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Doughty, CE

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Tropical forests are approaching critical temperature thresholds

Christopher E. Doughty[1], Jenna Keany[1], Benjamin C. Wiebe[1], Camilo Rey-Sanchez[2], Kelsey R. Carter[3,3.5], Kali B. Middleby[4], Alexander W. Cheesman[4], Michael L. Goulden[5], Humberto R. da Rocha[6], Scott D. Miller[7], Yadvinder Malhi[8], Sophie Fauset[9], Emanuel Gloor[10], Martijn Slot[11], Imma M. Oliveras Menor[8,12], Kristine Y. Crous[13], Gregory R. Goldsmith[14], Joshua B. Fisher[14]

[1]School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, AZ, USA

[2] Department of Marine, Earth and Atmospheric Sciences, North Carolina State University, Raleigh, NC, USA

[3] College of Forest Resources and Environmental Sciences, Michigan Technological University, Houghton, MI, USA

[3.5] Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM, USA

[4] Centre for Tropical Environmental and Sustainability Science, James Cook University, Cairns, QLD, Australia

[5]Department of Earth System Science, University of California, Irvine, California, USA

[6]Departamento de Ciencias Atmosfericas, Universidade de São Paulo, São Paulo, Brazil

[7]Atmospheric Sciences Research Center, State University of New York at Albany, Albany, NY, USA

[8]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

[9]School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK

[10] University of Leeds, Leeds, UK

[11] Smithsonian Tropical Research Institute, Balboa Ancon, Republic of Panama

[12] AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), CIRAD, CNRS, INRA, IRD, Université de Montpellier, Montpellier, France

[13]Western Sydney University, Hawkesbury Institute for the Environment, Penrith, NSW, Australia

[14]Schmid College of Science and Technology, Chapman University, Orange, CA 92866 USA

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Abstract –The critical temperature beyond which photosynthetic machinery in tropical trees
begins to fail averages ~46.7°C (T_{crit}) [1]. However, it remains unclear whether leaf temperatures
experienced by tropical vegetation approach this threshold or soon will under climate change.
We found that pantropical canopy temperatures independently triangulated from individual leaf
thermocouples, pyrgeometers, and remote sensing (ECOSTRESS) have midday-peak
temperatures of ~34°C during dry periods, with a long high-temperature tail that can exceed
40°C. Leaf thermocouple data from multiple sites across the tropics suggest that even within
pixels of moderate temperatures, upper-canopy leaves exceed T_{crit} 0.01% of the time. Further,
upper-canopy leaf warming experiments (+2, 3, and 4°C in Brazil, Puerto Rico and Australia)
increased leaf temperatures non-linearly with peak leaf temperatures exceeding T_{crit} 1.3% of the
time (11% >43.5°C, 0.3% >49.9°C). Using an empirical model incorporating these dynamics
(validated with warming experiment data), we found that tropical forests can withstand up to a
3.9 ± 0.5 °C increase in air temperatures before a potential tipping point in metabolic function,
but remaining uncertainty in the plasticity and range of T_{crit} in tropical trees and the impact of
leaf death on tree death could drastically change this prediction. The 4.0°C estimate is within the
"worst case scenario" (RCP-8.5) of climate change predictions[2] for tropical forests and therefore
it is still within our power to decide (e.g., by not taking the RCP 6.0 or 8.5 route) the fate of these
critical realms of carbon, water, and biodiversity [3,4].

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Introduction

Tropical forest mean temperatures are high, and their diel and seasonal variations are relative small, thus even a small change in temperature could more greatly impact tropical plant species than a large temperature change in other global regions [5]. Average temperatures have risen by 0.5 °C per decade in some tropical regions, and temperature extremes are becoming more pronounced (e.g. the El Niño of 2015 was 1.5 °C warmer than the El Niño of 1997)[6,7]. Since temperatures in tropical forests are near or above the temperature optimum for photosynthesis[8], further increased temperatures may close stomata, reducing transpirational cooling and exposing leaves to damaging temperatures. More than 150 years ago, Sachs (1864) first reported that leaves from different plant species could withstand temperatures up to 50 °C, but would die at temperatures even slightly higher [9]. In the era of climate change, this finding is still relevant. How close are forests to a high temperature threshold such as the one proposed by Sachs? Nowhere is such a question more pressing than in tropical forests, which serve as critical stores and sinks of carbon, play host to most of the world's biodiversity, and may be more sensitive to increasing temperatures than other ecoregions [3,4].

More recently, techniques to determine the ability for leaves to withstand high temperatures have advanced to focus on T_{crit}, or the temperature at which irreversible damage to the photosynthetic machinery occurs. Over the past few years, T_{crit} data have become increasingly available for tropical forests, specifically measured as the temperature at which the ratio of variable fluorescence yield to maximum fluorescence yield (F_v/F_m), reflecting photosystem II functioning, starts to decline [1,10]. The decline in F_v/F_m is often followed by development of necrosis and leaf death[11]. Heat tolerance, measured by T_{crit}, varies minimally among tropical species, mainly due to differences in growing environment and leaf traits. For instance, among 147 tropical tree species, the average T_{crit} was found to be 46.7 °C (5th–95th percentile: 43.5–49.7 °C) [1]. They also found that older tree lineages that experienced higher temperatures in the distant past did not have higher T_{crit} and thus, were not better acclimated to higher temperatures today. Across the planet, heat tolerance generally increases with higher mean growing temperatures. For example, as average temperatures increase by ~20 °C from the Arctic to the Tropics, heat tolerance was 9 °C greater in tropical plants than arctic plants [12]. Similarly, as temperatures decrease by 17 °C along a tropical elevation gradient, heat tolerance decreases by ~2 °C [10]. Heat tolerance also increases with increasing leaf mass area (LMA), suggesting that heat tolerance may be linked to construction costs of the leaves and their mean leaf lifetime [1].

With a much-improved understanding of T_{crit} across the Tropics, it is now important to know how close tropical leaves are to experiencing and surpassing these critical temperatures. In the past, tropical forest leaf and canopy temperatures were difficult and time consuming to measure, but new technologies like drones and thermal cameras are making the process much easier [13]. More recently, the ECOsystem Spaceborne Thermal Radiometer Experiment on Space Station (ECOSTRESS) sensor on the International Space Station (ISS) can provide unique high temporal and spatial resolution measurements of land surface temperatures at the global scale [14]. ECOSTRESS is an improvement over previous thermal satellite land surface temperature (LST) sensors because it has 5 spectral bands, a 70 m spatial resolution, and multiple diel overpass times, as well as improved algorithms.

99   Here we use data from the new ECOSTRESS sensor to estimate peak pantropical forest canopy
100 temperatures. We begin by ground truthing the satellite data with tower-based pyrgeometer data.
101 We then use these data to determine what causes variation in peak temperatures at the canopy
102 scale and show similar trends driving peak temperatures across all of the Tropics. Critically, we
103 show that for a given canopy temperature, individual leaf temperatures display a "long tail" of
104 values in the distribution, where the temperatures of a few individual leaves far exceed that of
105 the overall canopy, and that this skewed distribution persists under leaf warming experiments of
106 2, 3 and 4 °C. Finally, we develop a simple empirical model to explore the implications of
107 observed leaf temperatures on the fate of tropical forests under future climate change.

