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**Code availability** Code used for the analysis is available via Zenodo at <https://doi.org/10.5281/zenodo.10997880> (ref. 77) with examples of the open access datasets (as listed in the Data availability statement) needed to reproduce the results shown here. The mechanistic microclimate model is freely available to use in the microclimf package<sup>21</sup> for R (available at <https://github.com/ilyamaclean/microclimf>).

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# Novel temperatures are already widespread beneath the world's tropical forest canopies

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Tropical forest biodiversity is potentially at high risk from climate change, but most species reside within or below the canopy, where they are buffered from extreme temperatures. Here, by modelling the hourly below-canopy climate conditions of 300,000 tropical forest locations globally between 1990 and 2019, we show that recent small increases in below-canopy temperature (<1 °C) have led to highly novel temperature regimes across most of the tropics. This is the case even within contiguous forest, suggesting that tropical forests are sensitive to climate change. However, across the globe, some forest areas have experienced relatively non-novel temperature regimes and thus serve as important climate refugia that require urgent protection and restoration. This pantropical analysis of changes in below-canopy climatic conditions challenges the prevailing notion that tropical forest canopies reduce the severity of climate change impacts.

Humid tropical forests are global hotspots of terrestrial biodiversity<sup>1,2</sup>, playing critical roles in species conservation<sup>3</sup>, influencing climate regimes<sup>4</sup> and terrestrial carbon cycles<sup>5</sup>. Yet the ecological integrity of global tropical forests is being diminished by clearing, selective logging and wildfires<sup>6</sup>, and by increasingly frequent extreme weather events, such as blowdowns and droughts, driven by climate change<sup>7</sup>. Moreover, novel climates—those with no recent historic analogues—are predicted to appear first in the tropics and subtropics<sup>8–11</sup>.

It is generally assumed that the impact of climate change on the forest subcanopy and understorey will be lower than elsewhere on Earth because temperature conditions below the canopy are buffered from temperature extremes, reducing the severity of warming impacts<sup>12–14</sup>. Beneath forest canopies, direct sunlight is strongly reduced and evapotranspirative cooling is increased, dampening temperature fluctuations compared with open habitats and resulting in cooler below-canopy maximum temperatures, warmer minimum

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temperatures, and lower seasonal and interannual variability<sup>12,15</sup>. However, the relative stability in temperature regimes through evolutionary history means that tropical forest organisms evolved under a narrower range of climate conditions than extratropical biota and can therefore tolerate a smaller margin of warming above their thermal optima<sup>16–18</sup>. Key questions, therefore, are whether the range of below-canopy temperatures currently experienced by tropical forest biota are novel in relation to historic climate, and how novelty varies between structurally intact and degraded tropical forests.

There is little understanding of how microclimates beneath the forest canopy—the conditions actually experienced by tropical forest organisms—are changing pantropically. Recent efforts to monitor within-forest temperatures<sup>14,19</sup> have revealed that forests warm at a slower rate than non-forested areas, yet logging-induced canopy perforations increase understorey temperatures for up to 5 years relative to intact forest<sup>20</sup>. Although these are an important first step to quantifying below-canopy climate novelty, they provide only limited temporal coverage from a relatively small number of locations. Accordingly, mapping forest microclimates at a global scale has been identified as an important, yet unexplored, future research avenue<sup>13</sup>. Integrating a recently developed mechanistic microclimate model<sup>21</sup> with empirical temperature measurements and satellite-derived land-cover data, we quantify hourly below-canopy temperature (5 cm above the ground) at 5 km grid resolution between 1990 and 2019 across forests in the humid tropics, including tropical rainforest and tropical moist deciduous forest (hereafter tropical forests<sup>6</sup>). We tackle two key objectives: (1) quantifying recent temperature novelty of forests pantropically compared with a historic baseline, to map those most at risk from warming and those that are currently providing climate refugia; and (2) comparing how overall temperature change across the last 30 years affects the degree of below-canopy temperature novelty in (i) undisturbed forest within ecologically unfragmented areas (defined as wilderness areas<sup>22</sup>), (ii) undisturbed forest in more fragmented landscapes and (iii) degraded forest.

## Novelty is widespread across tropical forests

To accurately represent climate conditions experienced by the majority of forest-dwelling organisms, we modelled below-canopy, near-ground, hourly temperatures across the world's tropical forest regions (approximately 9.3 million km<sup>2</sup>). Temperature is a primary constraint on species distributions and ecological function<sup>23–25</sup>, and so we derived estimates of seven temperature-based bioclimatic variables widely shown to affect species distributions<sup>26</sup> (Methods). These variables represent annual trends, such as mean annual temperature and seasonality, and the incidence of extremes. Because tropical forests typically experience low temporal variability in temperature, small changes can result in climate conditions that lie entirely outside the normal range to which species are adapted. Consequently, we assume that temperature novelty is a better measure of climate vulnerability than the overall magnitude of temperature changes<sup>27</sup>. We derived an index of climate novelty from the fractional overlap in climate values between two time periods, representing the fraction of years in the most recent period (2005–2019) in which climate lies outside the range of conditions experienced in the historical baseline period (1990–2004); locations with high novelty are those with no historic climate analogue, making community disruption and species extinctions more likely<sup>28</sup>. We initially calculated novelty indexes for each temperature variable and a cumulative novelty index (the sum of novelty scores for all bioclimatic temperature variables, rescaled between 0 and 1) for undisturbed tropical forests<sup>6</sup>, that is, without any disturbances (degradation or deforestation) between 1982 and 2019.

Our results contradict the widely held belief that environments below forest canopies will be buffered from the worst impacts of warming<sup>12,14</sup>. Instead, our model suggests that, between 2005 and 2019, the majority of the world's undisturbed tropical forests experienced

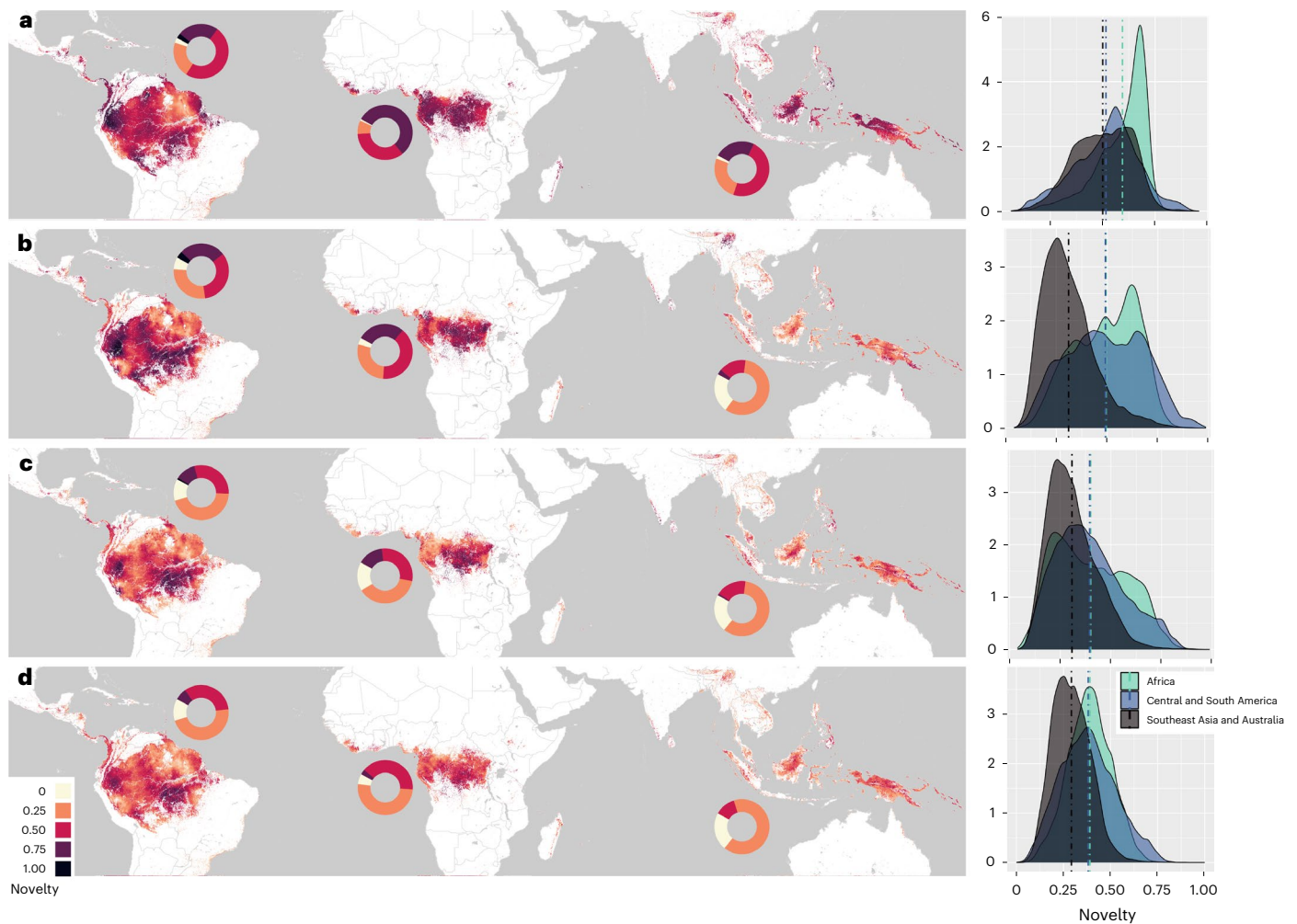
climate conditions at least partially outside the range of baseline historic conditions (>0.25 fractional novelty in bioclimatic variables) and substantial portions of undisturbed tropical forests transitioned to almost entirely novel climatic averages (>0.80 fractional novelty in bioclimatic variables). For swaths of the Amazon and Congo basins, and Sundaland (insular Southeast Asia), annual climate conditions were almost entirely unprecedented relative to historic baselines (Fig. 1 and Extended Data Fig. 1). Highly novel temperature regimes have not only occurred in the lowlands, but also in tropical mountain systems including the tropical Andes and the Mentarang range in Northern Borneo, where there have been particularly high levels of warming over the last 30 years.

