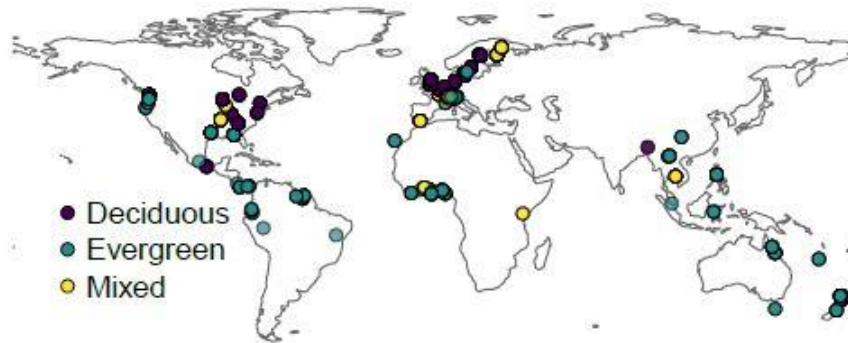
589 **Figure Legends**

590 **Fig. 1 | Forests buffer temperatures under canopies globally.** **a**, Distribution of the 98 study
591 sites and their vegetation type (deciduous, evergreen or mixed forests). **b**, Histograms display the
592 714 paired temperature offset values for maximum (T_{\max}), mean (T_{mean}) and minimum (T_{\min})
593 temperatures. Maximum and mean temperatures are consistently cooler, and minimum temperatures
594 consistently warmer, within forests compared to macroclimate temperatures. Offsets were always
595 calculated as temperatures inside minus macroclimate temperatures outside the forest such that
596 negative (positive) values reflect cooler (warmer) forest temperatures. Offset means and standard
597 errors are based on mixed-effects models with study as a random-effect term. Full statistical
598 analyses, data and code are reported in Supplementary Information and ref. 37.

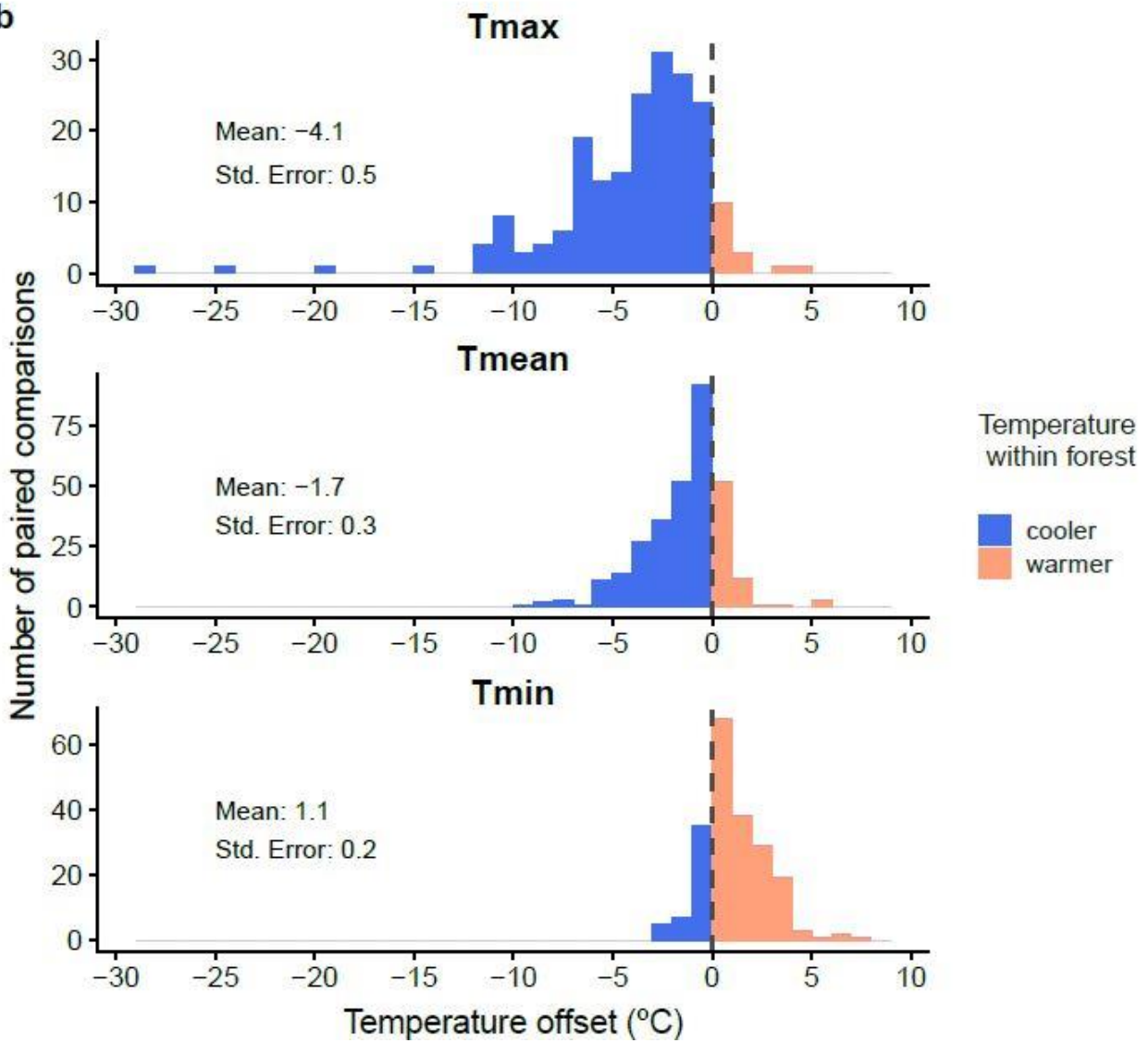
599 **Fig. 2 | Forest temperature offsets under canopies are negatively related to warming air**
600 **temperatures and dependent on the biome.** **a**, The magnitude of the temperature offset within
601 forests depends on ambient macroclimate temperature: the higher the warming, the more offsetting
602 of temperatures (T_{\max} and T_{mean}). For minimum temperatures, positive offsets increase with colder
603 temperatures. **b**, Study sites were classified into boreal, temperate or tropical, based on their latitude.
604 Offset values were always calculated as temperatures inside minus macroclimate temperatures
605 outside the forest such that negative (positive) values reflect cooler (warmer) forest temperatures.
606 Regression slopes, 95% confidence intervals (grey shading), and offset means (red lines), are based
607 on mixed-effects models with study as a random-effect term. Full statistical analyses, data and code
608 are reported in Supplementary Information and ref. 37.

609 Fig. 1 | Forests buffer temperatures under canopies globally

a

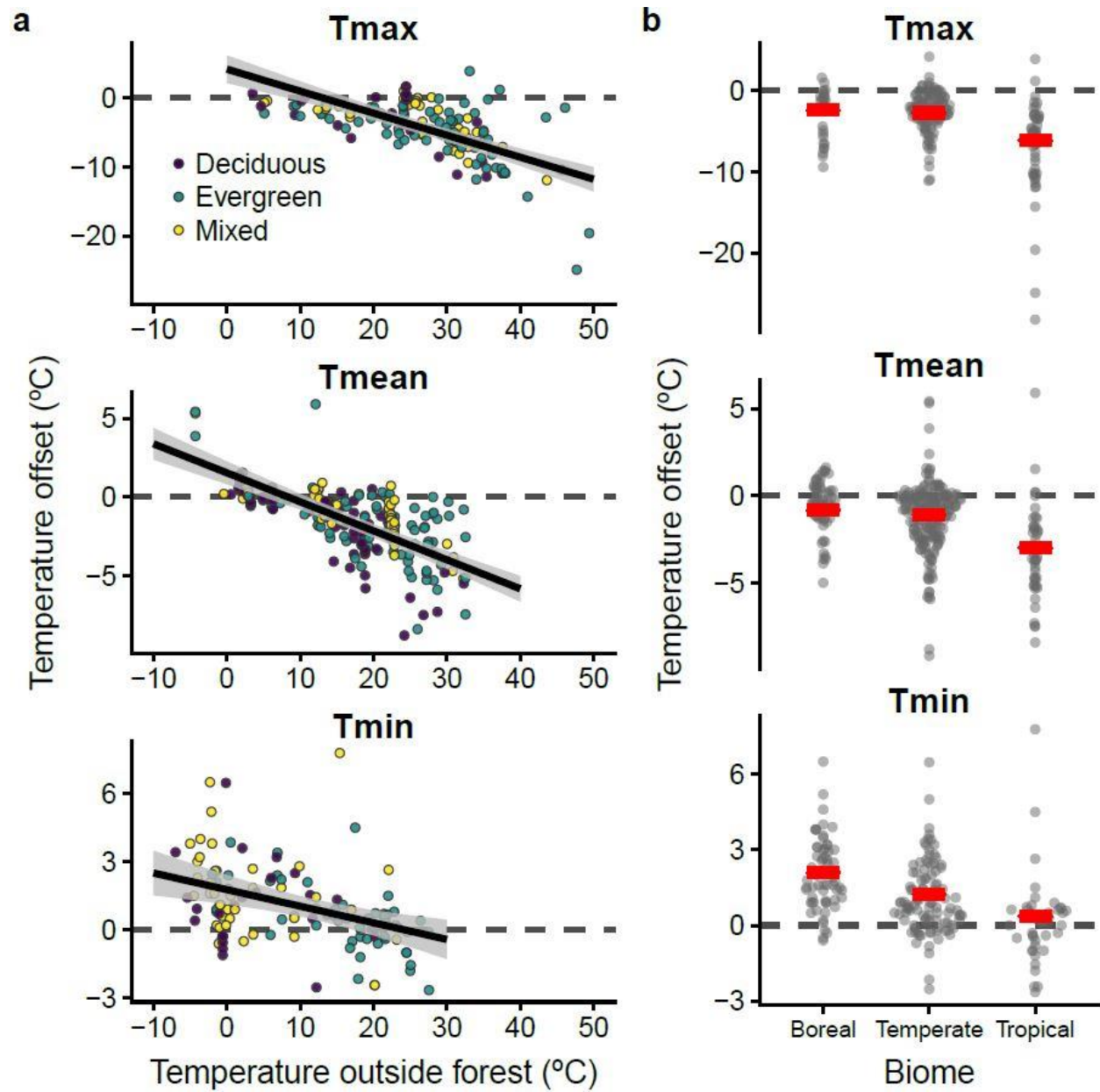


b



610
611

Fig. 2 | Forest temperature offsets under canopies are negatively related to warming air temperatures and dependent on the biome



612