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Ground validation using pyrgeometer data- We first ground-truth ECOSTRESS and find similar peak temperatures between a 3-year, 30-minute averaged canopy temperature pyrgeometer dataset for a lowland tropical rainforest site near the Tapajos River (KM 83) in Brazil and a broad region (Fig ED1a red box) of the Amazon Basin (Fig 1a; $r^2 = 0.75$, N=16, P < 0.0001, with ECOSTRESS having a slight cool bias (Fig ED2d) matching previous findings[15]). The pyrgeometer data at that site indicate that midday sunny canopy temperatures in the dry season (July to Dec) averaged 33.5 °C compared to 31.0 °C in the wet season (Jan to June) (Fig 1a). Sampling frequency (Fig ED3), latent heat flux (Fig ED 2c), air temperature (Fig ED2b), and soil moisture (Fig ED2a) all impacted canopy temperatures. The tower-mounted pyrgeometer inherently averages spatially (over an 8,000 m^2 footprint) and thus amalgamates individual peak leaf temperatures. Therefore, we used leaf thermocouples on three canopy tree species at the same site to assess individual leaf temperatures. The mean temperatures for 11 individual sun-exposed leaves over 54 sunny 20-minute periods also averaged ~33.2 °C (similar to that measured by the pyrgeometer) but with a "long tail" of high temperatures (> 40 °C) in the distribution (Fig 1b).

We then aggregated similar upper-canopy leaf thermocouple datasets from Brazil[16,17], Puerto Rico[18], Panama[19] and Australia[20] and all had "long tail distributions" (Fig 1c and ED4-5) with upper limits ~44 °C (43-48) (but see Fig ED5c for a cooler Atlantic forest example[16]). When we zoom in on the long tail of each dataset (insets in Fig ED4-5), the curve shows statistical regularity, which allows us to estimate T_{crit} as a percent of all canopy top leaves. For instance, when all data are aggregated across sites, we estimate that 0.01% (0.03% >43.5°C) of all leaves will surpass T_{crit} at least once a season (Fig 1c). Although infrequent, the occurrence of extreme temperatures may have a catastrophic effect on a leaf's physiology and may be thought of as a low probability, high impact event.

We then aggregated data from three in situ upper-canopy warming experiments where leaves were heated by 2, 3, and 4 °C (in Brazil[17], Puerto Rico[18], and Australia[20] respectively). Warmed leaf peak temperatures ranged between 51-54 °C (Fig ED4), an increase of ~8 °C above ambient highs (mean ~45 °C-; Fig ED4). The percentage of warmed leaves exceeding T_{crit} at least once a year increased to 1.3% of all warmed leaves (11% >43.5°C, 0.3% >49.9°C) (Fig 1c), because of a non-linear relationship between leaf and air temperatures in the warming experiments (Fig 1d). During the Brazilian warming experiment, individual leaves exceeded T_{crit} and T_{50} with noticeable signs of leaf necrosis, some for a duration of >8 mins (Fig ED6), and following this, net transpiration in warmed branches decreased significantly (P<0.0001) by an average of 27% (Fig 3a). In the warming experiments, leaves exceeded T_{crit} for extended periods (>8 minutes) 0.2% (0.6% for >6 minutes) of the time over the course of a season (Fig ED6), events that can cause leaf browning and necrosis.

Remote sensing data – We analyze ECOSTRESS LST data along with comparisons to VIIRS and MODIS, as well as SMAP soil moisture. At the landscape scale (Fig ED1 red box), peak ECOSTRESS LST (~36 °C) using all data corresponded with periods of low SMAP-measured soil moisture (~0.3 m^3 m^{-3}) (Fig 2a and b). A linear extrapolation of our pyrgeometer data to a soil moisture of 0.3 m^3 m^{-3} would predict a similar canopy temperature (~36 °C) (Fig ED2a). For the warmest datapoint (Fig 2c and d), we then expanded the area (Fig ED1 blue box) and applied the highest quality data flags (~6% of the data used – see methods and SI for an extensive

153   discussion of this), which reduced the median value to 34 °C. These average temperatures do not
154   reflect the extremes, as 0.5% of the data is >38 °C and 0.1% is > 40 °C (Fig 2d and Table 1).
155   We show the long tail distribution of temperatures (with a log10 scale) for Amazonia in Fig 2d.
156   Using less restrictive or no quality flags generally resulted in higher tails > 40 °C (Table S2). We
157   compare ECOSTRESS to other LST satellites (VIIRS, MODIS) (Fig ED9-10 and Table S1-2)
158   and show similar results, but with greater fidelity and ability to capture long tails with
159   ECOSTRESS. LST for Central Africa (Fig 2e and Fig ED7) and SE Asia (Fig 2f and Fig ED8)
160   during similar peak dry periods had similar peak temperatures (with data flags; Table 1). We
161   then estimated the highest temperatures during dry periods if temperature increased by 2 °C (to
162   simulate climate change) and found that the percent of time above threshold temperatures would
163   increase by an order of magnitude in all three regions. For example, the percent time Amazon
164   canopies spend at temperatures $\geq$ 38.0 °C would increase from 0.5 to 5% and the percent time $\geq$
165   40.0 °C would increase from 0.1 to 1% (Table 1).

166   *Model results* - An empirical model to explore the temperature thresholds of tropical trees was
167   parameterized using the temperature distributions of warmed and non-warmed leaves (Fig 1c)
168   from the combined tropical datasets (N=5). Assuming leaf death at T_{crit}, and evaporative cooling
169   as a linear function of the number of leaves, we show that enhanced warming could tip the forest
170   towards the death of all leaves and possible tree mortality (Fig 3b and Table 2). The modelled
171   impact of warming on reduced transpirational cooling approximately matched the measured
172   values; a 26 ($\pm$ 28) % (N=30 simulations) reduction of modelled evaporative cooling with ~2 °C
173   warming, versus a measured 27% average reduction after ~2 °C warming during the Brazilian
174   warming experiment (Fig 3a). The decline in transpiration occurred after leaf temperatures
175   exceeding both T_{crit} for >8 mins (Fig 3a inset) and T50. Mean initial modelled canopy
176   temperature was 33.7 $\pm$ 0.4 °C, matching the measured canopy average (33.5 °C) during peak
177   temperature periods (sunny, midday). When run using the most likely parameters, including a
178   T_{crit} of 46.7 °C[1], the model showed that most forests could withstand up to 3.9 $\pm$ 0.5 °C warming
179   before the death of all leaves and potential tree death (n =30 simulation runs; Fig 3b and Table
180   2), but a series of sensitivity studies give a temperature distribution between 2-8 °C (Table 2).
181   Due to the stochastic nature of droughts in our model, total leaf loss ranged over a wide
182   timespan. For instance, if temperatures increase by 0.03 °C per year, we estimate that the mean
183   time to leaf death would be 132 years, but extensive canopy leaf mortality could occur as early as
184   102 years and as late as 163 years (Fig 3b and Table 2).