Latin America experienced the highest overall cumulative temperature novelty, and the highest novelty in mean annual temperature, mean diurnal temperature range and temperature seasonality (Fig. 1). Here, 27% of undisturbed forest has recently experienced highly or entirely novel regimes in mean annual temperature (>0.61 fractional novelty) and 31% experienced highly or entirely novel mean diurnal temperature ranges. These mostly occurred in the northern tropical Andes and Pacific coast of South America—both of which are global biodiversity hotspots supporting high numbers of threatened and endemic species<sup>29</sup>. Additionally, 23% of undisturbed forests in Latin America, especially in the northern tropical Andes and the Brazilian Shield, have shifted to highly or entirely novel regimes in temperature seasonality; likely to be, in part, a consequence of increasing El Niño intensification<sup>30</sup>. In Africa, a high proportion of undisturbed forest locations (56%) transitioned to novel mean annual temperature regimes. These locations were primarily concentrated across the Congo Basin which also experienced strong shifts to novel mean diurnal temperature ranges and temperature seasonality. In Southeast Asia and Australia, cumulative temperature novelty was noticeably lower than in the rest of the global tropics. Nevertheless, high novelty in mean annual temperature was widespread, occurring across 24% of forest locations, predominantly across New Guinea, Sundaland and Wallacea biodiversity hotspots.

There are fragmented but substantial areas of tropical forest that have not recently transitioned to novel regimes in annual climate variables. Parts of the Guiana Shield region and much of the southwestern Amazon in Brazil and Peru have recently experienced annual climates similar to the historic baseline. In Africa, parts of the western Congo Basin, southwest Cameroon and the western Gulf of Guinea coastline have relatively stable climate regimes across multiple bioclimatic variables. Relative to the rest of the tropics, a high proportion (75%, compared with 46% in Latin America and 40% in Africa) of tropical forest locations in mainland Southeast Asia and Australia have not recently transitioned to highly novel temperature regimes; the mean fractional novelty in climate conditions relative to historic baselines is noticeably lower than elsewhere for most temperature variables. Papua New Guinea, coastal Indonesia and areas of continental Asia appear to be the locations most insulated from novel conditions as a result of climate change. A considerable proportion of these tropical forests are located along coastlines, where overall change in temperature across the 30 year period was less severe than within continental interiors.

## Contiguous forest does not prevent temperature novelty

Although many tropical forests have experienced extensive degradation by a variety of anthropogenic disturbances, they also form a considerable part of Earth's most ecologically unfragmented environments—wilderness areas<sup>22</sup>. Because these areas are, by definition, subjected to fewer forms of anthropogenic disturbance, any impacts caused by climatic changes are of particular concern. By contrast, degraded forest might be expected to undergo transitions to novel temperatures due to widespread perforations and reductions in canopy cover resulting from wildfires and selective logging. To investigate whether there were differences in temperature novelty between



**Fig. 1 | Below-canopy temperature novelty across global, undisturbed-only tropical forests. a–d,** Novelty at 5 km gridded resolution ( $n = 317,809$ ) mapped for mean annual temperature (a), mean diurnal temperature range (b), temperature seasonality (c) and cumulative temperature novelty (d) whereby novelty values for all temperature variables are summed and then rescaled between 0 and 1 to assess collective impact. The plots on the right show the distribution of novelty scores for each temperature variable and

continental group (Central and South America, Africa, and Southeast Asia and Australia). Dotted lines indicate mean values. Ring plots, inset with maps, show the percentage of undisturbed forest for each continental group experiencing minimal (0.0–0.2), low (0.21–0.4), moderate (0.41–0.6), high (0.61–0.8) and extreme (0.81 to 1.0) novelty scores with colours scaled to match novelty map colours: see Supplementary Table 5 for a detailed breakdown of percentages.

tropical forests with different degrees of human disturbance, we compared the novelty of: (1) undisturbed forest located in areas where habitat is largely unfragmented<sup>30</sup>; (2) all other undisturbed forested areas where there will be greater pressures from human activities; and (3) forested areas classified as degraded<sup>6</sup> in 2019 (that is, where a visual disturbance or repeated visual disturbances less than 2.5 years was observed = between 1982 and 2019).

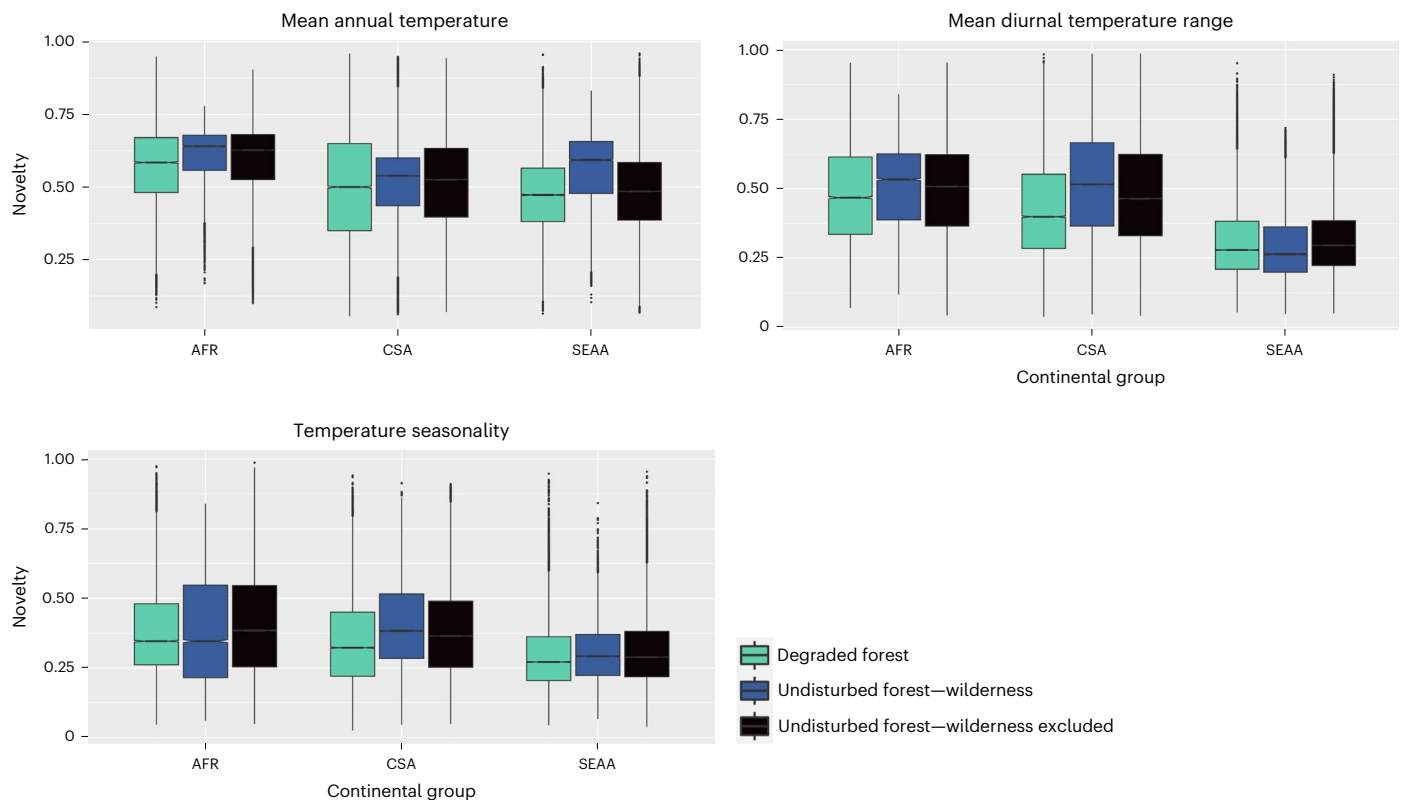
As expected, novelty in temperature regimes was more prevalent within tropical forests than outside of them (Supplementary Fig. 6). Moreover, we found no evidence that unfragmented, intact ecological areas provided additional mitigation against modelled novel temperatures. Indeed, the mean temperature novelty in unfragmented, ecologically intact forests was higher than in other undisturbed forests and degraded forests, albeit with greater spatial variance (Fig. 2, Supplementary Table 1 and Extended Data Fig. 2). This outcome can be attributed to lower interannual variability in thermal conditions within intact forests, whereby incremental changes in temperatures result in novel temperature regimes.

Tropical forests in Latin America's ecologically unfragmented areas were worst affected overall, having experienced highly novel temperature regimes across almost all bioclimatic variables, while

in Africa, Southeast Asia and Australia they experienced especially high novelty in mean annual temperatures (Supplementary Table 1). Pristine forests such as these, many of which form part of Indigenous peoples' lands, are vital for biodiversity conservation<sup>30</sup>. They support higher levels of biodiversity, reducing the risk of extinction for highly threatened taxa—especially terrestrial mammal species which are often otherwise in conflict with urban populations<sup>31</sup>—and providing spatial connectivity across environmental gradients allowing for gene flow and genetic adaptation under climate change<sup>32</sup>. Our findings suggest that the climate regimes of degraded tropical forests can still offer some resistance to rising temperatures. Fortunately, these forests have been shown to retain some conservation value and are especially important in regions with little remaining undisturbed forest<sup>33</sup>. Although forest disturbances will alter the climate by removing parts of the canopy, some studies have shown that disturbed forests can attain canopy closure very quickly and so the impacts on climate can be temporary<sup>20,34</sup>.

### Stable climates are more sensitive to long-term change

Our index of novelty represents the fraction of years in the recent period in which temperature lies outside the range of baseline historic



**Fig. 2 | The distribution of temperature novelty across undisturbed and degraded tropical forests.** Box plots of the distribution of temperature novelty scores in tropical forest across Africa (AFR,  $n = 80,599$ ), Central and South America (CSA,  $n = 208,002$ ), and Southeast Asia and Australia (SEAA,  $n = 85,596$ ) for mean annual temperature, mean diurnal temperature range and temperature seasonality. Climate novelty values are separated into three distinct forest

classifications: undisturbed tropical forest outside ecologically unfragmented areas, undisturbed tropical forest within ecologically unfragmented areas (defined by wilderness areas<sup>22</sup>) and degraded tropical forest only. The horizontal line within the box plot displays the median of the data, the box limits refer to the interquartile range, and the whiskers extend to the minimum and maximum values. The data points falling outside the whiskers are outliers.

conditions and is thus influenced by both absolute change and inter-annual variance. Because species are also sensitive to temperature thresholds<sup>35</sup>, we sought to establish the relative importance of absolute change in temperature, as opposed to interannual variability, on novelty. We calculated the mean change in bioclimatic variables below the canopy and then quantified the relationship between overall changes in each bioclimatic variable and recent fractional temperature novelty (Fig. 3 and Extended Data Fig. 3). We found statistically significant relationships between all mean changes in variables and their corresponding novelty indices (Supplementary Table 2). For instance, a  $<1$  °C increase in mean annual temperatures over the last three decades was equivalent to almost entirely novel below-canopy mean annual temperatures across most of the tropics. Consequently, those forest locations highlighted as having recently transitioned to a highly novel temperature regime (Extended Data Figs. 4 and 5) also typically experienced high temperature change over the last 30 years (Supplementary Fig. 4).