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Discussion

Several lines of remotely sensed, tower-based, and *in situ* evidence (ECOSTRESS, VIIRS, pyrgeometer, leaf thermocouples) suggest that hot periods in tropical forests with low soil moisture lead to canopy temperatures that average ~34 °C, with some pixels exceeding 40 °C [8,21]. Even within a given LST pixel, there is a long tail distribution with individual leaf temperatures exceeding 40 °C. Currently, 0.01% of upper canopy leaves from *in situ* measurements exceed T_{crit} at least once a season (N=5 sites); warming experiments (N=3) suggest 1.4% will exceed T_{crit} under future warming conditions (Figs S7-9). We posit that capturing the higher tail temperatures may be important for future climate change predictions in tropical forests because as individual leaves exceed T_{crit}, they die, thus reducing the net evaporative cooling potential for the canopy, as suggested in Fig 1d and 3a). This is supported by branch warming experiments where noticeable signs of leaf damage and a reduction of transpiration by 27% followed periods where leaf temperatures exceeded T_{crit} for extended periods (Fig 3a). Certain tropical regions, such as the Southeast Amazon, may already be experiencing critical thresholds[22]. Many recent large-scale drought studies have shown that the largest, most sun-exposed trees die disproportionately [23,24]. Moreover, there has been a recent increase in continental mortality rates across the Amazon basin (although not in the Congo basin and Table 1 shows the Congo basin experiences lower peak temperatures than the Amazon) [4] and carbon uptake across the basin has been reduced [25]. We propose that high leaf temperatures may play a role (along with carbon starvation and hydraulic limitation[34]) in those recent mortality events.

We make several assumptions in our model related to the broader tipping point results. The first key assumption is that within a given LST pixel, there is a long tail of high individual tropical leaf temperatures following Fig 1c. This is supported by several leaf thermocouple datasets (N=5, Fig 1, (Figs S7-9)), all of which show a long-tail, as well as first principles (SI text). Critically, warming experiments show non-linear trends (Fig 1c and d) where temperature increases of 2, 3, and 4 °C increase maximum leaf temperatures by larger amounts (+8.1 °C, +6.1 °C, 8.0 °C, respectively; Fig ED4). Many other studies have documented individual leaf temperatures approaching 46.7 °C [8,11,16,19].

The second assumption is that water-stressed pantropical median canopy temperatures can average ~34 °C with a spatial tail exceeding 40 °C (Fig 2). In other words, RS data suggest entire canopies and forests getting very warm and (our first assumption) that within these pixels, there is a long-tail distribution of individual leaf temperatures. ECOSTRESS and VIIRS LST data are both >1 °C warmer (34.7 and 33.9 °C) than older LST sensors like MODIS (32.7 °C) (ECOSTRESS has ~0.75 °C cold bias compared to VIIRS [15]). We assume ECOSTRESS and VIIRS will be more accurate than MODIS because there are more thermal bands, vegetation can be identified with emissivity (for ECOSTRESS and VIIRS, but not MODIS), and an improved algorithm [26] can accurately estimate temperatures within 1 K for many surfaces [27]. We further found that adding 2 °C (to replicate climate change) to the measured ECOSTRESS satellite data would increase the occurrence of high tail temperatures by about an order of magnitude (e.g., from 0.1 to 1% > 40 °C) (Table 1). Therefore, the change in percentage of time when temperatures exceeded >40 °C in response to a simple addition of 2 °C was not a simple linear change.

The third assumption is that leaves at temperatures > T_{crit} will die, and thus stop contributing to future transpiration (although transpiration often stops at temperatures lower than

232 T_{crit}), and that the sum of evaporative cooling is a linear function of the total number of
233 transpiring leaves. Our T_{crit} value is based on Slot et al. (2021), who found the mean (T_{crit}) was
234 46.7 °C (5th–95th percentile: 43.5–49.7 °C) and the temperature when F_v/F_m had decreased by
235 50% (T_{50}) was 49.9 °C (47.8–52.5 °C)[1]. T_{crit} variation is important because ~50% of the species
236 from Slot et al. (2021) had a T_{crit} <46.7 °C with negative consequences at lower temperatures for
237 those species. Incorporating this variation in our model demonstrated those consequences can
238 exacerbate conditions for other species as they die and their evaporative cooling is reduced,
239 leading to less future warming (~0.1 °C) needed to achieve leaf death when such variation is
240 included (Table 2). Branch warming experiments in Brazil showed large (27%) decreases in
241 transpiration when leaves reached either T_{50} or T_{crit} for an extended period (>8 minutes) (Fig 3).
242 It was not possible to determine which (T_{50}, extended T_{crit}, or a different variable) was more
243 critical for the decrease in transpiration in our dataset (but another recent study found leaf death
244 when leaf temperatures exceeded T_{crit} for between 10 and 40 minutes[28]). If a longer time is
245 necessary to exceed T_{crit} prior to leaf death, T_{crit} will be exceeded less often and our model
246 suggests that the forest canopies could resist an additional 0.7 °C increase in air temperatures
247 prior to leaf death (Table 2). Prior work had suggested that irreversible damage will often occur
248 at 45–60 °C [29].

249   T_{crit} was the largest source of uncertainty in the model and changed the tipping point
250 temperatures by between 2-8 °C (Table 2). T_{crit} has been adopted because it is relatively easy to
251 measure and can be standardized across ecosystems. However, the impact of T_{crit} on plant
252 hydraulics still needs more research[30]. Other uncertainties include the importance of T_{crit} vs T_{50}
253 on enzyme denaturation and how long exposure to high temperatures is needed for enzyme
254 denaturation to occur[1]. We also assumed that T_{crit} does not acclimate to warming—acclimation
255 has been observed in temperate species[31], but the few studies that examined acclimation in
256 tropical species, found no, or very limited evidence for upregulation of T_{crit} [11, 32] (although warm
257 selected tropical trees in Biosphere 2 did show acclimation of T_{crit}[33]). In a sensitivity study we
258 allowed acclimation by enabling leaves to increase T_{crit} by 0.5 °C or 1°C, which increased forest
259 resistance to warming by similar amounts (by 0.5 °C and 1°C).

260   An additional assumption was that if all leaves die at T_{crit}, the tree will die. However,
261 tropical trees may use non-structural carbohydrate (NSC) [34,35] reserves to reflush leaves in later
262 years, but this is highly uncertain. Given these uncertainties, we made the simple assumption that
263 leaf level T_{crit} is a general signal of enzyme denaturation (supported by [36]), which will have a
264 range of other impacts including reducing evaporative cooling and possibly leading to tree death.
265 It is clear that further studies are needed. However, in a sensitivity study, we tried to account for
266 high NSCs by allowing trees to reflush an LAI of 2 (e.g. increase total LAI to 7) which slightly
267 increased resilience by 0.2 °C (SI text). We also assume that all sunlit leaves have an equal
268 chance of dying, but leaf orientation likely impacts both leaf temperatures and T_{crit} and only
269 further studies may address this. If the assumptions above are robust, then our model suggests
270 that tropical forests may be approaching a high temperature threshold.

271   How close are future predictions of temperature increases in tropical forests to our
272 predictions of leaf death? An ensemble of CMIP5 models (with similar results from CMIP6[37]),
273 the "worst case scenario" (RCP 8.5), predicts temperature increases of 3.3 ± 0.6 °C by 2081–
274 2100 for tropical regions with land regions heating by ~5 °C by 2181 in RCP 6.0 and by 2081 in
275 RCP 8.5 [2]. This level of climate change is within the range of our most likely scenario of 3.9 ±
276 0.50 °C of temperature increases that lead to a tipping point. However, the 4 °C is out of the

277   range of the "best case scenario" (RCP 2.6) of 0.9 ± 0.3 °C, or 1.4 ± 0.5 °C for the land surface.

278   Tree death could come earlier through a combination of mechanisms and their interactions (e.g.,

279   carbon starvation, hydraulic limitation, fire, etc.). Further, even at lower temperatures, partial

280   canopy death can negatively affect CO_2 uptake feedbacks, which could accelerate climate change

281   effects. Our sensitivity study (Table 2) shows temperature ranges leading to leaf death between

282   ~ 2.0 and 8.1 °C (the lowest and highest scenarios plus error). Scenario uncertainty due to the

283   change in drought prevalence played a relatively small role, shifting our best estimate by ~0.4

284   °C. Most of this uncertainty is methodological (T_{crit} value and high temperature duration), which

285   could be reduced with further studies and method standardization of T_{crit} measurements.

286   **Conclusion** –Our work suggests that a tipping point in metabolic function in tropical forests

287   could occur with 3.9 ± 0.5 °C of additional warming, which is more than expected for tropical

288   forests under RCP 2.6, but less than under RCP 6.0 or 8.5. We use T_{crit} to simplify an

289   enormously complex process and we want to emphasize that even our great uncertainty (2-8 °C)

290   estimates may ignore critical feedbacks such as sensitivity of reproduction to high temperatures,

291   hydraulic failure due to embolisms, and more generally, other unexplored positive feedback

292   loops. Recent literature suggests a resilience of tropical forests to how warming impacts carbon

293   uptake [33] (but see [25]) and long-term drought [38]. However, T_{crit} acts as an absolute upper limit and

294   it seems that, if our assumptions in the model are correct, crossing such a threshold is within the

295   range of our most pessimistic future climate change scenarios (RCP 6.0 or 8.5). In addition,

296   deforestation and fragmentation can amplify local temperature changes[39]. The combination of

297   climate change and local deforestation may already be placing the hottest tropical forest regions

298   close to, or even beyond, a critical thermal thresholds[40]. Therefore, our results suggest the

299   combination of ambitious climate change mitigation goals and reduced deforestation can ensure

300   that these important realms of carbon, water, and biodiversity[3,4] stay below thermally critical

301   thresholds.

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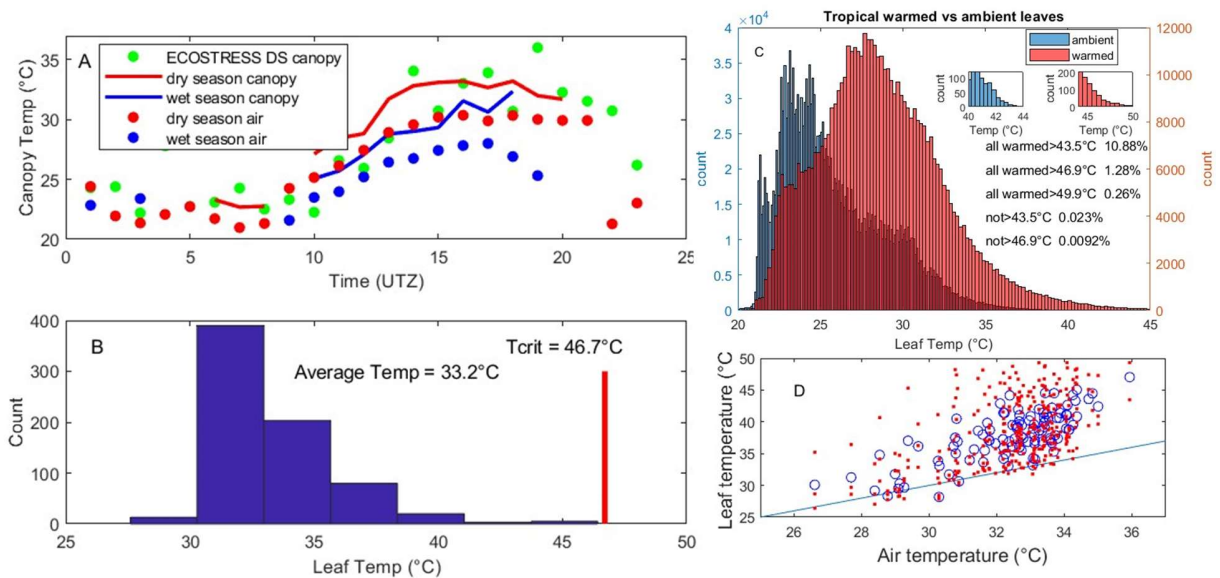
Fig 1 – In situ and warming experiment leaf temperatures compared to canopy temperatures - (A) Diurnal temperature patterns for the dry season (DS) for a region (SI Fig 1a) of the Amazon basin using ECOSTRESS data (green). Average canopy (solid line) and 40 m air temperatures (circles) from the km 83 eddy covariance tower for the dry season (red) and the wet season (blue) for sunny periods (when $solar_{in}/solar_{in,max}$ >90% for the hour). (B) A histogram of individual canopy top leaf thermocouples from 11 individual leaves from the same site as "A" over 54 sunny periods lasting 20 minutes (measurements taken every 2 min) and the average of these data (33.2 °C). T_{crit} is the temperature when the photosynthetic machinery breaks down and is shown as a red line. (C) We aggregated all leaf thermocouple data from SI Figure 7 for ambient (blue) and warmed leaves (red) and show the percentage of leaves at +2 (Brazil), +3 (Puerto Rico), and +4 °C (Australia) warming that were >T_{crit}. (D) Air temperature versus leaf temperature for a warming experiment for individual leaves (red dots), average leaf temperatures (blue circles), and one-to-one line (blue dotted).