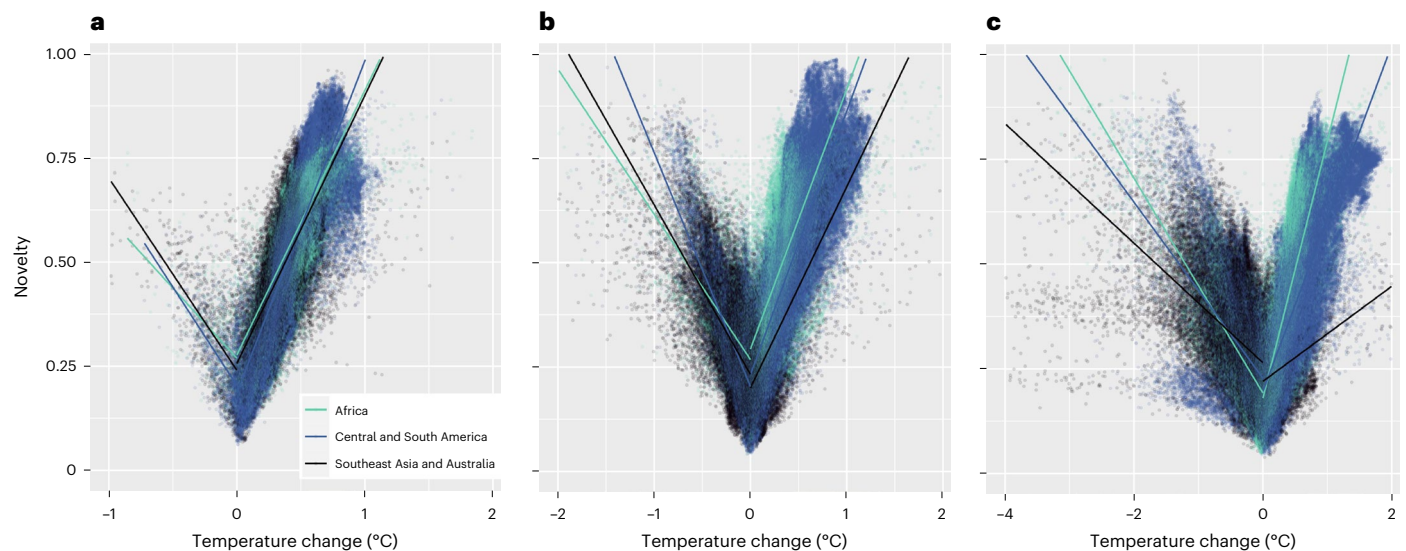
The relationship between novelty and absolute change was strongest across mean annual temperature and mean diurnal temperature regimes. Within undisturbed tropical forests, the average long-term change in mean annual temperature over the last three decades was highest in Africa (0.50 °C), followed by Latin America (0.41 °C), and Southeast Asia and Australia (0.37 °C). Across Latin America, mean annual temperatures in four of the recent years were up to 0.25 °C higher than those that occurred during the El Niño drought of 1997–1998, and the mean diurnal temperature range was up to 0.32 °C higher in all 15 recent years (Supplementary Table 4). However, there are forest regions, such as west of the Albertine Rift, which did not recently experience novelty in certain climate variables despite long-term changes

occurring, suggesting that interannual variability confers resilience to changing climate conditions in some areas.

## Conclusions

Tropical forests are the world's most diverse terrestrial ecosystems, hosting more than 62% of vertebrate species<sup>36</sup> and over 75% of flowering plant species<sup>1</sup>. Mechanistic modelling of the below-canopy environment suggests there have been pronounced shifts in below-canopy climate regimes to novel conditions in a significant proportion of tropical forests, including globally important national parks, Indigenous reserves and large tracts of ecologically unfragmented areas. Novel temperature regimes were frequently a signature of low-lying continental interiors where there is limited opportunity for species to access elevational climate gradients if thermal limits are breached<sup>18</sup>.

Although we cannot confidently draw conclusions on implications for biota that do not occur near the ground, recent research in largely undisturbed and/or primary lowland tropical has found changes in species composition<sup>37–39</sup> and significant declines in animal, insect and plant populations<sup>40–43</sup>. These changes are attributed to warming temperatures and are consistent with our findings. For instance, the abundance of terrestrial and near-ground insectivore bird species has declined in primary tropical forest in the Brazilian Amazon since the 1980s<sup>44</sup>, with evidence that these species respond to warming by closely tracking cooler microclimates<sup>16</sup>, while in Panama, most understorey bird species experienced large (>50%) proportional losses in estimated abundances since 1977, irrespective of ecology<sup>42</sup>. As a result of lower natural climate variability, many tropical forest species have narrow realized climate niches<sup>37</sup> and are not pre-adapted to warmer



**Fig. 3 | The relationship between the change in the mean of temperature variables and recent temperature novelty.** **a–c**, Scatterplots showing the correlation (as investigated using piecewise GLMs with a binomial logit) between the below-canopy novelty of each temperature variable and the change in the same variable (that is, the difference between the mean of 1990–2004 and the mean of 2005–2019) across undisturbed tropical forests ( $n = 317,809$ ) for mean annual temperature (**a**), mean diurnal temperature range (**b**) and temperature

seasonality (**c**). Each point represents one grid cell for Africa ( $n = 67,799$ ), Central and South America ( $n = 185,883$ ), and Asia and Australia ( $n = 64,127$ ). See Supplementary Table 2 for model results for each group. Tests were conducted using two-sided Wald tests with a significance level set at  $P < 0.01$ . No adjustments were made for multiple comparisons because each temperature variable was analysed and presented separately.

conditions<sup>45</sup>. The ongoing transition of tropical forest environments to almost entirely novel temperature regimes can easily precipitate changes in niche availability, favouring species with higher temperature affinity<sup>46</sup>, and triggering changes in community composition through trophic cascades<sup>47,48</sup>.

We also identified areas pantropically where temperature novelty has been low despite ongoing climatic change. Although many are highly fragmented<sup>49</sup> and dispersed across continents, especially in Africa, these tropical forests are the best candidates to act as climate refugia and are crucial to conservation efforts. Their usefulness as refugia will depend on their connectivity to areas with unfavourable climates, enabling species range-shifts<sup>50</sup>. Severe fragmentation will also influence temperature novelty as edge effects have been shown to reduce microclimatic temperature buffering up to 20 m into the interior<sup>51</sup>. It is paramount that distant wealth-related drivers of deforestation and degradation begin to be sufficiently addressed<sup>52</sup> and that intact candidate refugia are urgently and vigorously protected, via legal protection<sup>53</sup>, carbon payments<sup>54</sup> or empowering indigenous communities<sup>55</sup>. In turn, we urgently need to direct forest restoration programmes to improve the connectivity, overall size and interior (non-edge effected) area of fragmented refugia<sup>56,57</sup>. Notwithstanding the fundamental need for global carbon emission reductions, the prioritization and protection of refugia and the restoration of highly threatened forests is vital to mitigate further damage to global tropical forest ecosystems.

## Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-024-02031-0>.

## References

- Barlow, J. et al. The future of hyperdiverse tropical ecosystems. *Nature* **559**, 517–526 (2018).
- Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M. & Gascon, C. in *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas* (eds Zachos, F. E. & Habel, J. C.) 3–22 (Springer, 2011).
- Buchanan, G. M. et al. Using remote sensing to inform conservation status assessment: estimates of recent deforestation rates on New Britain and the impacts upon endemic birds. *Biol. Conserv.* **141**, 56–66 (2008).
- Bustamante, M. M. C. et al. Toward an integrated monitoring framework to assess the effects of tropical forest degradation and recovery on carbon stocks and biodiversity. *Glob. Change Biol.* **22**, 92–109 (2016).
- Anderson-Teixeira, K. J. et al. Carbon cycling in mature and regrowth forests globally. *Environ. Res. Lett.* **16**, 053009 (2021).
- Vancutsem, C. et al. Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Sci. Adv.* **7**, eabe1603 (2021).
- Feng, Y., Negrón-Juárez, R. I., Romps, D. M. & Chambers, J. Q. Amazon windthrow disturbances are likely to increase with storm frequency under global warming. *Nat. Commun.* **14**, 101 (2023).
- Abatzoglou, J. T., Dobrowski, S. Z. & Parks, S. A. Multivariate climate departures have outpaced univariate changes across global lands. *Sci. Rep.* **10**, 3891 (2020).
- García, R. A., Cabeza, M., Rahbek, C. & Araújo, M. B. Multiple dimensions of climate change and their implications for biodiversity. *Science* **344**, 1247579 (2014).
- Williams, J. W., Jackson, S. T. & Kutzbach, J. E. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl Acad. Sci. USA* **104**, 5738–5742 (2007).
- Dobrowski, S. Z. et al. Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes. *Commun. Earth Environ.* **2**, 198 (2021).
- De Frenne, P. et al. Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.* **3**, 744–749 (2019).

13. De Frenne, P. et al. Forest microclimates and climate change: importance, drivers and future research agenda. *Glob. Change Biol.* **27**, 2279–2297 (2021).
14. De Lombaerde, E. et al. Maintaining forest cover to enhance temperature buffering under future climate change. *Sci. Total Environ.* **810**, 151338 (2022).
15. Barry, R. G. & Blanken, P. D. *Microclimate and Local Climate* (Cambridge University Press, 2016).
16. Jirinec, V., Rodrigues, P. F., Amaral, B. R. & Stouffer, P. C. Light and thermal niches of ground-foraging Amazonian insectivorous birds. *Ecology* **103**, e3645 (2022).
17. Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. Putting the heat on tropical animals. *Science* **320**, 1296–1297 (2008).
18. Trew, B. T. & Maclean, I. M. D. Vulnerability of global biodiversity hotspots to climate change. *Glob. Ecol. Biogeogr.* **30**, 768–783 (2021).
19. Ismaeel, A. et al. Patterns of tropical forest understory temperatures. *Nat. Commun.* **15**, 549 (2024).
20. Mollinari, M. M., Peres, C. A. & Edwards, D. P. Rapid recovery of thermal environment after selective logging in the Amazon. *Agric. Meteorol.* **278**, 107637 (2019).
21. Maclean, I. M. D. Microclim: fast above, below or within canopy gridded microclimate modelling with R (2023); <https://github.com/ilyamaclean/microclimf>
22. Watson, J. E. M. et al. Catastrophic declines in wilderness areas undermine global environment targets. *Curr. Biol.* **26**, 2929–2934 (2016).
23. Deutsch, C. A. et al. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672 (2008).
24. Neate-Clegg, M. H. C., Jones, S. E. I., Tobias, J. A., Newmark, W. D. & Şekercioglu, Ç. H. Ecological correlates of elevational range shifts in tropical birds. *Front. Ecol. Evol.* <https://doi.org/10.3389/fevo.2021.621749> (2021).
25. Vieilledent, G. et al. Bioclimatic envelope models predict a decrease in tropical forest carbon stocks with climate change in Madagascar. *J. Ecol.* **104**, 703–715 (2016).
26. Hijmans, R. J. & Graham, C. H. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Change Biol.* **12**, 2272–2281 (2006).
27. Foden, W. B. et al. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS One* **8**, e65427 (2013).
28. Pacifici, M. et al. Assessing species vulnerability to climate change. *Nat. Clim. Change* **5**, 215 (2015).
29. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
30. Garnett, S. T. et al. A spatial overview of the global importance of Indigenous lands for conservation. *Nat. Sustain.* **1**, 369–374 (2018).
31. Fasullo, J. T., Otto-Bliesner, B. L. & Stevenson, S. ENSO's changing influence on temperature, precipitation, and wildfire in a warming climate. *Geophys. Res. Lett.* **45**, 9216–9225 (2018).
32. Sgrò, C. M., Terblanche, J. S. & Hoffmann, A. A. What can plasticity contribute to insect responses to climate change? *Annu. Rev. Entomol.* **61**, 433–451 (2016).
33. Edwards, F. A. et al. Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Anim. Conserv.* **17**, 163–173 (2014).
34. Senior, R. A., Hill, J. K., Benedick, S. & Edwards, D. P. Tropical forests are thermally buffered despite intensive selective logging. *Glob. Change Biol.* **24**, 1267–1278 (2018).
35. Doughty, C. E. et al. Tropical forests are approaching critical temperature thresholds. *Nature* **621**, 105–111 (2023).
36. Pillay, R. et al. Tropical forests are home to over half of the world's vertebrate species. *Front. Ecol. Environ.* **20**, 10–15 (2022).
37. Fadrique, B. et al. Widespread but heterogeneous responses of Andean forests to climate change. *Nature* **564**, 207–212 (2018).
38. Marimon, B. S. et al. Disequilibrium and hyperdynamic tree turnover at the forest–cerrado transition zone in southern Amazonia. *Plant Ecol. Divers.* **7**, 281–292 (2014).
39. Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez, T. M. & Zuleta, D. Climate-driven changes in the composition of New World plant communities. *Nat. Clim. Change* **10**, 965–970 (2020).
40. Blake, J. & Loiselle, B. Enigmatic declines in bird numbers in lowland forest of eastern Ecuador may be a consequence of climate change. *PeerJ* **3**, e1177 (2015).
41. Lister, B. C. & Garcia, A. Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl Acad. Sci. USA* **115**, E10397–E10406 (2018).
42. Pollock, H. S. et al. Long-term monitoring reveals widespread and severe declines of understory birds in a protected neotropical forest. *Proc. Natl Acad. Sci. USA* **119**, e2108731119 (2022).
43. Whitfield, S. M. et al. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proc. Natl Acad. Sci. USA* **104**, 8352–8356 (2007).
44. Stouffer, P. C. et al. Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. *Ecol. Lett.* **24**, 186–195 (2021).
45. Watson, J. E. M., Segan, D. B. & Tewksbury, J. in *Biodiversity and climate change* (eds Lovejoy, T. E. & Hannah, L.) Ch. 15, 196–207 (Yale University Press, 2019).
46. Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D. & Coomes, D. Advances in microclimate ecology arising from remote sensing. *Trends Ecol. Evol.* **34**, 327–341 (2019).
47. Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W. & Holt, R. D. A framework for community interactions under climate change. *Trends Ecol. Evol.* **25**, 325–331 (2010).
48. Lensing, J. R. & Wise, D. H. Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proc. Natl Acad. Sci. USA* **103**, 15502–15505 (2006).
49. Ma, J., Li, J., Wu, W. & Liu, J. Global forest fragmentation change from 2000 to 2020. *Nat. Commun.* **14**, 3752 (2023).
50. Senior, R. A., Hill, J. K. & Edwards, D. P. Global loss of climate connectivity in tropical forests. *Nat. Clim. Change* **9**, 623–626 (2019).
51. Ewers, R. M. & Banks-Leite, C. Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS One* **8**, e58093 (2013).
52. Carmenta, R. et al. Connected conservation: rethinking conservation for a telecoupled world. *Biol. Conserv.* **282**, 110047 (2023).
53. Roberts, C. M., O'Leary, B. C. & Hawkins, J. P. Climate change mitigation and nature conservation both require higher protected area targets. *Philos. Trans. R. Soc. B* **375**, 20190121 (2020).
54. Crossman, N. D., Bryan, B. A. & Summers, D. M. Carbon payments and low-cost conservation. *Conserv. Biol.* **25**, 835–845 (2011).
55. Sze, J. S., Carrasco, L. R., Childs, D. & Edwards, D. P. Reduced deforestation and degradation in Indigenous lands pan-tropically. *Nat. Sustain.* **5**, 123–130 (2022).
56. González del Pliego, P. et al. Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. *Biol. Conserv.* **201**, 385–395 (2016).
57. Strassburg, B. B. N. et al. Global priority areas for ecosystem restoration. *Nature* **586**, 724–729 (2020).

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## Methods

### Climate data and modelling

Using a recently developed grid version<sup>21</sup> of a previously published mechanistic microclimate model<sup>58</sup>, we quantified hourly below-canopy climate conditions across the global tropics (30° S to 30° N) between 1990 and 2019. The microclimate model was run in daily time increments and then hourly temperatures—at 0.05 m above the ground—were derived using the model's interpolation methods, which infer hourly data from daily minima and maxima using the diurnal cycle in the ambient temperatures provided as inputs to the model. Full details of the model are provided<sup>58</sup>, but in summary the following workflow is implemented. First, the model downscales hourly input climate-forcing data to the desired spatial resolution (in this case 5 km gridded resolution) using spatial interpolation and the application of an elevation- and humidity-dependent lapse rate correction. Temperature and water vapour at the desired height are modelled mechanistically using principles of energy conservation, that is, by assuming that components of the energy budget remain in balance, and by solving the energy budget to derive differences between near-ground and ambient temperature using the Penman–Monteith equation. Radiative fluxes through the canopy are estimated using Seller's two-stream approximation model<sup>59</sup>. Sensible and latent heat fluxes are assumed to depend on wind speed, which in turn is attenuated vertically by canopy foliage using the method described<sup>60</sup>. Wind speed is terrain-adjusted using the method described<sup>61</sup>. Latent heat fluxes are assumed additionally to depend on the stomatal conductance of leaves, which is quantified from the availability of photosynthetically active radiation using the method described<sup>62</sup>. Ground heat fluxes are quantified from canopy–soil temperature gradients, the latter contingent primarily on radiation absorbed by the ground using the method described<sup>63</sup>.

The hourly climate-forcing data required to drive the microclimate model were obtained from the ERA5 fifth-generation ECMWF atmospheric reanalysis of the global climate, using the single levels surface dataset<sup>64</sup> at a 0.25° gridded spatial resolution for the 30 year time period. The ERA5 climate data assimilate past climate observations with climate model predictions to generate a series of climate variables for atmospheric, land-surface and sea parameters. The following climate variables were extracted for the extent of the study area: (1) air temperature at 2 m, (2) dewpoint temperature at 2 m, (3) pressure at surface, (4) precipitation rate, (5) U-wind speed at 10 m (west to east component), (6) V-wind speed at 10 m (south to north component), (7) total cloud cover, (8) downward long-wavelength radiation and (9) downward solar radiation, which was partitioned into direct and diffuse components using the method described<sup>65</sup>.

Additionally, the following environmental predictors were obtained to drive the microclimate model: (1) annual habitat type, sourced from the European Space Agency Climate Change Initiative<sup>66</sup> at a gridded spatial resolution of 5 km; (2) annual vegetation height, sourced from ORNL DAAC<sup>67</sup> at a gridded spatial resolution of 5 km; (3) monthly plant area index, calculated as the sum of monthly leaf area index (LAI) and 20% of the monthly maximum LAI. Monthly LAI values were sourced from the National Oceanic and Atmospheric Administration<sup>68</sup> and spatially aggregated to a gridded spatial resolution of 5 km, with missing values estimated from the LAI at the same location in other months using a locally informed month effect accounting for seasonal cycles; (4) monthly canopy and ground reflectance at a spatial resolution of 5 km gridded resolution, calculated by first deriving the fractional canopy cover from surface albedo<sup>68</sup> and monthly LAI values and then using the fractional canopy cover to partition surface albedo between ground and canopy; both steps used the microclima<sup>69</sup> package for R v.4.2<sup>70</sup>; (5) soil type, sourced at a gridded spatial resolution of 250 m from soilgrids.org<sup>71</sup>, which was then resampled to a gridded spatial resolution of 5 km using the nearest-neighbour

method; (6) a digital elevation model, sourced from the US Geological Survey<sup>72</sup> at a gridded spatial resolution of 7.5 arcsec and resampled to 5 km using a bilinear method; and (7) a topographic wetness index at a gridded spatial resolution of 5 km, calculated by using the digital elevation model to derive flow accumulation. Inevitably the model is sensitive to uncertainty and error in the data used to drive the model. Sensitivity analysis indicated it was most sensitive to assumed LAI, although mostly at low LAI values, which are typically derived with greater accuracy<sup>73</sup>.

To assess whether the microclimate model was more accurate than ERA5 climate data and adequately represented below-canopy conditions, the hourly modelled microclimate temperatures and the ERA5 hourly temperatures were both compared to in situ measurements of temperature obtained from 70 locations under tropical forest canopies across the Americas, Africa and the Sundaland and represented in the SoilTemp database<sup>74</sup>. Below-canopy temperatures were modelled independently of our global results at a higher gridded resolution of 500 m (reflecting the higher-resolution LAI datasets available for recent years). Additionally, to avoid duplicating results, we did not use temperature loggers that were located in the same 500 m grid cell (Extended Data Fig. 6). For each temperature logger, microclimate was modelled as above using ERA5 reanalysis climate variables and vegetation parameters (Supplementary Table 6) which matched the time and duration of the empirical temperature observations (Supplementary Data 1). The average for each recorded time series of empirical temperatures—taken separately for microclimate and ERA5 reanalysis—was used to derive a single root mean square error (r.m.s.e.) to quantify similarity to the logger observations (Extended Data Fig. 7). As indicated by the r.m.s.e. from empirical observations, the microclimate model (r.m.s.e., 2.73) was more accurate than ERA5 (r.m.s.e., 3.62). Moreover, we derived a r.m.s.e. score for mean temperature at each logger location, separately for both microclimate and ERA5 reanalysis temperatures (Supplementary Data 1).