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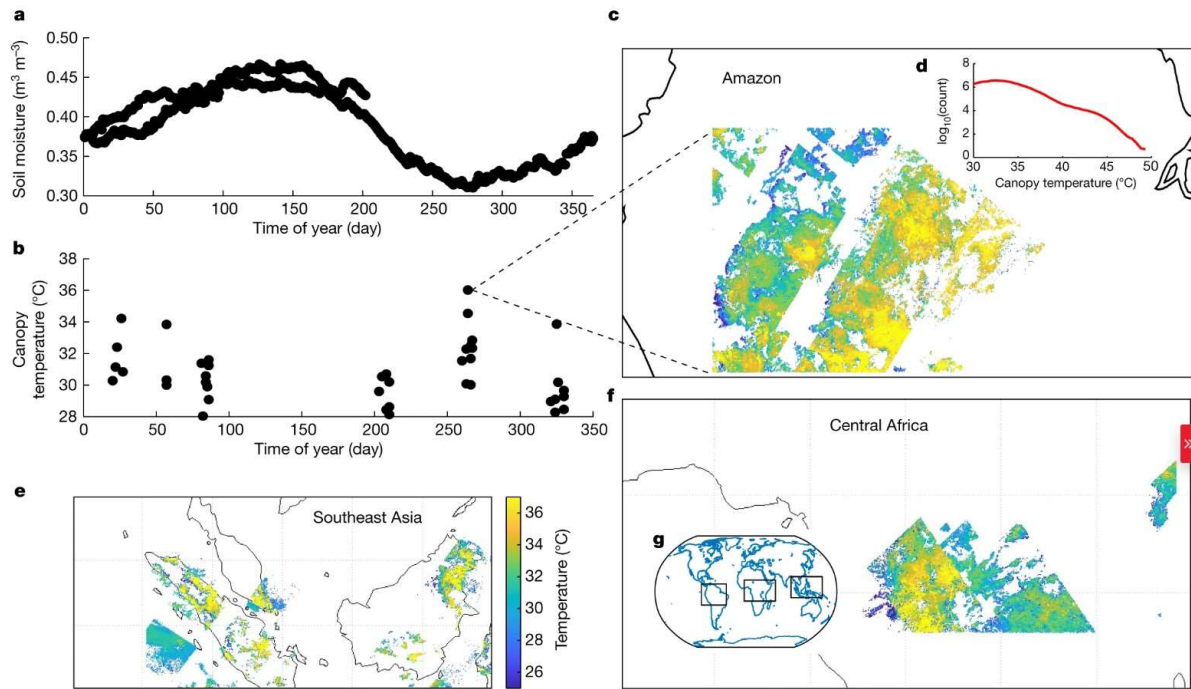
Figure 2 –Remotely sensed peak canopy temperature across the tropics - Seasonal patterns
of (A) soil moisture using SMAP and (B) canopy temperatures using ECOSTRESS for the
Amazon basin (Fig ED1a red). For the hot dry period shown by the arrows, we show a larger
spatial distribution (Fig ED1a green) (C) and log10 histogram focusing on the long tail of the
data (D) using only the highest quality data flag. We show trends for periods of low soil
moisture for (E) Southeast Asian region (Fig ED8) and (F) Central Africa (Fig ED7). G shows a
world map with focal areas boxed in red.

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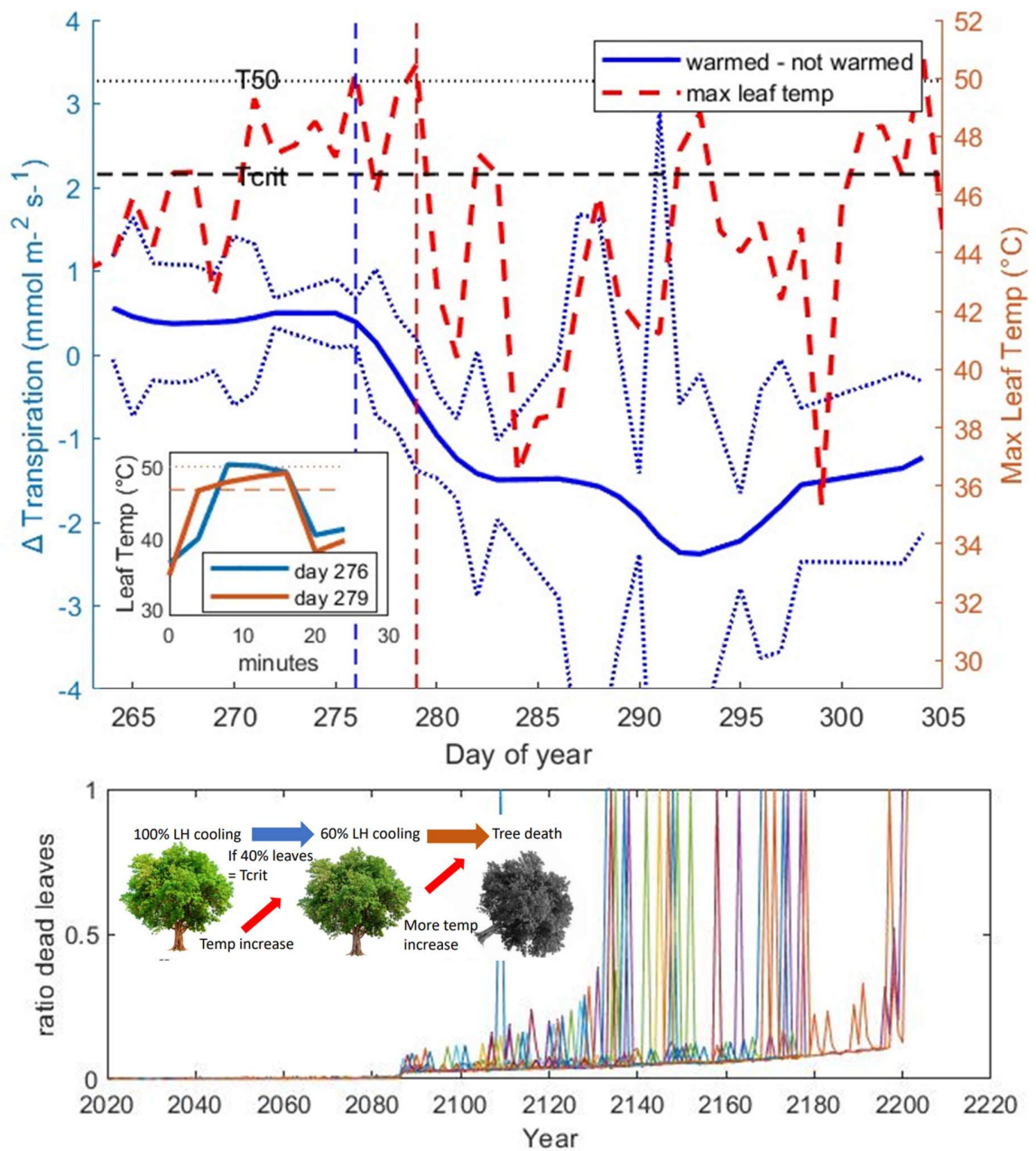
Figure 3 – Modelled impact of future warming on tropical forests - (top) Warmed branch sap flow (N=9 branches) minus non-warmed (N=4 branches) sap flow (blue line) ± propagated error (blue dotted line) for sunny (irradiance >1200 mmol m^{-2} s-1) midday periods (10:30–14:00 h local time) on six tree species using passive black plastic heaters in a heating experiment conducted at Floresta National do Tapajos, Brazil. Maximum daily temperatures for individual leaves (red stippled line) from a co-occurring leaf warming experiment during the same time period. Horizontal red lines indicate T_{crit} (dashed) and T50 (dotted). The subset figure shows the duration of warm periods for day 276 and 279 (marked as vertical red and blue lines). Around

432 this period (between 276 and 279) transpiration decreases in warmed branches relative to the
433 non-warmed branches. (bottom) Dead leaves as a ratio of total leaves over time with climate
434 change for 30 simulations (one color per simulation). (Inset) Diagram of our model showing
435 impact of T_{crit} on change in average canopy temperature as temperatures increase over time,
436 where LH is latent heat.   Tree image is from canva.com under a free content license.