### Temperature novelty analysis

The hourly modelled below-canopy climate conditions were used to calculate the annual bioclimatic variables detailed<sup>75</sup>, namely: (1) mean annual temperature, (2) mean diurnal temperature range, (3) isothermality (diurnal range/annual range × 100), (4) seasonality, (5) maximum temperature of the warmest month, (6) minimum temperature of the coldest month and (7) annual temperature range. The annual bioclimatic variables were then split into a baseline historical time period (1990–2004) and the most recent time period (2005–2019). For each grid cell, we derived an index of novelty for each bioclimatic variable ( $n = 7$ ) from the fractional overlap in each variable's values between the two periods<sup>76</sup>. Specifically, for each bioclimatic variable, we measured the fractional overlap between two sets of 15 annual values. This was done by computing the frequency distribution curves of the annual values across historical and recent time periods separately, and then novelty was derived as 1 minus the proportion of overlap in annual values between the two periods, calculated as:

$$\text{novelty} = 1 - (2 \times \text{intersection area} / \text{total area of both curves})$$

This novelty index represents the fraction of years in the recent period (2005–2019) in which the climate lies outside the range of conditions that occurred in the baseline historical period (1990–2004). For example, if both mean annual temperatures and interannual variance in mean annual temperature were identical in both periods, the novelty index would be zero. If two-thirds of the mean annual temperatures in the latter period lay outside the range of temperatures in the historic period, then the novelty index would be 0.6667. Thus, the locations with novelty indexes closer to 1 are those with no recent climate analogue relative to the recent historical baseline.

To exclude forest in which climate change could be amplified by interacting human activities such as deforestation, novelty index values for each of the seven bioclimatic variables were extracted for the locations of tropical moist forest which were still undisturbed in 2019<sup>6</sup>, defined as all closed forests in the humid tropics including the tropical rainforest and the tropical moist deciduous forest without any observed disturbances (degradation or deforestation) across the full observation period defined by the available Landsat data (1982–2019). The definition is not based on percentage of canopy cover and does not discriminate between primary- and secondary-growth tropical forest because there are no Landsat data available prior to 1982. However, it is probable that undisturbed tropical forest cover as estimated here is close to the true extent of primary tropical forest due to the amount of time that they have been undisturbed.

We investigated whether climate novelty differed between tropical forests with different degrees of human disturbance using three categories of forest: (1) undisturbed forested areas in ecologically unfragmented areas<sup>30</sup>, (2) undisturbed forested areas outside of ecologically unfragmented areas, and (3) tropical forests classified as degraded<sup>6</sup> in 2019 (where a visual disturbance or repeated visual disturbances have been observed from space between 1982 and 2019, but each disturbance event lasted <2.5 years and was therefore not classified as deforestation). In this study, we considered deforested locations as no longer able to meet the biological requirements of a tropical forest and so these locations were not included in our analyses.

Finally, we calculated the overall change in each bioclimatic variable ( $n = 7$ ) as the difference between the mean value for each time period (baseline period, 1990–2004; recent period, 2005–2019). We used a generalized linear model (GLM) with a binomial logit to fit the relationship between overall changes in each bioclimatic variable and recent fractional temperature novelty for each grid cell.

### Reporting summary

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

### Data availability

Global hourly climate data are available at <https://cds.climate.copernicus.eu/>. Environmental parameters include: (1) LAI and surface reflectance available at <https://www.ncei.noaa.gov/data/avhrr-land-leaf-area-index-and-fapar/>, (2) global habitat types available at <https://www.esa-landcover-cci.org/>, (3) vegetation height available at <https://webmap.ornl.gov/ogc/>, (4) soil types available at <https://www.soilgrids.org>, (5) digital elevation model available at <https://www.usgs.gov/centres/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm-1>. The microclimate model is freely available for download and adaptation via a GitHub repository at <https://github.com/ilyamaclean/microclimf>. The global tropical forest monitoring dataset is available at <https://forobs.jrc.ec.europa.eu/TMF>. Temperature records used for validation are available from the global SoilTemp dataset on request at <https://www.soiltempproject.com/the-soiltemp-database/>.

### Code availability

Code used for the analysis is available via Zenodo at <https://doi.org/10.5281/zenodo.10997880> (ref. 77) with examples of the open access datasets (as listed in the Data availability statement) needed to reproduce the results shown here. The mechanistic microclimate model is freely available to use in the microclimf package<sup>21</sup> for R (available at <https://github.com/ilyamaclean/microclimf>).

### References

58. Maclean, I. M. D. & Klings, D. H. Microclimc: a mechanistic model of above, below and within-canopy microclimate. *Ecol. Modell.* **451**, 109567 (2021).

59. Sellers, P. J. Canopy reflectance, photosynthesis and transpiration. *Int. J. Remote Sens.* **6**, 1335–1372 (1985).
60. Raupach, M. R. Simplified expressions for vegetation roughness length and zero-plane displacement as functions of canopy height and area index. *Boundary Layer Meteorol.* **71**, 211–216 (1994).
61. Ryan, B. C. A mathematical model for diagnosis and prediction of surface winds in mountainous terrain. *J. Appl. Meteorol. Climatol.* **16**, 571–584 (1977).
62. Kelliher, F. M., Leuning, R., Raupach, M. R. & Schulze, E. D. Maximum conductances for evaporation from global vegetation types. *Agric. Meteorol.* **73**, 1–16 (1995).
63. Campbell, G. S. & Norman, J. M. *An Introduction to Environmental Biophysics* 2nd edn (Springer, 1998).
64. Hersbach, H. et al. The ERA5 global reanalysis. *Q. J. R. Meteorol. Soc.* **146**, 1999–2049 (2020).
65. Skartveit, A., Olseth, J. A. & Tuft, M. E. An hourly diffuse fraction model with correction for variability and surface albedo. *Sol. Energy* **63**, 173–183 (1998).
66. *Land Cover CCI Product User Guide, Version 2* (ESA, 2017); [https://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2\\_2.0.pdf](https://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf)
67. Dubayah, R. O. et al. *GEDI L3 Gridded Land Surface Metrics, Version 2* (ORNL DAAC, 2021); <https://doi.org/10.3334/ORNLDAAC/1952>
68. Vermote, E. et al. *NOAA Climate Data Record (CDR) of AVHRR Surface Reflectance, Version 4* (NOAA National Centers for Environmental Information, 2014); <https://doi.org/10.7289/V5TM782M>
69. Maclean, I. M. D., Mosedale, J. R. & Bennie, J. J. Microclima: an R package for modelling meso- and microclimate. *Methods Ecol. Evol.* **10**, 280–290 (2019).
70. R Core, T. R. *A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2021).
71. Hengl, T. et al. SoilGrids250m: global gridded soil information based on machine learning. *PLoS One* **12**, e0169748 (2017).
72. Danielson, J. J. and Gesch, D. B. *Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010)*, Report 2011-1073 (US Geological Survey, 2011).
73. Claverie, M., Matthews, J. L., Vermote, E. F. & Justice, C. O. A 30+ year AVHRR LAI and FAPAR climate data record: algorithm description and validation. *Remote Sens.* **8**, 263 (2016).
74. Lembrechts, J. J. et al. SoilTemp: a global database of near-surface temperature. *Glob. Change Biol.* **26**, 6616–6629 (2020).
75. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
76. Maclean, I. M. D. Predicting future climate at high spatial and temporal resolution. *Glob. Change Biol.* **26**, 1003–1011 (2020).
77. Trew, B. T. & Maclean, I. M. D. Novel climates are already widespread beneath the world's tropical forest canopies. *Zenodo* <https://doi.org/10.5281/zenodo.10997880> (2024).

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### Author contributions

B.T.T., I.M.D.M., D.P.E. and A.C.L designed the research. B.T.T. performed the climate modelling and analysed the results. D.H.K. analysed temperature logger data to validate the climate modelling. M.S., R.P., R.M, J.O., A.N., M.B., J.S., E.B., J.F., R.O.N., E.E.M, J.S.B and J.B. collected and processed temperature logger data for model validation. B.T.T., I.M.D.M., D.P.E., A.L and R.E wrote the paper with contributions from all coauthors.

### Competing interests

The authors declare no conflicts of interest.