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443 **Table 1– Current and future temperature extremes across the tropics.** The percent of time
444 that canopy temperatures are estimated to exceed thresholds of $\geq$ 38.0, 40.0 and 45.0 °C for low
445 soil moisture regions of the Amazon, Central Africa, and Borneo. We then increase temperature
446 by 2 °C to estimate the impact of climate change and show the same estimates for the three
447 regions. Canopy temperatures are observed by ECOSTRESS and are limited to only the highest
448 quality data.
449

	$\geq$ 38.0 °C		$\geq$ 40.0 °C		$\geq$ 45.0 °C	
	Current	+2 °C	Current	+2 °C	Current	+2 °C
South America	0.50%	5%	0.10%	1%	0.00%	0.10%
Central Africa	0.60%	2%	0.06%	0.60%	0%	0.01%
SE Asia (Borneo)	3%	8%	1%	3%	0.01%	0.30%

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453 **Table 2** –**Results from model sensitivity studies.** An individual-based model showing
454 estimated amount of climate change under different scenarios before leaf death. We first show
455 results from the "most likely scenario" with an LAI of 5, 10% drought probability, 46.7 °C T_{crit},
456 T_{crit} range=0, T_{crit} duration=1, a soil moisture exponent of -33.6, and maximum evaporative
457 cooling of 4.4 °C. We then show the results of contrasting extreme scenarios as a means of a
458 sensitivity analysis where we keep all other variables as in the "most likely scenario", but vary
459 the one mentioned. Temperature increase results represent means ± 1 SD, while time-scale
460 results represent means and range in parentheses (n = 30 simulation runs).

Most likely scenario (Tcrit=46.7)		Drought		T_{crit}		T_{crit} range	T_{crit} duration	Soil moisture coefficient	Max evap cooling
	LAI 5	20%	5%	45 °C	49.9 °C	46.7 ±2 °C	>3 periods	-38.2	3.7 °C
Total temperature increase (°C)	**3.9 ± 0.5**	3.6 ± 0.7	4.9 ± 1.1	2.6 ± 0.6	7.3 ± 0.8	3.9 ± 0.7	4.7 ± 0.8	4.1 ± 0.7	5.2 ± 0.5
Time scale until leaf death (years)	**132 (102-163)**	120 (88-170)	163 (108 - 238)	89 (69-133)	244 (204-300)	131 (100 - 185)	159 (129-220)	138 (91-183)	173 (145-202)

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Methods

Field Data - We estimate canopy temperature at the km 83 eddy covariance tower in the Tapajos region of Brazil [1–3] using a pyrgeometer (Kipp and Zonen, Delft, Netherlands) mounted at 64 m to measure upwelling longwave radiation ($L\uparrow$ in W m^{-2}) with an estimated radiative-flux footprint of 8,000 m^2 [4]. Data were collected every 2 seconds and averaged over 30-minute intervals between August 2001 and March 2004. We estimated canopy temperature with the following equation:

Eq 1 – Canopy temperature (°C) = ($L\uparrow$ /(**E***5.67e-8))^0.25-273.15

We chose an emissivity value (**E**) of 0.98 for the tower data, as this was the most common value used in the ECOSTRESS data (SDS_Emis1-5 (ECO2LSTE.001) and the broader literature for tropical forests [5]. We compared canopy temperature derived from the pyrgeometer to eddy covariance derived latent heat fluxes (flux footprint ~1 km^2), air temperature at 40 m, which is the approximate canopy height (model 076B, Met One, Oregon, USA; and model 107, Campbell Scientific, Logan, Utah, USA) and soil moisture at depths of 40 cm (model CS615, Campbell Scientific, Logan, Utah, USA). Further details on instrumentation and eddy covariance processing can be found in [1,3]. This site was selectively logged, which had a minor overall impact on the forest [6], but did not affect any trees near the tower.

Leaf thermocouple data - We measured canopy leaf temperature at a 30 m canopy walk-up tower between July to December of 2004 and July to December of 2005 at the same site. We initially placed 50 thermocouples on canopy-exposed leaves of *Sextonia rubra, Micropholis sp., Lecythis lurida*) (originally published in Doughty and Goulden 2008). Fine wire thermocouples (copper constantan 0.005 Omega, Stamford, CT) were attached to the underside of leaves by threading the wire through the leaf and inserting the end of the thermocouple into the abaxial surface. The thermocouples were wired into a multiplexer attached to a data logger (models AM25T and 23X, Campbell Scientific, Logan, UT, USA) and the data were recorded at 1 Hz. Additional upper-canopy leaf thermocouple data from Brazil[7], Puerto Rico[8], Panama[9], Atlantic forest Brazil[10] and Australia[11], were generally collected in a similar manner.

Satellite data - *ECOSTRESS data (*ECO2LSTE.001) – The ECOsystem Spaceborne Thermal Radiometer Experiment on Space Station (ECOSTRESS) mission is a thermal infrared (TIR) multispectral scanner with five spectral bands at 8.28, 8.63, 9.07, 10.6, and 12.05 μm. The sensor has a native spatial resolution of 38 m x 68 m, resampled to 70 m x 70 m, and a swath width of 402 km (53°). Data are collected from an average altitude of 400 ± 25 km on the International Space Station (ISS). ECOSTRESS is an improvement over other thermal sensors because no other sensors provide TIR data with sufficient spatial, temporal, and spectral resolution to reliably estimate LST at the local-to-global scale for a diurnal cycle [12]. To ensure the highest quality data, we used ECOSTRESS quality flag 3520, which identifies the best quality pixels (no cloud detected), a minimum-maximum difference (MMD) indicative of vegetation or water[13], and nominal atmospheric opacity. We accessed ECOSTRESS LST data through the AppEEARS website (https://lpdaac.usgs.gov/tools/appeears/) for the following products and periods: SDS_LST (ECO2LSTE.001) from a long longitudinal swath of the Amazon for 25 December 2018 to 20 July 2020 (SI Fig 1a red box) and then a larger area of the

western Amazon for 18 September to 29 September 2019 (SI Fig 1a green box), Central Africa for 1 August to 30 August 2019 (SI Fig 1b), and SE Asia for 15 January to 30 February 2020 (SI Fig. 1c). The dates were chosen as all ECOSTRESS data available at the start of the study for the smaller regions and for warm periods with low soil moisture for the larger areas. We calculated "peak median," which is defined as the average of the highest three medians of each granule (i.e., for the Amazon SI Fig. 1a, there were 934 granules) for each hour period.