### Additional information

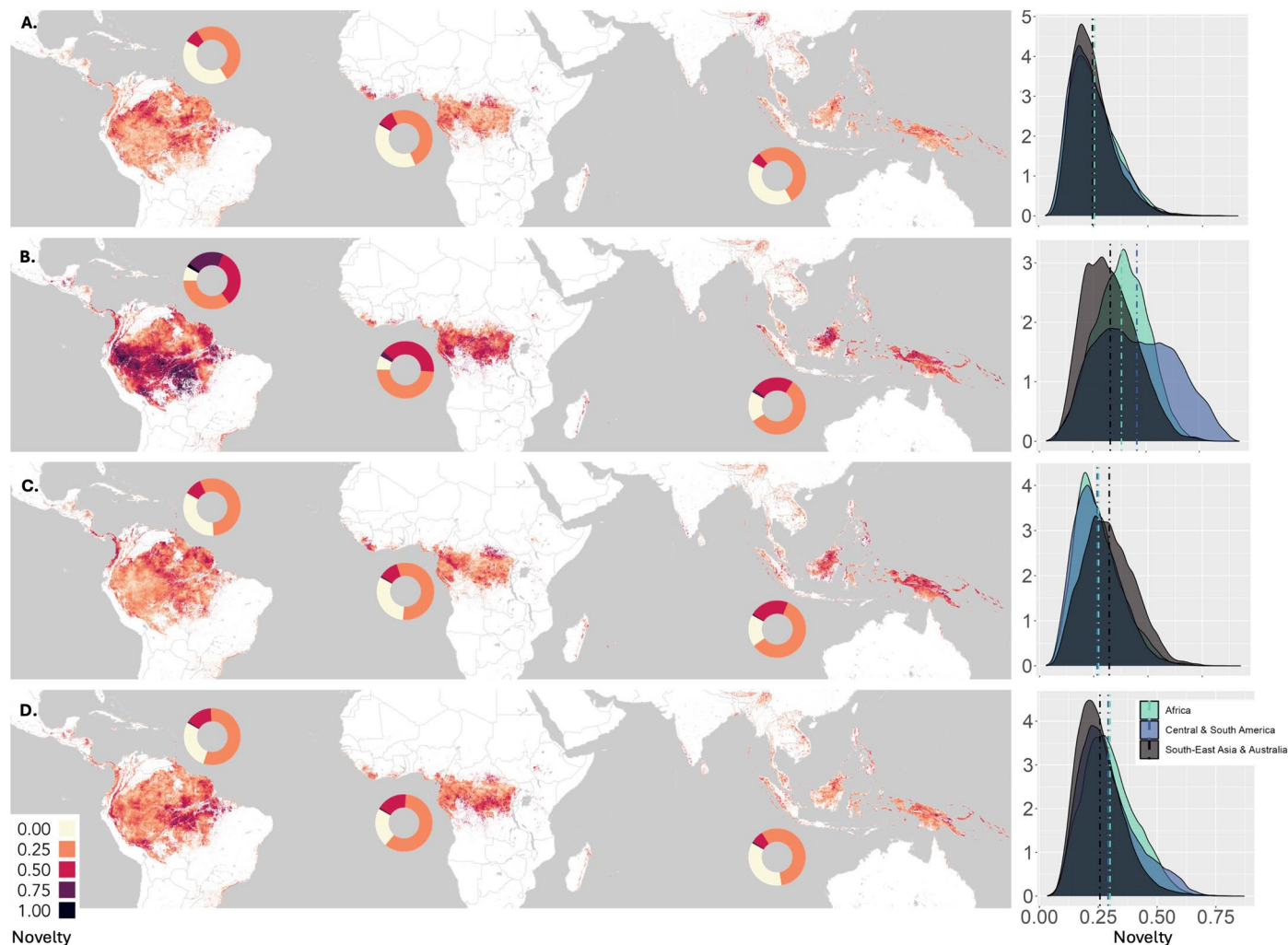
**Extended data** is available for this paper at <https://doi.org/10.1038/s41558-024-02031-0>.

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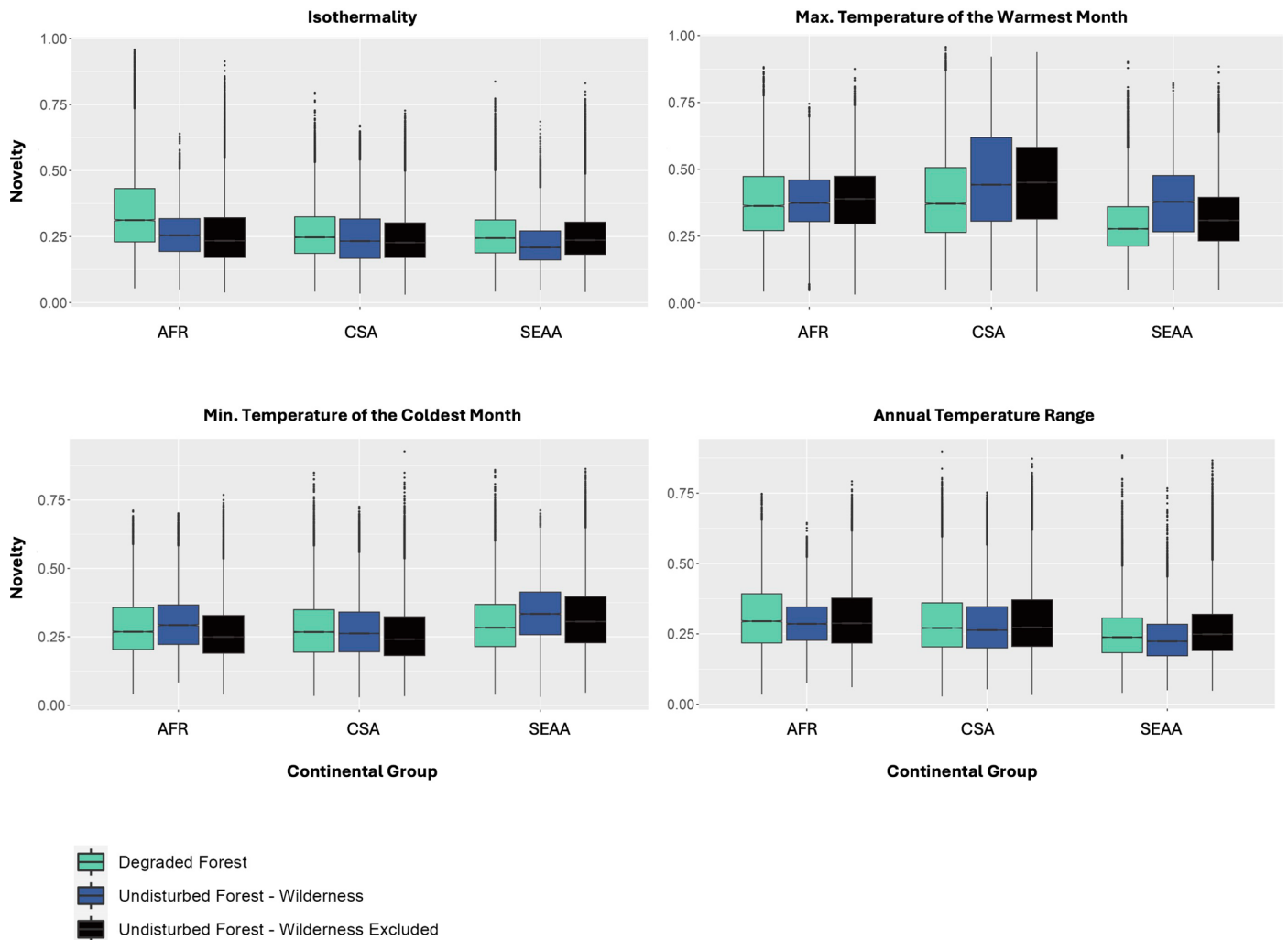
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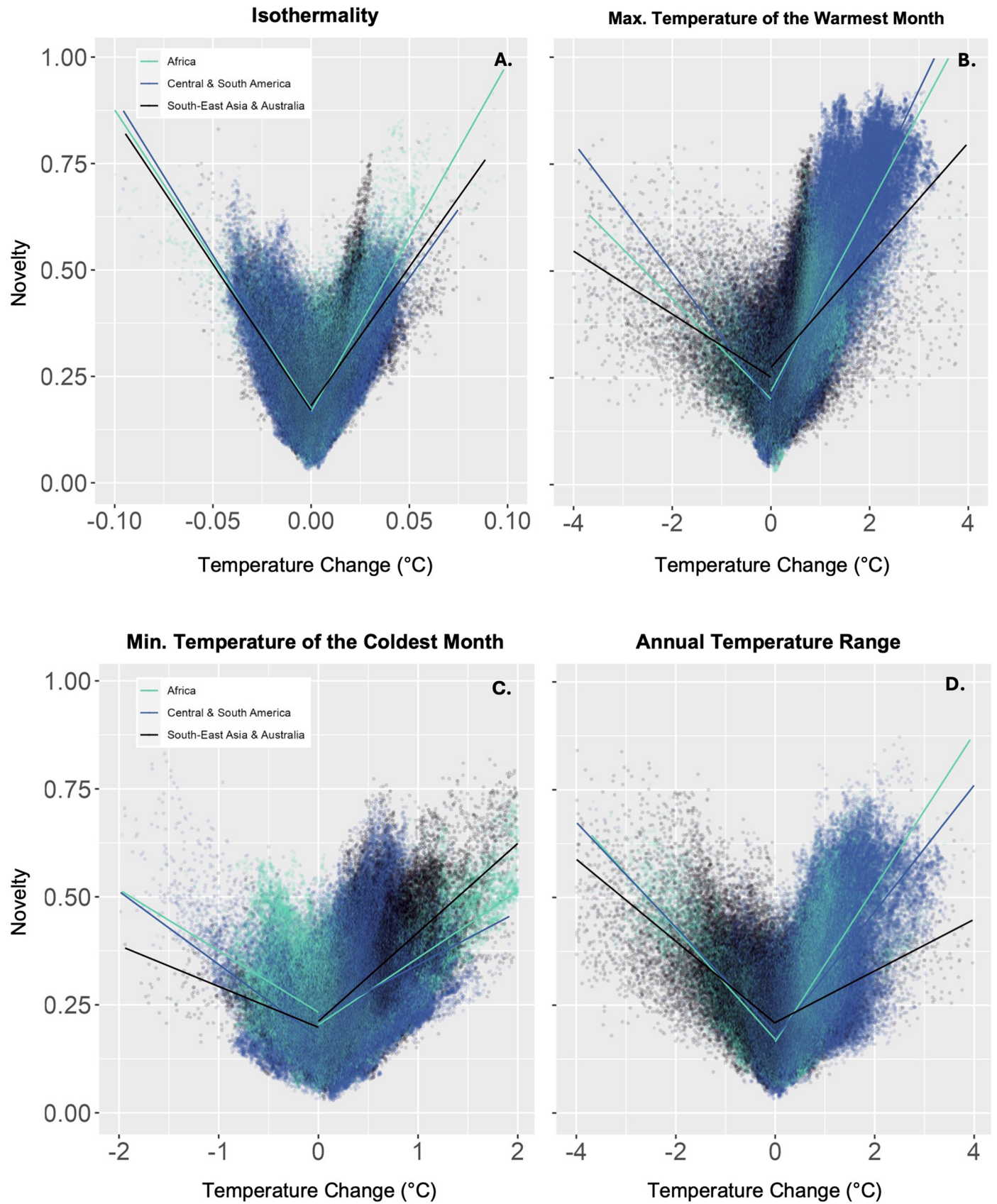
**Extended Data Fig. 1 | Below-canopy temperature novelty across global, undisturbed-only tropical forests.** Novelty at 5 km gridded resolution ( $n = 317,809$ ) mapped for (A) isothermality, (B) maximum temperature of the warmest month, (C) minimum temperature of the coldest month, and (D) annual range of temperature. Plots, inset right, show the distribution of novelty scores for each temperature variable and continental group (Central & South America,

Africa, and Southeast Asia & Australia). Dotted lines indicate mean values. Ring plots, inset with maps, show the percentage of undisturbed forest for each continental group experiencing minimal (0.0–0.2), low (0.21–0.4), moderate (0.41–0.6), high (0.61–0.8) and extreme (0.81 to 1.0) novelty scores with colours scaled to match novelty map colours: see supplementary table S5 for a detailed breakdown of percentages.



**Extended Data Fig. 2 | The distribution of temperature novelty across undisturbed and degraded tropical forests.** Box plots of the distribution of temperature novelty scores in tropical forest across Africa (AFR,  $n = 80,599$ ), Central and South America (CSA,  $n = 208,002$ ), and Southeast Asia and Australia (SEAA,  $n = 85,596$ ) for: isothermality, maximum temperature of the warmest month, minimum temperature of the coldest month, and annual range of temperature. Climate novelty values are separated into three distinct forest

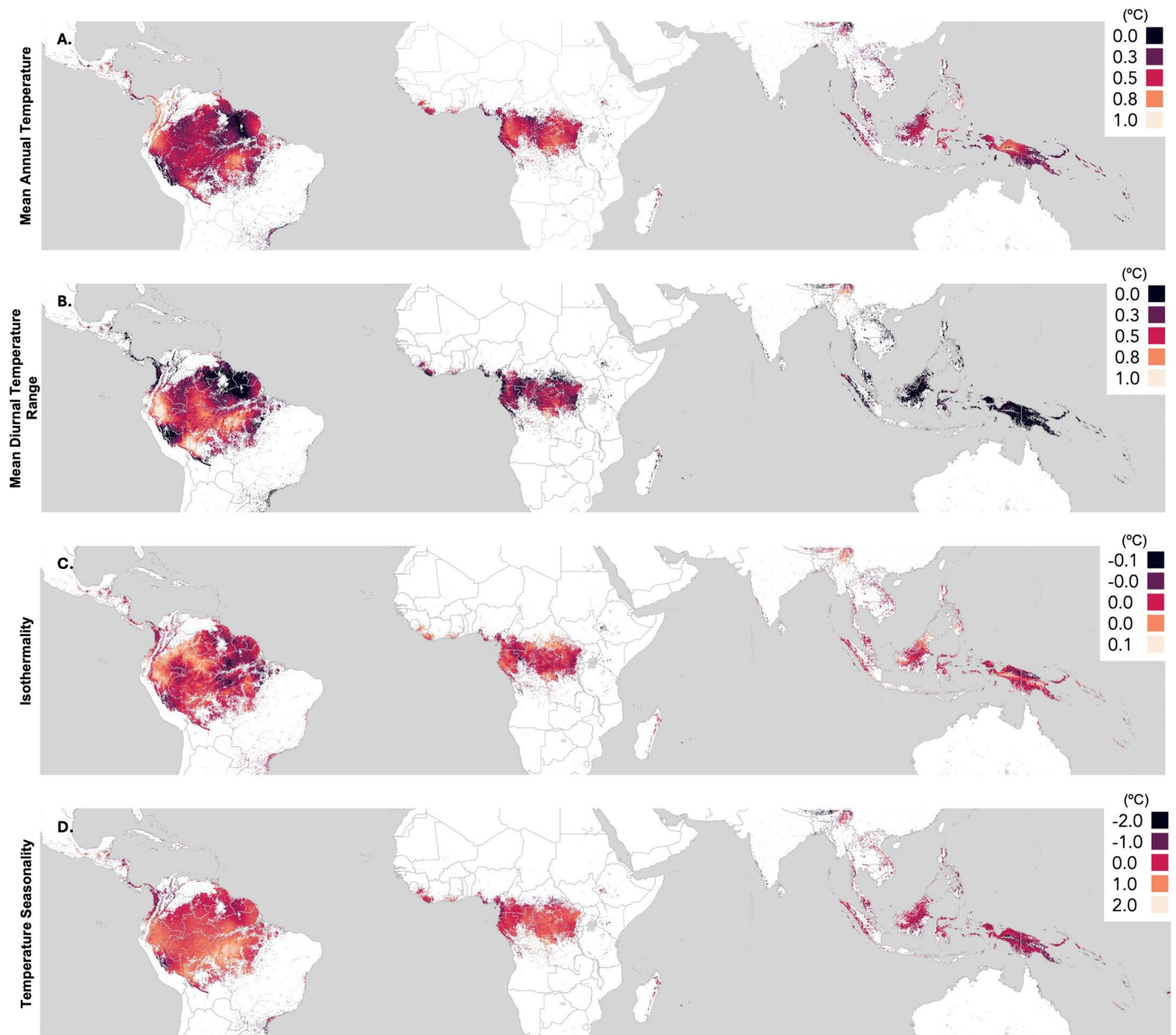
classifications: undisturbed tropical forest outside ecologically unfragmented areas, undisturbed tropical forest within ecologically unfragmented areas (defined by wilderness areas<sup>22</sup>), and degraded tropical forest only. The horizontal line within the box plot displays the median of the data, the box limits refer to the interquartile range (IQR), and the whiskers extend to the minimum and maximum values. The data points falling outside the whiskers are outliers.



Extended Data Fig. 3 | See next page for caption.

**Extended Data Fig. 3 | The relationship between change in the mean of temperature variables and recent temperature novelty.** Scatterplots showing the correlation (as investigated using piecewise generalised linear models with a binomial logit; GLMs) between the below-canopy novelty of each temperature variable and the change in the same variable (that is the difference between the mean of 1990–2004 and the mean of 2005–2019) across undisturbed tropical forests (n = 317,809) for isothermality, maximum temperature of the

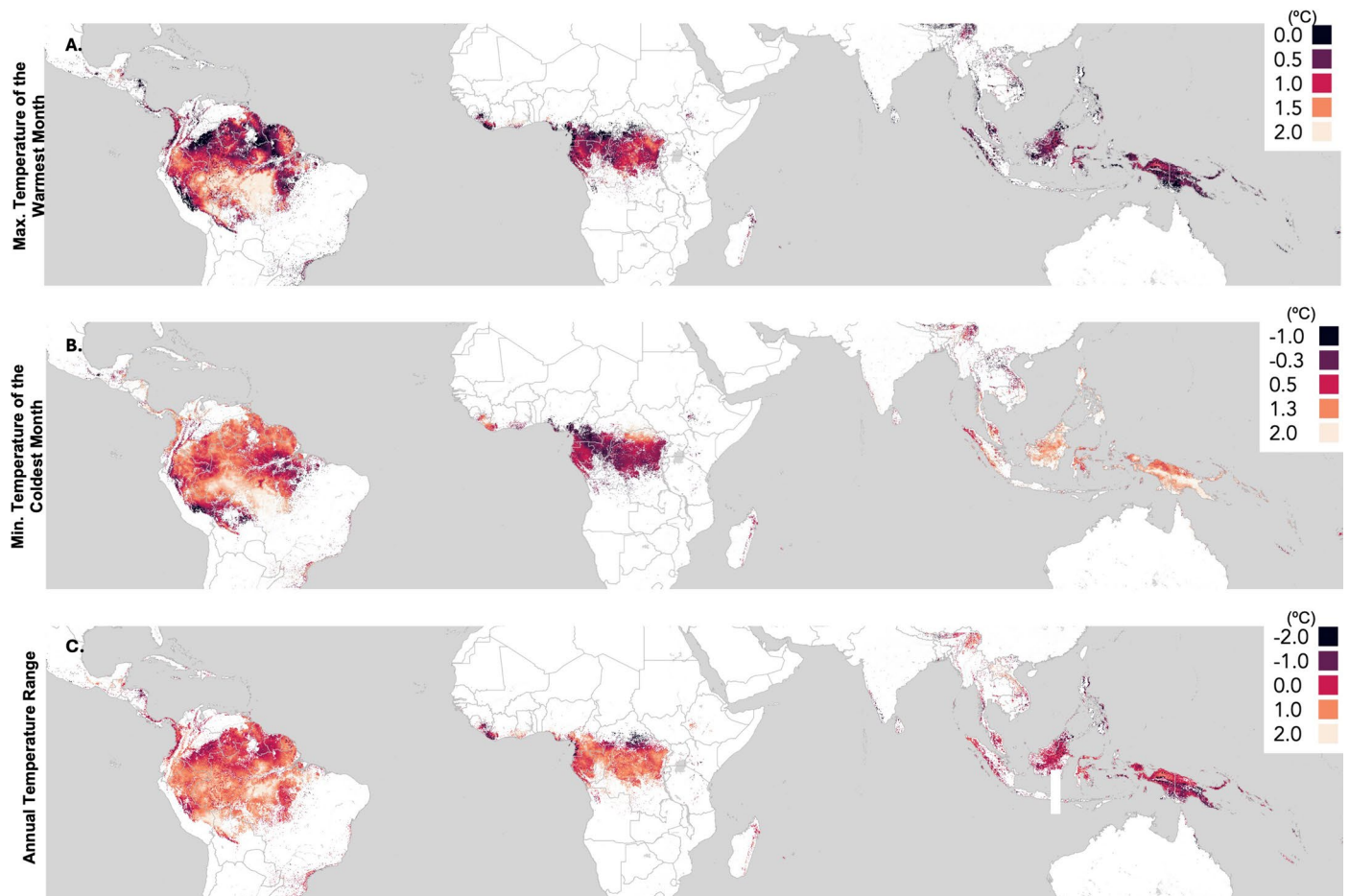
warmest month, minimum temperature of the coldest month, and annual range of temperature. Each point represents one grid cell for Africa (n = 67,799), Central and South America (n = 185,883), and Asia and Australia (n = 64,127). Please see supplementary table S2 for model results for each group. Tests were conducted using two-sided Wald tests with a significance level set at  $p < 0.01$ . No adjustments were made for multiple comparisons as each temperature variable was analysed and presented separately.