Comparison of LST data – We compared ECOSTRESS LST to VIIRS LST (VNP21A1D.001) and MODIS LST (MYD11A1.006). A more detailed comparison and description of these sensors can be found in Hulley et al 2021[14]. Details for the sensors and quality flags used are given in Table S1. Broadly, G1 for ECOSTRESS and VIIRS is classified as vegetation (using emissivity) and of medium quality. G2 is classified as vegetation, but of the highest quality. MODIS landcover classifies this region as almost entirely broadleaf evergreen vegetation, but using MMD (emissivity) only 18% (VIIRS) and 12% (ECOSTRESS) of the data are classified as vegetation, rather than as soils and rocks (Table S2). Therefore, we use the vegetation classification (from MMD) as a very conservative estimate of complete forest canopy cover and not farms, urban, or degraded forest where rocks or soils are more likely to appear to satellites.

SMAP data – To estimate pantropical soil moisture, we use the Soil Moisture Active Passive (SMAP) sensor and the product Geophysical_Data_sm_rootzone (SPL4SMGP.005). SMAP measurements provide remote sensing of soil moisture in the top 5 cm of the soil [15] and the L4 products combine SMAP observations and complementary information from a variety of sources. We accessed SMAP data from the AppEEARS website for the following products and periods: Amazon for 25 December 2018 to 20 July 2020 (SI Fig 1a), Central Africa for 25 December 2019 to 20 July 2020 (SI Fig 1b), and Borneo for 25 December 2018 to 20 July 2020 (SI Fig 1c).

Warming experiments – For model validation, we used the results of three upper-canopy leaf and branch warming experiments of 2°C (Brazil)[7], 3°C (Puerto Rico)[8], and 4°C (Australia)[11]. The first experiment (Brazil), were 4 individual leaf resistant heaters on each of 6 different upper-canopy species at the Floresta National (FLONA) do Tapajos as part of the Large-Scale Biosphere–Atmosphere Ecology Program (LBA-ECO) in Santarem, Brazil[14]. On the same six species, black plastic passively heated branches by an average ~2°C. Initially, heat balance sap flow sensors and the passive heaters were added to 40 branches, but we had confidence in the data from 9 heated and 4 control in the final analysis. The second experiment (Puerto Rico) had two species (*Ocotea sintenisii* (Mez) *Alain* and *Guarea guidonia (L.) Sleumer* where leaves were heated by 3 °C at the Tropical Responses to Altered Climate Experiment (TRACE) canopy tower site at Sabana Field Research Station, Luquillo, Puerto Rico[8]. The final experiment (Australia), which increased leaf temperatures by 4 °C, was conducted at Daintree Rainforest Observatory (DRO) in Cape Tribulation, Far North Queensland, Australia[11]. Leaf heaters were installed using a pair of 30-gauge copper-constantan thermocouples, one reference leaf and one heated with a target temperature differential of 4 °C. There were two pairs in the upper canopy of each tree crown installed in 2-3 individuals across four species with the thermocouples installed on the underside of the leaves. Two absolute 36-gauge copper-constantan thermocouples were installed in each species to measure the leaf temperatures of the reference leaves. Thermocouple wires

548 connected into an AM25T multiplexer from Campbell Scientific connected to a CR1000
549 Campbell datalogger. More details about the experiment and sensors can be found in [16].

550

551 **Model** – We created a model of individual leaves on a tree (100 by 100 grid where each leaf is a
552 pixel) using matlab (mathworks version 2022a) to estimate the upper limit of tropical canopy
553 temperatures with projected changes in climate. At the start of the simulation, we randomly
554 applied the measured distribution (ambient Fig 1c) of canopy leaf temperatures >31.2 °C (chosen
555 to give a mean canopy temperature of 33.2 ± 0.4 °C, matching the canopy average Fig 1b) to the
556 entire grid. Each year we increased the mean air temperatures by 0.03°C to simulate a warming
557 planet. As air temperatures reached +2, 3 and 4°C, we applied the leaf temperature distributions
558 (but subtracted out the air temperature increases) from the different warming experiments (+2°C
559 (Brazil), +3°C (Puerto Rico), and +4°C (Australia), respectively (Fig ED4)). We ran the model
560 at a daily time step with leaves flushing once a year (all dead leaves reset to living each year).

561 In addition, to take into account the effect of climate inter-annual variation - specifically drought,
562 these mean canopy temperatures were further increased or decreased by deviations from mean
563 maximum air temperatures at 40 m pulled each day from the Tapajos eddy covariance tower[1–3]
564 and soil moisture at 40 cm depth $(m^3 m^{-3})$ which controlled canopy temperatures following
565 equation 2 (Fig ED3a).

566 **Eq 2** – Canopy temperature (°C) = 46.5-33.6*soil moisture $(m^3 m^{-3})$
567
568 For example, in a non-drought year, on a day where max air temperatures were 0.1 °C higher
569 than average and soil moisture was 0.01 $m^3 m^{-3}$ lower than average (which would add 0.3 °C to
570 canopy temperatures (Eq 2)), we would add 0.4 °C to the grid canopy temperature that day.
571 Every year, there was a 10% random probability of either a minor (80% probability) drought
572 which reduced soil moisture by 0.1 $m^3 m^{-3}$ and increased air temperatures by 0.5 °C or severe
573 drought (20% probability), which reduced soil moisture by 0.2 $m^3 m^{-3}$ and increased air
574 temperatures by 1 °C. This is similar to the Amazon-wide temperature increases during the last
575 El Niño [17].

576 If an individual leaf temperature increases to above 46.7 °C (T_{crit}) the leaf died, following Slot et
577 al. (2021). Prior research has suggested that irreversible damage could begin at 45 °C [18] and T_{50}
578 for tropical species is 49.9 °C [19], and we use these values in a sensitivity study. We further
579 explore the impact of duration of T_{crit} on mortality in a sensitivity study (ranging between
580 needing a single exposure to four exposures to T_{crit} to die). Over the season, if a leaf died, then it
581 did not contribute towards canopy evapotranspiration. We ran simulations as a 3D canopy with
582 an LAI of 5 where if the top leaf died, then it was replaced by a shade-adapted leaf with a T_{crit} 1
583 °C lower [20]. If each of the 5 LAIs died, then all leaves in that grid cell were dead and canopy
584 evaporative cooling decreased by that percentage. Several lines of evidence suggest that under
585 normal hydraulic conditions, when radiation load increases from ~350 to 1100 W m^{-2} (e.g.
586 between shady and sunny conditions) average canopy temperature increases by ~3 °C and
587 therefore, evaporative cooling for a full 1100 W m^{-2} is ~4.4°C[4,21] (we vary this in a sensitivity
588 study between 3.7 and 5.1°C). For example, if, over a year, 1000 leaves (10% of all leaves)
589 surpass T_{crit} and die, evaporative cooling for all leaves in the grid will be reduced by 10%
590 (1000/(100 by 100 grid)) or 0.44 °C and 0.44 °C will be added to mean canopy temperature.

591 Therefore, mean canopy temperature could heat up by a maximum of 4.4°C either due to a
592 reduction of soil moisture or from an increase in dead leaves. We ran each simulation until the
593 point where all leaves were dead and repeated this 30 times. We assumed loss of tree function
594 following the death of all leaves, but we discuss this further in the discussion. We then ran
595 sensitivity studies for several of the key variables (bold indicates the standard model parameter)
596 including: drought (0.05, **0.1,** to 0.2 m^3 m^{-3} decrease in soil moisture), change in T_{crit} (T_{crit}: 45,
597 **46.7**, 49.9 °C), T_{crit} range (100 by 100 grid =random distribution of 46.7±2, **100 by 100 grid**
598 **=46.7±0)** , Max evaporative cooling (3.7, **4.4**°C), (T_{crit} duration (**exceed Tcrit once,** exceed
599 Tcrit more than 3 times) and soil moisture coefficient (**-33.6** -38.2; i.e. change the slope from Fig
600 ED2a by ± 1 sd).

601

602   Data availability – We provide key data as an attachment: Fig1leaftempshared.csv, Fig2data.csv,
603   Fig3data.csv

604   Code availability - Data and code to produce all figures are available at the following link-
605   URL: https://doi.org/doi:10.5061/dryad.fqz612jx1.

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667 **Author contributions** – CED, GG, IO, YM, and JF designed the study. CED and JK analyzed
668 the RS data. CED, MG. HR, SM, SF, EG, CRS, MS, KRC, KYC, KM and AWC collected and
669 analyzed the empirical data. CED created the model. CED and BCW prepared the public data
670 and code. CED wrote the paper with contributions from GG, KRC, JF, and IO.

671 **Additional Information**: Supplementary Information is available for this paper.

672 Correspondence and requests for materials should be addressed to chris.doughty@nau.edu.

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674 The authors declare no competing interests.

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Extended data figure captions

Fig ED 1 – Regions of interest. Tropical forest regions in A) Amazon, B) Central Africa and C) SE Asia used for the retrieval of ECOSTRESS LST and SMAP data. The red area was used to ground-truth ECOSTRESS LST with the pyrgeometer.

Fig ED 2 – Impacts on canopy temperature. (A) Linear regression of canopy temperature versus soil moisture (40 cm depth) at the km 83 eddy covariance tower ($r^2 = 0.46$, P=7e-10, N=62). (B) Linear regression of canopy temperature as a function of air temperature during sunny periods during the wet (green circles) and dry (red circles) season at the km 83 eddy covariance tower in the Tapajos region of Brazil. Red line shows a linear fit for the dry season ($r^2 = 0.96$, P=3e-21, N=29) and the lower line is a one-to-one line. (C) Linear regressions of canopy temperature as a function of latent heat flux for warm (>30°C) periods (r^2=0.50, P=0.009, N=11) at the km 83 eddy covariance tower in the Tapajos region of Brazil. (D) Linear regression (r^2=0.75, P=2e-5, N=16) using data from Figure 1a comparing ECOSTRESS dry season to pyrgeometer dry season data from the Tapajos (Km 83).

Fig ED 3 – Histograms of canopy temperature. Histograms of the canopy temperatures as (top) 30 min average periods and (bottom) two second instantaneous observations, where total shortwave energy load is >1000 W m^{-2}, as measured by a downward facing pyrgeometer in the Tapajos region of Brazil.

Fig ED 4 – Leaf thermocouple data from warming experiments. Canopy top tropical leaf thermocouple measurements for normal (blue) and warmed leaves (red) for Brazil (+2°C) (a), Puerto Rico (+3°C) (b), and Australia (+4°C) (c). Insets show the long tail distribution of temperatures and text records the highest leaf temperature.

Fig ED 5 – Leaf thermocouple data. Canopy top tropical leaf thermocouple measurements for (top) Brazil km 67, (middle) Panama and (bottom) the Atlantic Forest in Brazil. Insets show the long tail distribution of temperatures and text records the highest leaf temperature. The resampled assumes a similar number of samples (~N=400) at 38°C for both sites and fits a curve to extrapolate the long tail. The Atlantic forest is a cooler forest (at ~1000m) and the median temperature of the Amazon is ~4°C higher than the Atlantic forest.

Fig ED 6 –Duration of warming. Periods when the leaves were warmed by >8 minutes during the Tapajos warming experiment for individual leaves (thin lines) and averaged (thick red line). Text in figure indicates the percent of time leaves exceeded Tcrit for greater than 6 and 8 minutes.

Fig ED 7–Finding African peak temperatures. Procedure for finding peak canopy temperatures using ECOSTRESS data for central Africa. (A) Histogram of temperatures for (B) a region of Central Africa. A diurnal curve showing all ECOSTRESS LST data for central Africa versus (C) time of day and (D) time of year. (E) SMAP soil moisture (m^2 m^{-2}) data showing periods of (red lines) dry weather.

Fig ED 8 - Finding SE Asian peak temperatures. Procedure for finding peak canopy temperatures using ECOSTRESS data for SE Asia. (A) Histogram of temperatures for (B) a

723 region of SE Asia. A diurnal curve showing all ECOSTRESS LST data for SE Asia versus (C)
724 time of day and (D) time of year. (E) SMAP soil moisture data (m^2 m^{-2}) showing periods of (red
725 lines) dry weather.
726
727 **Fig ED 9** – **Comparison of LST temperature data.** We show the spatial distribution of LST
728 data for three sensors (VIIRS, MODIS, and ECOSTRESS) for similar time periods (Sept 18-28,
729 2019) for similar areas in the Amazon basin. The difference between the left, middle and right
730 are different data quality flags for no flag (left), QF g1 from Table S1 (middle) and QF g2
731 (right). We used three levels of quality flags (ECOSTRESS – G1 - 3522 and 3520, G2 =3520,
732 VIIRS – G1 – 12001, 15841, 11745, 32225 and G2 = 32225, and MODIS – G1 - 0 and 65 and
733 G2 -0) for the region depicted in SI Fig 1b during the same period (18 September to 28
734 September 2019). Quality flags were complex with 136 for ECOSTRESS and 229 for VIIRS
735 (but only 8 for MODIS).
736
737 **Fig ED 10** – **Histogram of LST temperature data.**   (top) We show histograms of LST data for
738 three sensors (VIIRS, MODIS, and ECOSTRESS) for similar time periods (Sept 18-28, 2019)
739 for similar areas in the Amazon basin. The difference between the left, middle and right are
740 different data quality flags for no flag (left), QF g1 from Table S1 (middle) and QF g2 (right).
741 We used three levels of quality flags (ECOSTRESS – G1 - 3522 and 3520, G2 =3520, VIIRS –
742 G1 – 12001, 15841, 11745, 32225 and G2 = 32225, and MODIS – G1 - 0 and 65 and G2 -0) for
743 the region depicted in SI Fig 1b during the same period (18 September to 28 September 2019).
744 (bottom) - A scaled in comparison for the same dataset showing the much higher resolution of
745 ECOSTRESS versus VIIRS and MODIS LST.
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