**Extended Data Fig. 4 | Mean overall change in temperature variables across global, undisturbed-only tropical forests.** Change in temperature ( $^{\circ}\text{C}$ ) is mapped at 5 km gridded resolution ( $n = 317,809$ ) for (A) mean annual

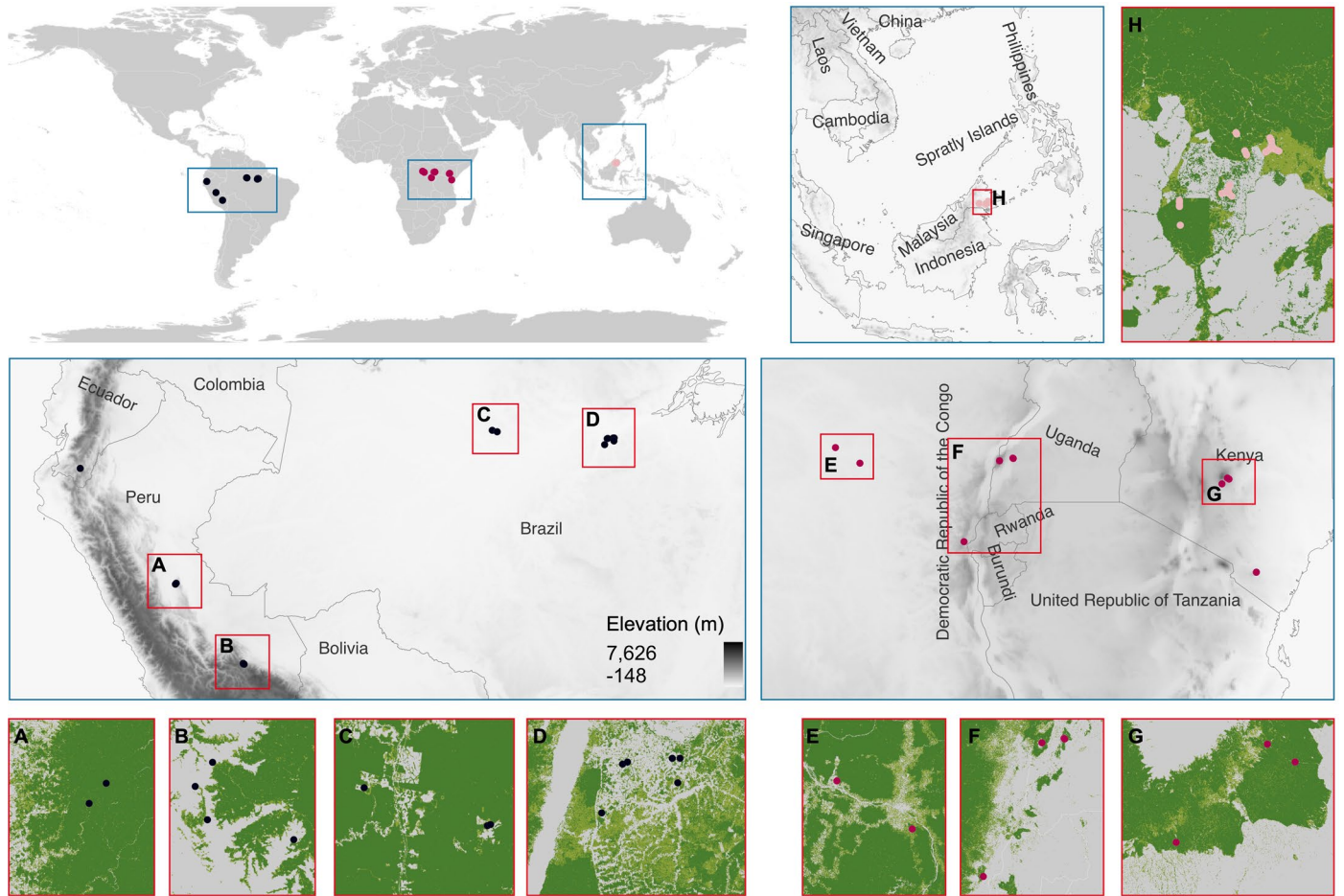
temperature; (B) mean diurnal temperature range; (C) isothermality, and (D) temperature seasonality. Change is defined as the difference between the mean of the temperature variable for 1990–2004 and the mean for 2005–2019.



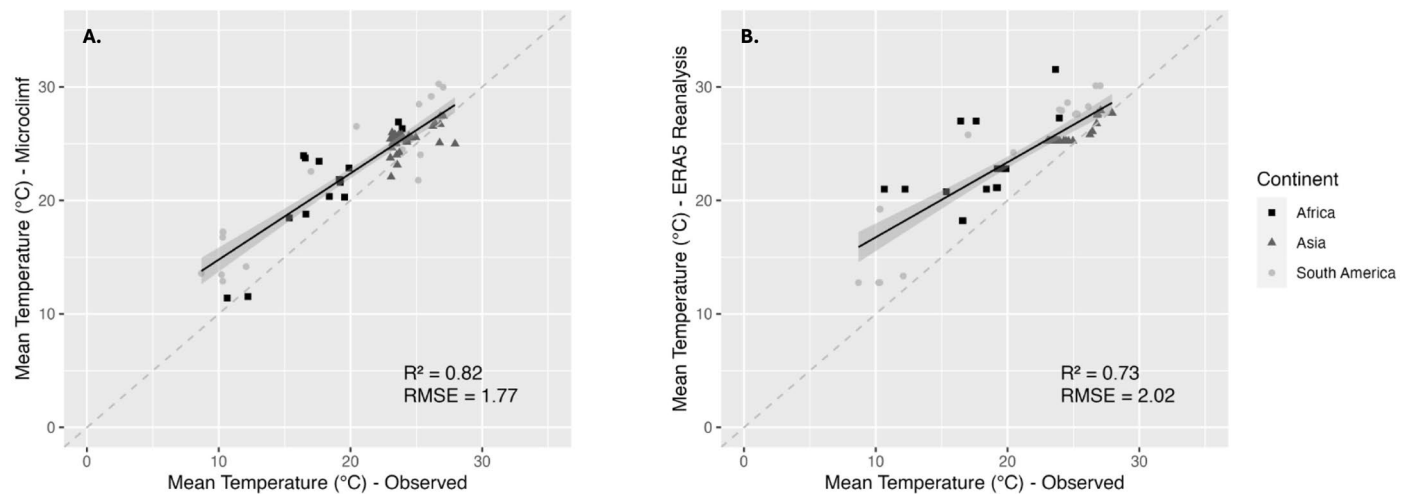


**Extended Data Fig. 5 | Mean overall change in temperature variables across global, undisturbed-only tropical forests.** Change in temperature ( $^{\circ}\text{C}$ ) is mapped at 5 km gridded resolution ( $n = 317,809$ ) for (A) maximum temperature

of the warmest month, (B) minimum temperature of the coldest month, and (C) annual temperature range. Change is defined as the difference between the mean of the temperature variable for 1990–2004 and the mean for 2005–2019.



**Extended Data Fig. 6 | Pantropical locations for all the temperature loggers used to validate the microclimate model.** Inset windows A-H show locations of loggers within undisturbed and degraded tropical forest in 2019 as defined in the methods.



**Extended Data Fig. 7 | Relationship between modelled and observed mean temperatures.** (A) The correlation between mean temperatures modelled using *microclimf* and mean temperatures recorded by in-situ temperature loggers. (B) The correlation between mean temperature from the ERA5 reanalysis dataset

and mean temperatures recorded by in-situ temperature loggers. These results pertain to beneath tropical forest canopies across South America, Africa and South-East Asia. The grey shaded areas represent 95% confidence intervals.

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Policy information about [availability of computer code](#)

Data collection

Microclimate modelling was conducted using R software (2021) and the mechanistic microclimate model is freely available to use in the microclimf package for R: <https://github.com/ilyamaclean/microclimf>. The full code used here to model microclimate is published online (10.5281/zenodo.8246818) with examples of the open access datasets needed to reproduce the results shown here (those listed in the data availability statement).

Data analysis

Code used for the novelty analysis is published online (10.5281/zenodo.8246818) with examples of the open access datasets needed to reproduce the results shown here (those listed in the data availability statement). Data analysis was conducted using R software (2021).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

## Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

Global hourly climate data is available from <https://cds.climate.copernicus.eu/>. Environmental parameters include: (a) leaf area index & surface reflectance available from <https://www.ncei.noaa.gov/data/avhrr-land-leaf-area-index-and-fapar/>, (b) global habitat types available from <https://www.esa-landcover-cci.org/>, (c) vegetation height available from <https://webmap.ornl.gov/ogc/>, (d) soil types available from <https://www.soilgrids.org>, (e) digital elevation model available from: <https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm-1>. The microclimate model is freely available for download and adaptation via a GitHub repository: <https://github.com/ilyamaclean/microclimf>. The global tropical forest monitoring dataset is available from <https://forobs.jrc.ec.europa.eu/TMF>. Temperature records used for validation are available from the global SoilTemp dataset on request: <https://www.soiltempproject.com/the-soiltemp-database/>.

## Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

### Reporting on sex and gender

*Use the terms sex (biological attribute) and gender (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data where this information has been collected, and consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.*

### Population characteristics

*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*

### Recruitment

*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*

### Ethics oversight

*Identify the organization(s) that approved the study protocol.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences  Behavioural & social sciences  Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

### Study description

Microclimate modelling of historical climate conditions across global tropical forests to assess recent climate novelty (2005 to 2019), compared to a baseline historical time period (1990 to 2004).

### Research sample

Undisturbed tropical forest = 317,809; degraded tropical forest = 56,388; total: 374,197 grid cells. The spatial extent of which is defined by Vancutsem et al., (2021) (as below).

### Sampling strategy

To exclude forest where climate change could be amplified by interacting human activities like deforestation, global tropical moist forest which remained undisturbed at the end of 2019 was included in the study and defined by Vancutsem et al., (2021) as all closed forests in the humid tropics including the tropical rainforest and the tropical moist deciduous forest without any observed disturbances (degradation or deforestation) across the full observation period defined by the available Landsat data (1982 - 2019). We also included degraded tropical forest in our analysis which was classified by Vancutsem et al., (2021) as degraded in 2019 (where a visual disturbance or repeated visual disturbances have been observed from space between 1982 and 2019. However, each disturbance event lasted less than 2.5 years and was therefore not classified as deforestation).

### Data collection

The microclimate model was run in daily time increments and then hourly temperatures – at 0.05 m above the ground - were derived

Data collection	using the model's interpolation methods, which infer hourly data from daily minima and maxima using the diurnal cycle in the ambient temperatures provided as inputs to the model. Data needed to drive the model is freely available from the databases listed in the data availability statement.
Timing and spatial scale	Microclimate modelling of hourly temperatures between 01.01.1990 to 31.12.2019. Spatial resolution is 5km gridded.
Data exclusions	Deforested locations were excluded form the analyses as they are no longer able to meet the biological requirements of a tropical forest.
Reproducibility	Reproducible code available at: 10.5281/zenodo.8246818. The mechanistic microclimate model is freely available to use in the microclimf package for R: <a href="https://github.com/ilyamaclean/microclimf">https://github.com/ilyamaclean/microclimf</a> . All data driving the model is open access and freely available from those databases listed in the data availability statement.
Randomization	None
Blinding	None

Did the study involve field work?  Yes  No

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

- | n/a                                 | Involvement in the study                               |
|-------------------------------------|--|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies                    |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms   |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern  |

### Methods

- | n/a                                 | Involvement in the study                        |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq               |
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| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |