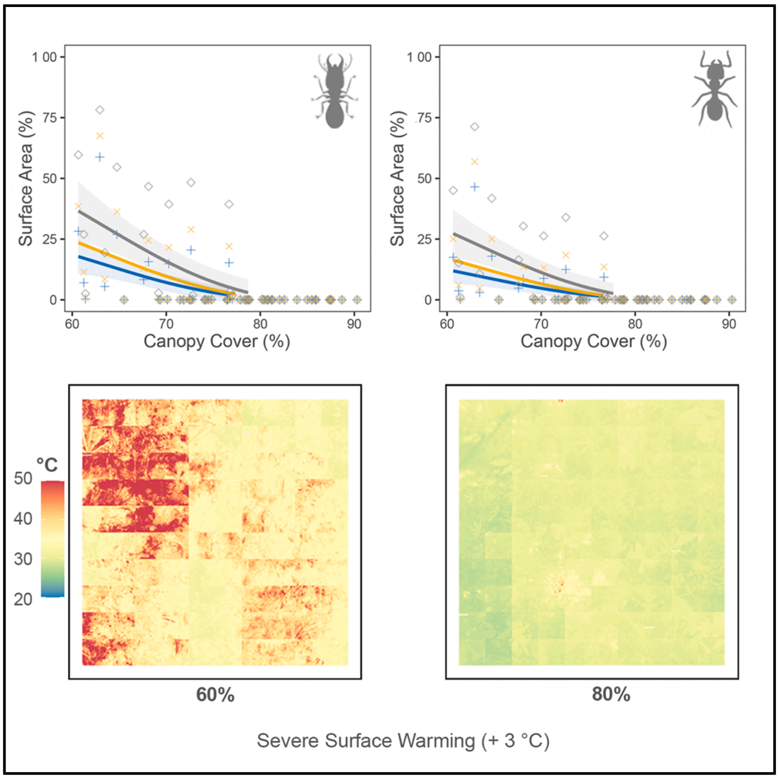
iScience

Article

Narrow thresholds of canopy disturbance determine the microclimate buffering potential of tropical forests

Graphical abstract



Authors

Michael J.W. Boyle, Joseph Williamson, Stephen J. Rossiter, ..., Eleanor M. Slade, Arthur Y.C. Chung, Robert M. Ewers

Correspondence

mjwboyle@hku.hk

In brief

Ecology; Environmental science; Plant ecology

Highlights

- Logged tropical forests are hotter, which may impact biodiversity in the future
- We measured the surface niche space available to invertebrates in a tropical forest
- Niche space was reduced by up to 40% in disturbed patches following severe warming
- High canopy cover forests buffered all invertebrates even following severe warming

Boyle et al., 2026, iScience *29*, 113936
February 20, 2026
https://doi.org/10.1016/j.isci.2025.113936

CellPress

iScience

CellPress
OPEN ACCESS

Article

Narrow thresholds of canopy disturbance determine the microclimate buffering potential of tropical forests

Michael J.W. Boyle,[1,2,3,18,*] Joseph Williamson,[4,5] Stephen J. Rossiter,[5] Marion Pfeifer,[2,6] Rosie Drinkwater,[5,7] Joel S. Woon,[8,9] Louise A. Ashton,[1,9] Michiel van Breugel,[10,11] Paul Eggleton,[9] Theodore A. Evans,[3,12] Owen T. Lewis,[13] Sarab S. Sethi,[2,14,15] Eleanor M. Slade,[16] Arthur Y.C. Chung,[17] and Robert M. Ewers[2]

[1]School of Biological Sciences, University of Hong Kong, Hong Kong SAR, China
[2]Georgina Mace Centre, Imperial College London, Silwood Park, Ascot, UK
[3]Department of Biological Sciences, National University of Singapore, Singapore, Singapore
[4]Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, UK
[5]Centre for Biodiversity and Sustainability, School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK
[6]School of Biology, Newcastle University, Newcastle Upon Tyne, UK
[7]Faculty of Vetinary Medicine, Ludwig Maximilian University, Munich, Germany
[8]School of Environmental Sciences, University of Liverpool, Liverpool, UK
[9]Department of Life Sciences, Natural History Museum London, London, UK
[10]Department of Geography, National University of Sinagpore, Singapore, Singapore
[11]Smithsonian Tropical Research Institue, Panama, Panama
[12]School of Biological Sciences, The University of Western Australia, Crawley, WA, Australia
[13]Department of Zoology, University of Oxford, Oxford, UK
[14]Department of Mathematics, Imperial College London, London, UK
[15]Dyson School of Design Engineering, Imperial College London, London, UK
[16]Asian School of the Environment, Nanyang Technological University, Singapore City, Singapore
[17]Forest Research Centre, Sabah Forestry Department, Sepilok, Sabah, Malaysia
[18]Lead contact
*Correspondence: mjwboyle@hku.hk

https://doi.org/10.1016/j.isci.2025.113936

SUMMARY

The importance of protecting logged and recovering tropical forests has gained much attention. Disturbed forests can, however, have hotter microclimates, exacerbating the effects of future climate change. Using thermal imaging we captured understory surface temperatures along a gradient of tropical forest disturbance, and compared these to the upper thermal limits (CT*max*) of invertebrates within the same forests. Surface temperatures exceeding the CT*max* of invertebrate groups occurred once canopy cover fell below 76%. In highly degraded forests, surface niche space was reduced by 22% for the most sensitive taxa, and this doubled following simulated warming of +3°C. In contrast, all invertebrate groups were buffered in sites that retained 80% canopy cover or higher even following severe warming. We demonstrate a narrow threshold of canopy disturbance beyond which microclimate buffering is significantly diminished. These findings illustrate the importance of conserving high canopy cover forests to protect tropical biodiversity in a hotter future.

INTRODUCTION

With continuing degradation of tropical habitats, considerable attention has been paid to the conservation value of logged tropical forests, providing powerful arguments for their inclusion in the conservation estate.[1–4] However, the ability of these already-disturbed environments to provide refuge for biodiversity following climate change remains poorly understood.[5–7] Tropical landscapes that were recently dominated by old-growth forests now largely appear as mosaics of old growth, varying quality logged and recovering forest alongside pasture and plantation.[8] Such landscape modification has been shown to increase local temperatures,[9] which can have profound impacts on tropical forest organisms and the functions they perform.[10] It is therefore likely that projected increases in global temperatures will disproportionately affect forest-adapted species living in human-modified tropical landscapes, thus reducing the future conservation potential of these forests, although the ecological effects of local and global climate changes acting in concert remain unclear.

Microclimate change arising because of human disturbance can define the community composition and activity of tropical forest organisms.[10] Microclimates also impact a variety of ecosystem processes such as decomposition,[11] plant germination,[12] biogeochemical cycling,[13] and soil respiration.[14] Disturbance arising from timber extraction opens forest

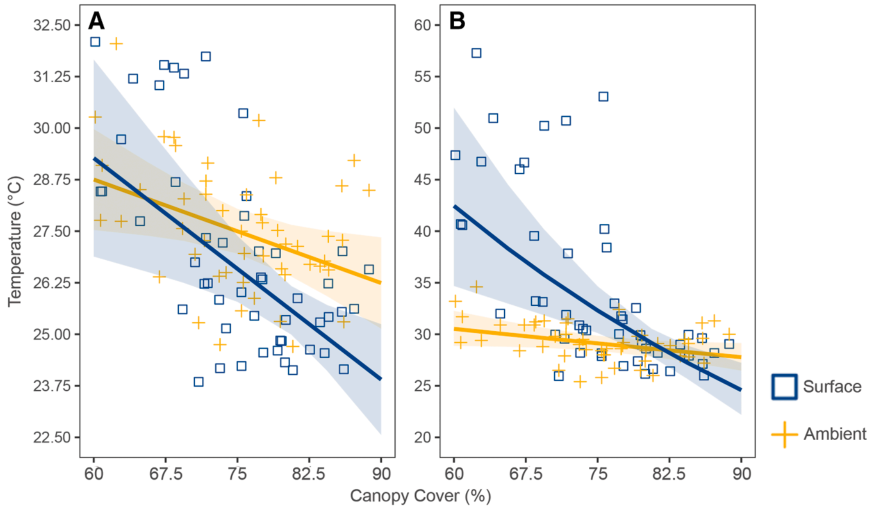


Figure 1. Mean and maximum air and surface temperatures in relation to canopy cover

(A) Mean air and surface temperatures in relation to canopy cover. Both measurements of temperature decline significantly with increasing canopy cover, although mean surface temperatures decline more rapidly.

(B) Maximum air and surface temperature in relation to canopy cover. Maximum air temperatures showed no significant relationship with canopy cover, but maximum surface temperatures increased dramatically as canopy cover decreased. Points represent individual sampling plots, fitted lines are from linear (LMER) or generalized linear (GLMER) mixed effects regression, with shaded polygons representing 95% confidence intervals.

canopies and thereby changes radiation[15] and air fluxes,[16] leading to considerable changes in microclimate at ground level.[17,18] In contrast, the intact canopy and high leaf density in undisturbed forests intercepts most solar radiation, and combined with high rates of evapotranspiration, creates relatively cool and homogenous conditions on the forest floor.[19] These structural differences mean that air temperatures in logged tropical forests are higher and more variable than those in unlogged tropical forests, with an average increase of 1.1°C globally.[9] Studying changes to tropical forest microclimates is therefore fundamental if we wish to develop our understanding of the resilience of these ecosystems to disturbance and climate change.[7,20]

Most animal species are ectotherms[21] including in the tropics, where invertebrates are numerically and functionally dominant.[22,23] As ectotherms, tropical invertebrates are physiologically and behaviorally constrained by local environmental temperatures.[10] However, ambient air temperatures may not reflect the thermal environment experienced by invertebrates such as small insects, for which body temperatures are directly influenced by radiation, reflection, and conductance from the boundary layers of the surfaces they encounter.[24] For example, on forest floors, surface temperatures modulate the foraging of ants,[25–27] which are the primary drivers of predation[28] and resource removal in the tropics.[29] Similarly, on leaf surfaces in the forest understory, spatial patterns of temperature determine the behavior and distribution of phytophagous insects,[30,31] which are important agents of herbivory and exert control over plant community dynamics.[32] While air temperatures beneath tropical canopies are becoming better understood,[19,20] surface temperatures at the microscale within tropical forests remain less well studied (but see in the studies by Scheffers et al. and Senior et al.[33,34]) despite being a crucial determinant of insect body temperature. Moreover, while some recent studies have relativized tropical microclimate dynamics using plant biotic responses,[35] only rarely are microclimate data in these habitats made relative to the thermal physiology of animal species such as insects.[36] This knowledge gap constrains our ability to quantify the buffering potential of tropical forest canopies for biodiversity.[7,37]

Here, we investigate the impact of disturbance on the microclimatic buffering capacity of tropical forests at the scale of functionally important invertebrates. We used thermal imaging to capture the two-dimensional landscape of surface temperatures on the forest floor along a gradient of forest disturbance from 90%–60% canopy cover (Figure in STAR Methods). From the same locations we collected over 5000 individuals from 129 invertebrate taxa representing a range of trophic and functional groups, including ants, termites, dung beetles, non-coprophagic beetles, moths and leeches, and measured their upper thermal limits (*CTmax*). To test how reductions in canopy closure affected microclimate buffering, we calculated the percentage surface area of forest floor and understory that would exceed the thermal limits of the different invertebrate groups, under both current conditions and simulated future warming scenarios of +1°C and +3°C. We then determined how decreasing canopy cover altered the available surface niche area available to invertebrates, thus allowing us to investigate the combined effects of logging and potential climate warming on biodiversity. Specifically, we hypothesized that while air temperatures may be buffered even in relatively disturbed forests, surface temperatures would exceed the upper thermal limits of invertebrates in degraded forest patches, and that this effect would be exacerbated by simulated warming.

RESULTS

Surface vs. air temperatures

Air temperatures varied from 23.7°C to 36.1°C (mean 27.6°C), and surface temperatures varied from 22°C to 57.3°C (mean 27°C) across sites. Canopy closure varied by 29.7%, from a high of 90.3% in old-growth forest to 60.7% in the most disturbed logged forest sites.

Reductions in canopy closure led to differences in mean air and surface temperatures, with surface measurements showing a greater magnitude of change over the same gradient of changing canopy closure (air slope = −0.1, se = 0.5, surface slope = −0.20, se = 0.64, $p < 0.0001$, $R^2_m = 0.30$, $R^2_c = 0.65$) (Figure 1). For each 5% reduction in canopy closure, mean air

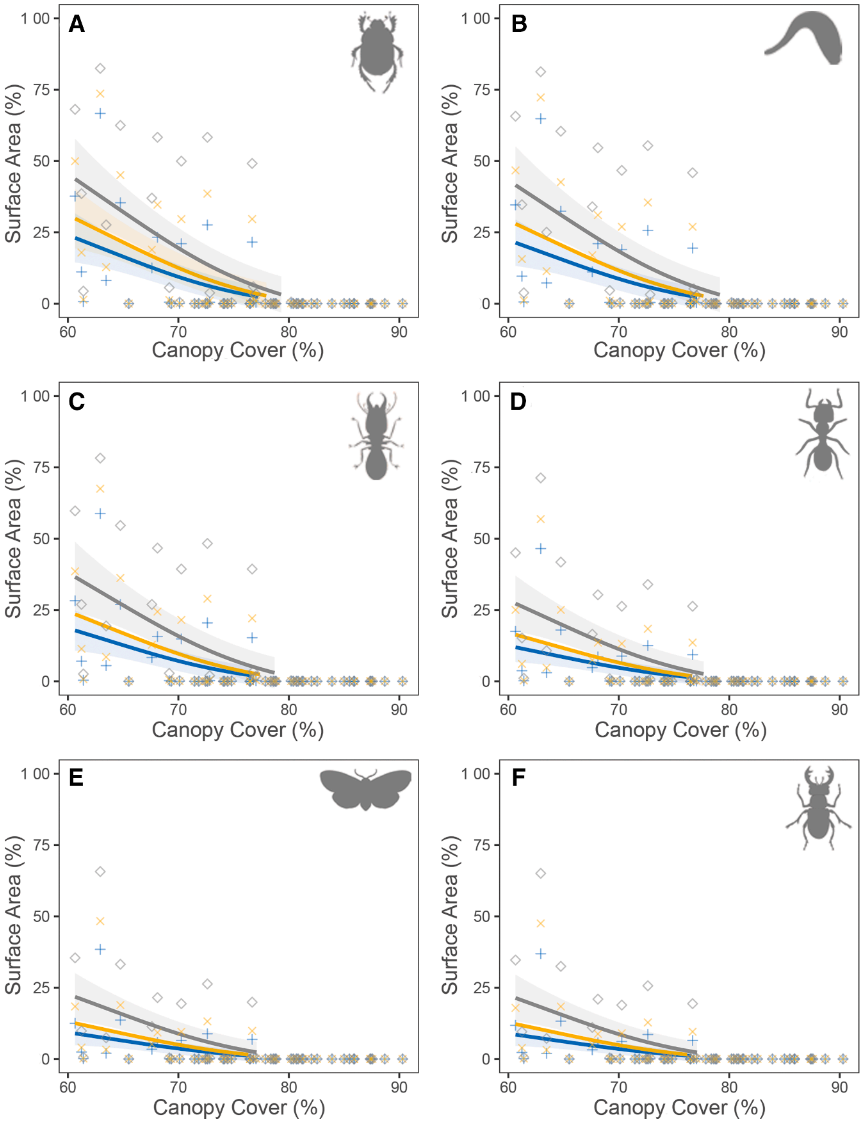


Figure 2. The relationship between the amount of surface area that has surface temperatures exceeding *CTmax* and forest cover for six invertebrate groups

(A) dung beetles, (B) leeches, (C) termites, (D) ants, (E) moths, and (F) non-coprophagic beetles. Three warming scenarios are shown (Present climate, moderate warming (+1°C) and severe warming (+3°C). Points represent individual sampling plots. Lines are predicted from generalized additive models (GAMM), with predicted lines representing where the trend is significantly different from zero, i.e., the point along the *x* axis where at least 1% of the total surface becomes hotter than *CTmax*, with shaded polygons representing 95% confidence intervals.

temperatures increased by 0.5°C (se = 0.5, $p < 0.05$, $R^2_m = 0.16$, $R^2_c = 0.53$) and mean surface temperatures increased by 1°C (se = 0.64, $p < 0.01$, $R^2_m = 0.26$, $R^2_c = 0.76$) (Figure 1).

Reductions in canopy closure also led to differences in maximum air and surface temperatures, again with surface measurements showing a much greater magnitude of change (air slope = −0.1, se = 1.02, surface slope = −0.82, se = 1.1, $p < 0.0001$, $R^2_m = 0.47$, $R^2_c = 0.65$) (Figure 1). A reduction in canopy closure of 5% did not lead to a significant increase in maximum air temperature ($p = 0.08$), but maximum surface temperatures increased substantially by 4.1 °C (se = 1.1, $p < 0.0001$, $R^2_m = 0.34$, $R^2_c = 0.8$) (Figure 1).

Surface temperatures vs. CT*max*

For all invertebrate groups, reductions in canopy closure below 76% led to a significant increase in the amount of surface area exceeding CT*max* (Figure 2). In the most degraded plots, with 60% canopy closure, 22% of the surface area exceeded the CT*max* of the most sensitive invertebrate groups during the hottest parts of the day. In contrast, plots with canopy closure above 80% experienced no deleterious surface temperatures for any invertebrate group. This threshold was further highlighted following simulated surface warming, with the most degraded areas experiencing a total reduction in thermally buffered surfaces of 42% for the most sensitive taxa following 3 degrees of warming. In contrast, forests with canopy cover of 80% or above withstood all simulated climate warming with none of the surface area surpassing the CT*max* for any of the invertebrate groups measured (Table 1; Figure 2).

DISCUSSION

Understanding the impacts of forest canopy disturbance on surface microclimates has important implications for our understanding of microhabitat availability of forest-adapted ectotherms in human-modified tropical landscapes. As hypothesized we found that the availability of buffered surfaces, i.e., available microhabitat for temperature-sensitive understory ectotherms, diminished with increasing canopy openness, though these trends were non-linear. Importantly, our results highlight a very narrow threshold of microclimate buffering for all taxa in our study. When canopy cover falls below 76%, surface temperatures—both currently and following moderate or severe surface warming—exceeded the community level thermal limits of all invertebrate groups measured. In contrast, forests retaining canopy cover above 80% may be able to buffer organisms from extreme temperatures, even following severe climate change. While more sensitive taxa were expected to experience a greater reduction in buffered surface space overall, this narrow threshold of disturbance was observed across all groups, regardless of thermal

Table 1. Model outputs from GAMM models of canopy cover vs. surface area exceeding CT*max*

Taxa	Individuals	CT*max* (C)	Time Period	N	F value	Significance	R2
Dung Beetles	543	40	Current	51	15.38	***	0.32
		sd = 1.3	Near Future	51	17.15	***	0.34
			Future	51	20.42	***	0.38
Leeches	39	40.3	Current	51	14.91	**	0.31
		sd = 1.3	Near Future	51	16.62	***	0.34
			Future	51	19.96	***	0.38
Termites	1305	41	Current	51	13.91	***	0.29
		sd = 1.8	Near Future	51	15.51	***	0.32
			Future	51	18.82	***	0.36
Ants	2359	42.4	Current	51	12.1	**	0.25
		sd = 1.6	Near Future	51	13.37	***	0.28
			Future	51	16.51	***	0.33
Moths	424	43.3	Current	51	11.15	**	0.23
		sd = 1.4	Near Future	51	12.25	**	0.25
			Future	51	14.97	***	0.31
Beetles	368	43.4	Current	51	11.13	**	0.23
		sd = 2.3	Near Future	51	12.13	**	0.25
			Future	51	14.87	***	0.31

Six invertebrate groups are represented, and models were run for three warming scenarios per group; none, moderate (+1°C) and severe (+3°C). In all cases the effect of reducing canopy cover led to significant increases in the amount of surface area exceeding CT*max*.

sensitivity. As a result of human activities, logged and fragmented forests are now a ubiquitous feature of the tropical landscape,[8] and these habitats are a research and policy focus because of their potential for biodiversity conservation.[4] Our results suggest that the ability of forests to conserve biodiversity in a warmer future will depend on recent logging intensity and canopy openness, whereas old growth forests and logged forests that have undergone sufficient canopy regeneration could provide crucial refugia even following severe warming.

Our results suggest that a narrow threshold of microclimate buffering is crossed in tropical forests following reductions in canopy closure of between 15% and 20%, a pattern that could lead to abrupt and synchronous loss of biodiversity in heavily degraded forests following climate change.[38] This value is remarkably similar to the threshold of 17% biomass removal that has been highlighted as a tipping point below which tropical forests experience rate changes of biodiversity loss.[39] Previous studies have highlighted narrow thresholds of disturbance affecting communities of organisms including fishes,[40] mammals,[41] amphibians,[41] cavity-nesting birds,[42] and decomposing invertebrate guilds,[43] suggesting that such tipping points may be common in tropical forest ecosystems. Our results imply that such thresholds of disturbance exist not only in terms of immediate impacts on species assemblages, but also in the ability of tropical forests to buffer organisms from further climate warming.

Forecasting biodiversity responses to warming using thermal physiology data are complex,[44] but remains a vital tool in predicting biodiversity responses to climate change and identifying taxa at risk of extinction.[45–47] Thresholds in thermal exposure across a gradient of forest disturbance may be a product of the relationship between microclimate and vegetation structure but are also likely driven by the sensitivity of organisms to warming. If species share similar abiotic tolerances, we might expect threshold responses to environmental change at the community-level, as species are exposed to stressful conditions at similar levels of warming.[48] This could occur via macro-scale climate change, localized microclimate change driven by habitat disturbance or both. It is important to note that thermal limits do vary within the diverse invertebrate taxa studied here, but overall they exhibit remarkably similar thermal limits that could drive clustering in their tolerances to warming.[48] While thermal exposure estimates are not perfect, they are likely correlated with the true tolerances of these taxa to warming. Indeed, we know that at least for dung beetles and ants, these thermal limits do predict the response of taxa to logging gradients and microclimate change in this landscape.[10,49] Accordingly, while it is difficult to define absolutely accurate climate tipping points using physiological thermal limits, our findings provide evidence for threshold responses following disturbance and relativize microclimate warming to ecologically relevant scales.

While general temperature increases are expected to generate stressful conditions for tropical organisms in the future, extreme events such as heatwaves and El Niños may already be exerting significant pressure on biodiversity in these ecosystems.[50–52] Recently, heatwaves have been implicated in driving observed declines in bird diversity even within primary tropical forests,[50,53] yet forest canopies were previously expected to be able to buffer bird communities from climate change.[54] Similarly, stronger El Niños are likely to be responsible for parallel declines in invertebrates in undisturbed forests where canopy structure is intact.[51] Alarmingly, these invertebrate declines are also mirrored in declining ecosystem functions such as leaf herbivory,[51] which is fundamental for the maintenance of plant community composition in tropical forests. While our findings imply that intact canopies can buffer organisms from gradual, wholesale increases to temperature over time, the effects of extreme events are more difficult to forecast. We expect that such events are already having significant impacts on biodiversity and ecosystem functioning across the tropics, and that such effects are likely to be even more pronounced in heavily degraded forests.[52]

Although natural processes such as tree falls can reduce canopy closure and alter microclimates at a local scale,[55] logging can alter the structure and abiotic conditions of forests at a landscape scale,[9] with over a fifth of tropical forests being logged between 2000 and 2005 alone.[56] There is evidence to suggest that tropical forests canopies can regenerate following logging, with an accompanying recovery of the microclimate,[34] though it is expected to take multiple decades and potentially well over a century for canopy structure to return fully to a pre-logging state.[57,58] Assumptions about the buffering potential of tropical forests are also predicated on the existing canopy remaining intact, but increasing droughts and heatwaves are leading to tree dieback and reduced seedling recruitment,[59] generating uncertainty about the structure of primary forest canopies in a warmer future.[19] Protection of high-quality logged forests and the increased uptake of selective and reduced impact logging practices in active concessions will be crucial to maintain sufficient coverage of intact canopies at the landscape scale. In more degraded forests, interventions such as active restoration through planting may be necessary to facilitate the recovery of microclimate buffering.[60] This will be crucial for the resilience for tropical biodiversity in a hotter future.

Shifting microclimates following disturbance represent a powerful and relatively understudied form of anthropogenic climate change.[6,7,10] How this interacts with larger scale temperature changes brought about by global climate warming is unclear, but it seems probable that species existing within disturbed forests will have to cope with the combined stresses of global climate change on top of an already elevated thermal environment.[5] Our results suggest that intact tropical forest canopies might be even more crucial for buffering the effects of climate change than previously thought, and that emerging microclimatic conditions in recently logged or heavily disturbed tropical forests may be even more hostile to several rainforest organisms than anticipated. While the preservation of old growth forests will therefore be fundamental for maintaining tropical biodiversity in a warming world, these findings also raise a powerful argument for adding high canopy cover logged forests to the conservation estate, and for the targeted restoration of highly degraded landscapes.

Limitations of the study

One limitation of our study is the lack of temporal replication. Working in remote tropical forest sites, it was not practically feasible to take repeat measurements at each location over the course of the day and night. Instead we focused on maximizing spatial replication and measured temperatures at the hottest time of the day, when we expect the most thermally stressful conditions to occur. Nonetheless, acute thermal stress is only one aspect of thermal sensitivity: chronic thermal stress and elevated nocturnal temperatures are understudied and fundamental components of thermal biology.[61,62] Similarly, we were only able to measure temperatures and sample organisms for thermal testing at the ground layer. Tropical forests have complex three-dimensional structure, and a significant proportion of biodiversity occurs in the canopy layer.[23] Organisms living in the canopy are likely to experience more extreme microclimate variability than those at the ground layer, with understudied consequences for community composition and function under habitat degradation and climate change. We encourage future research to investigate chronic and nocturnal thermal stress, and to extend measurements to the forest canopy within human modified tropical landscapes.

RESOURCE AVAILABILITY

Lead contact

Michael J. W. Boyle, mjwboyle@hku.hk

Materials availability

No novel materials were generated in this study.

Data and code availability

- Ants CTmax Database: https://doi.org/10.5281/zenodo.4297673
- Dung Beetles CTmax Database: https://doi.org/10.5281/zenodo.6477719.
- Termites CTmax Database: https://doi.org/10.5281/zenodo.1198695.
- Leeches CTmax Database: https://doi.org/10.5281/zenodo.2536269.
- For raw thermal images, analysis code, moth and non-coprophagic beetle *CTmax* please contact the corresponding author.

ACKNOWLEDGMENTS

M.J.W.B. was funded by the National Natural Science Foundation of China Excellent Young Scientist Award (AR215206), the Hong Kong University Grants Committee Collaborative Research Fund (C7048-22GF) and the University of Hong Kong 46th Round Fellowship. Original data collection was funded by the Sime Darby Foundation. EMS was funded by the Climate Transformation Program, Ministry of Education, Singapore, under its MOE AcRF Tier 3 Award MOET32022-0006. Research was facilitated by the South-East Asia Rainforest Research Partnership (SEARRP) and the Maliau Basin Management Committee (MBMC). All research in Borneo was authorized by the Sabah Biodiversity Council (SABC research permit numbers: JKM/MBS.1000-2/2 JLD.16 (174), JKM/MBS.1000-2/2 JLD.14 (40), JKM/MBS.1000-2/2 JLD.12 (106), JKM/MBS.1000-2/2 JLD.10 (185), JKM/MBS.1000-2/2 JLD.10 (185), JKM/MBS.1000-2/2 JLD.8 (55)). We would like to extend special thanks to Ms Anjulie Binti Abdul Razak, who's hard work was instrumental in generating data for this project, but who we are unable to contact.

AUTHOR CONTRIBUTIONS

M.J.W.B., R.M.E. and M.P. conceptualized the study. M.J.W.B. and M.P. developed the methods. R.M.E., L.A.A., S.J.R., M.V.B., T.A.E., P.E., O.T.L., M.P. and E.M.S. supervised the study. R.M.E., L.A.A., S.J.R., O.T.L., and E.M.S. secured funding. A.Y.C.C. acted as local collaborator in Malaysia. M.J.W.B., J.W., R.D., J.S.W. and L.A.A. contributed data. M.J.W.B. and S.S.S. curated the data. M.J.W.B. undertook the statistical analyses and created the figures. M.J.W.B. wrote the first version of the manuscript. All authors contributed to writing, editing and revising subsequent versions of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- METHOD DETAILS
  - Study site
  - Microclimate
  - Simulated warming
  - Canopy cover
  - Invertebrate CT*max*
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2025.113936.

Received: September 9, 2025
Revised: September 11, 2025
Accepted: October 30, 2025
Published: November 3, 2025

REFERENCES

1. Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., et al. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. USA *104*, 18555–18560. https://doi.org/10.1073/pnas.0703333104.
2. Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., Castello, L., Economo, E.P., Ferreira, J., Guénard, B., et al. (2018). The future of hyperdiverse tropical ecosystems. Nature *559*, 517–526. https://doi.org/10.1038/s41586-018-0301-1.
3. Woodcock, P., Edwards, D.P., Fayle, T.M., Newton, R.J., Khen, C.V., Bottrell, S.H., and Hamer, K.C. (2011). The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. Philos. Trans. R. Soc. Lond. B Biol. Sci. *366*, 3256–3264. https://doi.org/10.1098/rstb.2011.0031.
4. Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., Ahmad, N., Magintan, D., Khen, C.V., Maryati, M., et al. (2010). The high value of logged tropical forests: lessons from northern Borneo. Biodivers. Conserv. *19*, 985–997. https://doi.org/10.1007/s10531-010-9779-z.
5. Tuff, K.T., Tuff, T., and Davies, K.F. (2016). A framework for integrating thermal biology into fragmentation research. Ecol. Lett. *19*, 361–374. https://doi.org/10.1111/ele.12579.
6. De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M.B., Christiansen, D.M., Decocq, G., De Pauw, K., et al. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. Glob. Change Biol. *27*, 2279. https://doi.org/10.1111/gcb.15569.
7. Jucker, T., Jackson, T.D., Zellweger, F., Swinfield, T., Gregory, N., Williamson, J., Slade, E.M., Phillips, J.W., Bittencourt, P.R.L., Blonder, B., et al. (2020). A Research Agenda for Microclimate Ecology in Human-Modified Tropical Forests. Front. For. Glob. Change *2*, 92. https://doi.org/10.3389/ffgc.2019.00092.
8. Lewis, S.L., Edwards, D.P., and Galbraith, D. (2015). Increasing human dominance of tropical forests. Science *349*, 827–832.
9. Senior, R.A., Hill, J.K., González del Pliego, P., Goode, L.K., and Edwards, D.P. (2017). A pantropical analysis of the impacts of forest degradation and conversion on local temperature. Ecol. Evol. *7*, 7897–7908. https://doi.org/10.1002/ece3.3262.
10. Boyle, M.J.W., Bishop, T.R., Luke, S.H., van Breugel, M., Evans, T.A., Pfeifer, M., Fayle, T.M., Hardwick, S.R., Lane-Shaw, R.I., Yusah, K.M., et al. (2021). Localised climate change defines ant communities in human-modified tropical landscapes. Funct. Ecol. *35*, 1094–1108. https://doi.org/10.1111/1365-2435.13737/SUPPINFO.
11. Gottschall, F., Davids, S., Newiger-Dous, T.E., Auge, H., Cesarz, S., and Eisenhauer, N. (2019). Tree species identity determines wood decomposition via microclimatic effects. Ecol. Evol. *9*, 12113–12127. https://doi.org/10.1002/ece3.5665.
12. Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., and Franklin, J.F. (1999). Microclimate in Forest Ecosystem and Landscape Ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes. Bioscience *49*, 288.
13. Medinets, S., Gasche, R., Kiese, R., Rennenberg, H., and Butterbach-Bahl, K. (2019). Seasonal dynamics and profiles of soil NO concentrations in a temperate forest. Plant Soil *445*, 335–348. https://doi.org/10.1007/s11104-019-04305-5.
14. Hursh, A., Ballantyne, A., Cooper, L., Maneta, M., Kimball, J., and Watts, J. (2017). The sensitivity of soil respiration to soil temperature, moisture, and carbon supply at the global scale. Glob. Change Biol. *23*, 2090–2103. https://doi.org/10.1111/gcb.13489.
15. Pfeifer, M., Boyle, M.J.W., Dunning, S., and Olivier, P.I. (2019). Forest floor temperature and greenness link significantly to canopy attributes in South Africa's fragmented coastal forests. PeerJ *7*, e6190. https://doi.org/10.7717/peerj.6190.
16. Raupach, M.R., Finnigan, J.J., and Brunet, Y. (1996). Coherent eddies and turbulence in vegetation canopies: the mixing-layer analogy. Boundary-Layer Meteorol. *78*, 351–382. https://doi.org/10.1007/BF00120941.
17. Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R., and Ewers, R.M. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. Agric. For. Meteorol. *201*, 187–195. https://doi.org/10.1016/j.agrformet.2014.11.010.
18. Jucker, T., Hardwick, S.R., Both, S., Elias, D.M.O., Ewers, R.M., Milodowski, D.T., Swinfield, T., Coomes, D.A., and David Coomes, C.A. (2018). Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. Glob. Change Biol. *24*, 5243–5258. https://doi.org/10.1111/gcb.14415.
19. Ismaeel, A., Tai, A.P.K., Santos, E.G., Maraia, H., Aalto, I., Altman, J., Doležal, J., Lembrechts, J.J., Camargo, J.L., Aalto, J., et al. (2024). Patterns of tropical forest understory temperatures. Nat. Commun. *15*, 549. https://doi.org/10.1038/s41467-024-44734-0.
20. Trew, B.T., Edwards, D.P., Lees, A.C., Klinges, D.H., Early, R., Svátek, M., Plichta, R., Matula, R., Okello, J., Niessner, A., et al. (2024). Novel temperatures are already widespread beneath the world's tropical forest canopies. Nat. Clim. Chang. *14*, 753–759. https://doi.org/10.1038/s41558-024-02031-0.
21. Bar-On, Y.M., Phillips, R., and Milo, R. (2018). The biomass distribution on Earth. Proc. Natl. Acad. Sci. USA *115*, 6506–6511. https://doi.org/10.1073/PNAS.1711842115.
22. Ewers, R.M., Boyle, M.J.W., Gleave, R.A., Plowman, N.S., Benedick, S., Bernard, H., Bishop, T.R., Bakhtiar, E.Y., Chey, V.K., Chung, A.Y.C., et al. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. Nat. Commun. *6*, 6836. https://doi.org/10.1038/ncomms7836.
23. Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., et al. (2012). Arthropod Diversity in a Tropical Forest. Science *1979*, 1481–1485.
24. Kaspari, M., Clay, N.A., Lucas, J., Yanoviak, S.P., and Kay, A. (2015). Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Glob. Change Biol. *21*, 1092–1102. https://doi.org/10.1111/gcb.12750.

25. Ruano, F., Tinaut, A., and Soler, A.J.J. (2000). High surface temperatures select for individual foraging in ants. Behav. Ecol. *11*, 396–404. https://doi.org/10.1093/beheco/11.4.396.

26. Jayatilaka, P., Narendra, A., Reid, S.F., Cooper, P., and Zeil, J. (2011). Different effects of temperature on foraging activity schedules in sympatric Myrmecia ants. J. Exp. Biol. *214*, 2730–2738. https://doi.org/10.1242/jeb.053710.

27. Bestelmeyer, B.T. (2008). The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J. Anim. Ecol. *69*, 998–1009. https://doi.org/10.1111/j.1365-2656.2000.00455.x.

28. Floren, A., Biun, A., and Linsenmair, E.K. (2002). Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia *131*, 137–144. https://doi.org/10.1007/s00442-002-0874-z.

29. Griffiths, H.M., Ashton, L.A., Walker, A.E., Hasan, F., Evans, T.A., Eggleton, P., and Parr, C.L. (2018). Ants are the major agents of resource removal from tropical rainforests. J. Anim. Ecol. *87*, 293–300. https://doi.org/10.1111/1365-2656.12728.

30. Pincebourde, S., and Casas, J. (2006). Multitrophic biophysical budgets: Thermal ecology of an intimate herbivore insect-plant interaction. Ecol. Monogr. *76*, 175–194. https://doi.org/10.1890/0012-9615(2006)076[0175:MBBTEO]2.0.CO;2.

31. Pincebourde, S., and Casas, J. (2019). Narrow safety margin in the phyllosphere during thermal extremes. Proc. Natl. Acad. Sci. USA *116*, 5588–5596. https://doi.org/10.1073/pnas.1815828116.

32. Bagchi, R., Gallery, R.E., Gripenberg, S., Gurr, S.J., Narayan, L., Addis, C.E., Freckleton, R.P., and Lewis, O.T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature *506*, 85–88. https://doi.org/10.1038/nature12911.

33. Scheffers, B.R., Edwards, D.P., Macdonald, S.L., Senior, R.A., Andriamahohatra, L.R., Roslan, N., Rogers, A.M., Haugaasen, T., Wright, P., and Williams, S.E. (2017). Extreme thermal heterogeneity in structurally complex tropical rain forests. Biotropica *49*, 35–44. https://doi.org/10.1111/btp.12355.

34. Senior, R.A., Hill, J.K., Benedick, S., and Edwards, D.P. (2018). Tropical forests are thermally buffered despite intensive selective logging. Glob. Change Biol. *24*, 1267–1278. https://doi.org/10.1111/gcb.13914.

35. Zellweger, F., de Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., et al. (2020). Forest microclimate dynamics drive plant responses to warming. Science *368*, 772–775. https://doi.org/10.1126/SCIENCE.ABA6880/SUPPL_FILE/ABA6880-ZELLWEGER-SM.PDF.

36. Pincebourde, S., and Suppo, C. (2016). The Vulnerability of Tropical Ectotherms to Warming Is Modulated by the Microclimatic Heterogeneity. Integr. Comp. Biol. *56*, 85–97. https://doi.org/10.1093/ICB/ICW014.

37. De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., and Lenoir, J. (2019). Global buffering of temperatures under forest canopies. Nat. Ecol. Evol. *3*, 744–749. https://doi.org/10.1038/s41559-019-0842-1.

38. Trisos, C.H., Merow, C., and Pigot, A.L. (2020). The projected timing of abrupt ecological disruption from climate change. Nature, 496–496501. https://doi.org/10.1038/s41586-020-2189-9.

39. Ewers, R.M., Orme, C.D.L., Pearse, W.D., Zulkifli, N., Yvon-Durocher, G., Yusah, K.M., Yoh, N., Yeo, D.C.J., Wong, A., Williamson, J., et al. (2024). Thresholds for adding degraded tropical forest to the conservation estate. Nature *631*, 808–813. https://doi.org/10.1038/S41586-024-07657-W.

40. Wilkinson, C.L., Yeo, D.C.J., Tan, H.H., Fikri, A.H., and Ewers, R.M. (2018). Land-use change is associated with a significant loss of freshwater fish species and functional richness in Sabah, Malaysia. Biol. Conserv. *222*, 164–171. https://doi.org/10.1016/J.BIOCON.2018.04.004.

41. Burivalova, Z., Şekercioğlu, Ç., and Koh, L.P. (2014). Thresholds of Logging Intensity to Maintain Tropical Forest Biodiversity. Curr. Biol. *24*, 1893–1898. https://doi.org/10.1016/J.CUB.2014.06.065.

42. Costantini, D., Edwards, D.P., and Simons, M.J.P. (2016). Life after logging in tropical forests of Borneo: A meta-analysis. Biol. Conserv. *196*, 182–188. https://doi.org/10.1016/J.BIOCON.2016.02.020.

43. Luke, S.H., Fayle, T.M., Eggleton, P., Turner, E.C., and Davies, R.G. (2014). Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. Biodivers. Conserv. *23*, 2817–2832. https://doi.org/10.1007/s10531-014-0750-2.

44. Clusella-Trullas, S., Garcia, R.A., Terblanche, J.S., and Hoffmann, A.A. (2021). How useful are thermal vulnerability indices? Trends Ecol. Evol. *36*, 1000–1010. https://doi.org/10.1016/J.TREE.2021.07.001.

45. Pinsky, M.L., Eikeset, A.M., McCauley, D.J., Payne, J.L., and Sunday, J.M. (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. Nature, 108–108111. https://doi.org/10.1038/s41586-019-1132-4.

46. Pottier, P., Kearney, M.R., Wu, N.C., Gunderson, A.R., Rej, J.E., Rivera-Villanueva, A.N., Pollo, P., Burke, S., Drobniak, S.M., and Nakagawa, S. (2025). Vulnerability of amphibians to global warming. Nature *639*, 954–961. https://doi.org/10.1038/s41586-025-08665-0.

47. da Silva, C.R.B., Beaman, J.E., Youngblood, J.P., Kellermann, V., and Diamond, S.E. (2023). Vulnerability to climate change increases with trophic level in terrestrial organisms. Sci. Total Environ. *865*, 161049. https://doi.org/10.1016/J.SCITOTENV.2022.161049.

48. Williamson, J., Lu, M., Camus, M.F., Gregory, R.D., Maclean, I.M.D., Rocha, J.C., Saastamoinen, M., Wilson, R.J., Bridle, J., and Pigot, A.L. (2025). Clustered warming tolerances and the nonlinear risks of biodiversity loss on a warming planet. Phil. Trans. B *380*, 20230321. https://doi.org/10.1098/RSTB.2023.0321.

49. Williamson, J., Teh, E., Jucker, T., Brindle, M., Bush, E., Chung, A.Y.C., Parrett, J., Lewis, O.T., Rossiter, S.J., and Slade, E.M. (2022). Local-scale temperature gradients driven by human disturbance shape the physiological and morphological traits of dung beetle communities in a Bornean oil palm–forest mosaic. Funct. Ecol. *36*, 1655–1667. https://doi.org/10.1111/1365-2435.14062.

50. Wolfe, J.D., Luther, D.A., Jirinec, V., Collings, J., Johnson, E.I., Bierregaard, R.O., and Stouffer, P.C. (2025). Climate change aggravates bird mortality in pristine tropical forests. Sci. Adv. *11*, 8086. https://doi.org/10.1126/SCIADV.ADQ8086/SUPPL_FILE/SCIADV.ADQ8086_SM.PDF.

51. Sharp, A.C., Boyle, M.J.W., Bonebrake, T.C., Guo, Y., Kitching, R.L., Stork, N.E., Zeng, X., and Ashton, L.A. (2025). Stronger El Niños reduce tropical forest arthropod diversity and function. Nature *645*, 946–951. https://doi.org/10.1038/s41586-025-09351-x.

52. Boyle, M.J.W., Bonebrake, T.C., Dias da Silva, K., Dongmo, M.A.K., Machado França, F., Gregory, N., Kitching, R.L., Ledger, M.J., Lewis, O.T., Sharp, A.C., et al. (2025). Causes and consequences of insect decline in tropical forests. Nat. Rev. Biodivers. *1*, 315–331. https://doi.org/10.1038/s44358-025-00038-9.

53. Kotz, M., Amano, T., and Watson, J.E.M. (2025). Large reductions in tropical bird abundance attributable to heat extreme intensification. Nat. Ecol. Evol. *9*, 1897–1909. https://doi.org/10.1038/s41559-025-02811-7.

54. Betts, M.G., Phalan, B., Frey, S.J.K., Rousseau, J.S., and Yang, Z. (2018). Old-growth forests buffer climate-sensitive bird populations from warming. Divers. Distrib. *24*, 439–447. https://doi.org/10.1111/DDI.12688.

55. Brown, N. (1993). The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. J. Trop. Ecol. *9*, 153–168. https://doi.org/10.1017/S0266467400007136.

56. Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R., and Emerson, R. (2009). A Contemporary Assessment of Change in Humid Tropical Forests. Conserv. Biol. *23*, 1386–1395. https://doi.org/10.1111/J.1523-1739.2009.01333.X.

57. Milodowski, D.T., Coomes, D.A., Swinfield, T., Jucker, T., Riutta, T., Malhi, Y., Svátek, M., Kvasnica, J., Burslem, D.F.R.P., Ewers, R.M., et al. (2021). The impact of logging on vertical canopy structure across a gradient of

tropical forest degradation intensity in Borneo. J. Appl. Ecol. *58*, 1764–1775. https://doi.org/10.1111/1365-2664.13895.

58. Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F., Chazdon, R.L., Farrior, C.E., Kambach, S., Meave, J.A., et al. (2021). Multidimensional tropical forest recovery. Science *374*, 1370–1376. https://doi.org/10.1126/SCIENCE.ABH3629/SUPPL_FILE/SCIENCE.ABH3629_SM.PDF.
59. Pfeifer, M., Gonsamo, A., Woodgate, W., Cayuela, L., Marshall, A.R., Ledo, A., Paine, T.C.E., Marchant, R., Burt, A., Calders, K., et al. (2018). Tropical forest canopies and their relationships with climate and disturbance: results from a global dataset of consistent field-based measurements. For. Ecosyst. *5*, 7–14. https://doi.org/10.1186/S40663-017-0118-7/FIGURES/4.
60. Cerullo, G.R., and Edwards, D.P. (2019). Actively restoring resilience in selectively logged tropical forests. J. Appl. Ecol. *56*, 107–118. https://doi.org/10.1111/1365-2664.13262.
61. Rezende, E.L., Bozinovic, F., Szilágyi, A., and Santos, M. (2020). Predicting temperature mortality and selection in natural Drosophila populations. Science *369*, 1242–1245. https://doi.org/10.1126/SCIENCE.ABA9287/SUPPL_FILE/ABA9287_REZENDE_REPRODUCIBILITY_CHECKLIST.PDF.
62. Halsch, C.A., Shapiro, A.M., Fordyce, J.A., Nice, C.C., Thorne, J.H., Waetjen, D.P., and Forister, M.L. (2021). Insects and recent climate change. Proc. Natl. Acad. Sci. USA *118*, e2002543117. https://doi.org/10.1073/PNAS.2002543117/SUPPL_FILE/PNAS.2002543117.SAPP.PDF.
63. Leong, C.M., Tsang, T.P.N., and Guénard, B. (2022). Testing the reliability and ecological implications of ramping rates in the measurement of Critical Thermal maximum. PLoS One *17*, e0265361. https://doi.org/10.1371/JOURNAL.PONE.0265361.
64. The MathWorks Inc (2022). MATLAB. https://www.mathworks.com.
65. Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L., and Turner, E.C. (2011). A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philos. Trans. R. Soc. Lond. B Biol. Sci. *366*, 3292–3302. https://doi.org/10.1098/rstb.2011.0049.
66. Pfeifer, M., Kor, L., Nilus, R., Turner, E., Cusack, J., Lysenko, I., Khoo, M., Chey, V.K., Chung, A.C., and Ewers, R.M. (2016). Mapping the structure of Borneo's tropical forests across a degradation gradient. Remote Sens. Environ. *176*, 84–97. https://doi.org/10.1016/J.RSE.2016.01.014.
67. Struebig, M.J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., and Bell, D. (2013). Quantifying the Biodiversity Value of Repeatedly Logged Rainforests: Gradient and Comparative Approaches from Borneo. Adv. Ecol. Res. *48*, 183–224. https://doi.org/10.1016/B978-0-12-417199-2.00003-3.
68. Fisher, B., Edwards, D.P., Larsen, T.H., Ansell, F.A., Hsu, W.W., Roberts, C.S., and Wilcove, D.S. (2011). Cost-effective conservation: calculating biodiversity and logging trade-offs in Southeast Asia. Conserv. Lett. *4*, 443–450. https://doi.org/10.1111/j.1755-263X.2011.00198.x.
69. Walsh, R.P., and Newbery, D.M. (1999). The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. Philos. Trans. R. Soc. Lond. B Biol. Sci. *354*, 1869–1883. https://doi.org/10.1098/rstb.1999.0528.
70. Ewers, R.M., and Banks-Leite, C. (2013). Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. PLoS One *8*, e58093. https://doi.org/10.1371/journal.pone.0058093.
71. Humes, K.S., Kustas, W.P., Moran, M.S., Nichols, W.D., and Weltz, M.A. (1994). Variability of emissivity and surface temperature over a sparsely vegetated surface. Water Resour. Res. *30*, 1299–1310. https://doi.org/10.1029/93WR03065.
72. Tattersall, G.J. (2016). Infrared thermography: A non-invasive window into thermal physiology. Comp. Biochem. Physiol. Mol. Integr. Physiol. *202*, 78–98. https://doi.org/10.1016/J.CBPA.2016.02.022.
73. Dillon, M.E., Wang, G., and Huey, R.B. (2010). Global metabolic impacts of recent climate warming. Nature *467*, 704–706. https://doi.org/10.1038/nature09407.
74. Ma, C.S., Ma, G., and Pincebourde, S. (2021). Survive a Warming Climate: Insect Responses to Extreme High Temperatures. Annu. Rev. Entomol. *66*, 163. https://doi.org/10.1146/annurev-ento-041520-074454.
75. Hijmans, R. (2025). raster: Geographic Data Analysis and Modeling, R package version 3.6-32.
76. Pincebourde, S., and Woods, H.A. (2020). There is plenty of room at the bottom: microclimates drive insect vulnerability to climate change. Curr. Opin. Insect Sci. *41*, 63. https://doi.org/10.1016/j.cois.2020.07.001.
77. Ashton, L.A., Nakamura, A., Basset, Y., Burwell, C.J., Cao, M., Eastwood, R., Odell, E., de Oliveira, E.G., Hurley, K., Katabuchi, M., et al. (2015). Vertical stratification of moths across elevation and latitude. J. Biogeogr. *43*, 59–69. https://doi.org/10.1111/jbi.12616.
78. Bruhl, C.A., Gunsalam, G., and Linsenmair, K.E. (1998). Stratification of ants (Hymenoptera , Formicidae) in a primary rain forest in Sabah , Borneo. J. Trop. Ecol. *14*, 285–297.
79. Lembrechts, J.J., Aalto, J., Ashcroft, M.B., De Frenne, P., Kopecký, M., Lenoir, J., Luoto, M., Maclean, I.M.D., Roupsard, O., Fuentes-Lillo, E., et al. (2020). SoilTemp: A global database of near-surface temperature. Glob. Change Biol. *26*, 6616–6629. https://doi.org/10.1111/gcb.15123.
80. Pincebourde, S., and Salle, A. (2020). On the importance of getting fine-scale temperature records near any surface. Glob. Change Biol. *26*, 6025. https://doi.org/10.1111/gcb.15210.
81. Davies-Barnard, T., Catto, J.L., Harper, A.B., Imron, M.A., and Frank van Veen, F.J. (2023). Future fire risk under climate change and deforestation scenarios in tropical Borneo. Environ. Res. Lett. *18*, 024015. https://doi.org/10.1088/1748-9326/ACB225.
82. Geiger, R. (1967). The climate near the ground. Q. J. R. Meteorol. Soc. *93*, 150. https://doi.org/10.1002/qj.49709339529.
83. Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., and Coomes, D. (2019). Advances in Microclimate Ecology Arising from Remote Sensing. Trends Ecol. Evol. *34*, 327–341. https://doi.org/10.1016/J.TREE.2018.12.012.
84. Saudreau, M., Ezanic, A., Adam, B., Caillon, R., Walser, P., and Pincebourde, S. (2017). Temperature heterogeneity over leaf surfaces: the contribution of the lamina microtopography. Plant Cell Environ. *40*, 2174–2188. https://doi.org/10.1111/PCE.13026.
85. Environnement Mediterranéen et Modélisation des Agro-Hydrosystèmes (2024). CAN-EYE. https://can-eye.paca.hub.inrae.fr/welcome.
86. Drinkwater, R., Williamson, J., Swinfield, T., Deere, N.J., Struebig, M.J., Clare, E.L., Coomes, D., and Rossiter, S.J. (2019). Occurrence of blood-feeding terrestrial leeches (Haemadipsidae) in a degraded forest ecosystem and their potential as ecological indicators. Biotropica. https://doi.org/10.1111/btp.12686.
87. Woon, J.S., Boyle, M.J.W., Ewers, R.M., Chung, A., and Eggleton, P. (2018). Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests. Insectes Soc. *66*, 57–64. https://doi.org/10.1007/s00040-018-0664-1.
88. Weaving, H., Terblanche, J.S., Pottier, P., and English, S. (2022). Meta-analysis reveals weak but pervasive plasticity in insect thermal limits. Nat. Commun. *13*, 5292. https://doi.org/10.1038/s41467-022-32953-2.
89. Terblanche, J.S., Deere, J.A., Clusella-Trullas, S., Janion, C., and Chown, S.L. (2007). Critical thermal limits depend on methodological context. Proc. Biol. Sci. *274*, 2935–2942. https://doi.org/10.1098/rspb.2007.0985.
90. R Core Team (2024). R: A Language and Environment for Statistical Computing. https://www.R-project.org.
91. Nakagawa, S., and Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. *4*, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.
92. Simpson, G. (2024). derivatives.R. https://github.com/gavinsimpson/gratia/blob/main/R/derivatives.R.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Ant CTmax	Zenodo	https://doi.org/10.5281/zenodo.4297673
Dung Beetle CTmax	Zenodo	https://doi.org/10.5281/zenodo.6477719
Termite CTmax	Zenodo	https://doi.org/10.5281/zenodo.1198695
Leech CTmax	Zenodo	https://doi.org/10.5281/zenodo.2536269
Software and algorithms		
R version 3.4.1	R Core Team[63]	https://www.r-project.org
MATLAB (v R2018b)	The MathWorks, Inc.[64]	https://www.mathworks.com/products/matlab.html
CAN-EYE (v 6.3.8)	EMMAH[64]	https://can-eye.paca.hub.inrae.fr
Global LAI Project	Pfeifer[37]	https://globallai.wordpress.com

METHOD DETAILS

Study site

All data were collected in the Stability of Altered Forest Ecosystems (SAFE) project experimental area[65] and Maliau Basin Conservation Area in Sabah, Malaysian Borneo. We selected six sampling blocks structurally representing humid tropical rainforests and the disturbances they have been facing over large parts of their distribution. These fell within old-growth dipterocarp rainforest at Maliau Basin Conservation Area (2 blocks), selectively logged forest within the Ulu Segama Forest Reserve (1 block), and salvage logged forest within the Kalabakan Forest Reserve (3 blocks). Sampling blocks in old-growth forest had never been logged, with an average aboveground biomass of 400 $t.ha^{-1}$ and average canopy cover of 80 %.[66] The Ulu Segama logged forest block was initially logged in the 1970s and then re-logged between 2000 and 2008, removing around 150 m^3 of timber per hectare, or ∼50 % of the original aboveground biomass.[66,67] Kalabakan logged blocks were also initially logged in the 1970s and then underwent three rounds of extraction between 2000 - 2008, removing a cumulative total of up to 179 m^3 of timber per hectare, or roughly 75 % of the original above ground biomass.[22,67] As such, sites within logged forest covered a gradient from lightly to heavily disturbed in comparison to regional averages.[68] The elevation of sampling locations at the SAFE project is standardised, with mean elevation of 450 m and an interquartile range of 72 m. The local climate is relatively aseasonal, with no distinct wet or dry season.[69] No forest plots at the SAFE project lie less than 50m from a forest edge, therefore there were no microclimatic edge effects to account for in our study.[70]

Microclimate

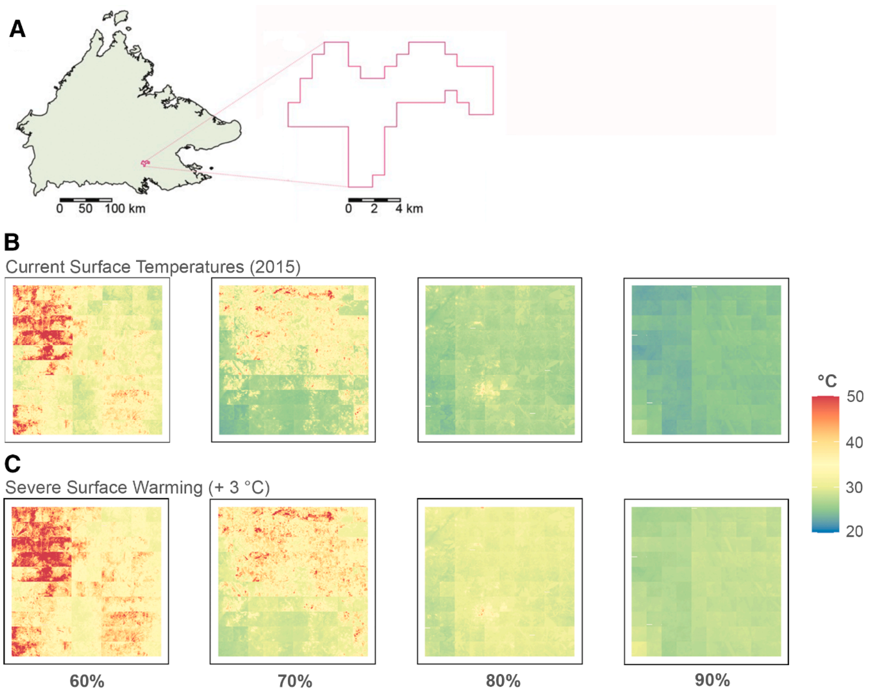
Sampling blocks were separated by a minimum of 1,780 m and within each block we established three microclimate plots, which were separated by a minimum of 178 m. One plot within one of the old-growth forest blocks was deemed unsafe because of landslide risk, resulting in data being collected from a total of 17 plots (5 old-growth, 3 selectively logged, 9 salvage logged). At each plot we set up a 5 x 5 m grid that was divided into 50 x 50 cm subplots. We used a thermal imaging camera (Flir E6) pointing directly downwards over each subplot from a height of 1.2 m, resulting in 100 images per plot. We retained the factory emissivity settings of 0.95 on the camera, which falls within the range of emissivity values of bare sandy soil (0.93) partial vegetation cover (0.96) and green vegetation (0.98)[71] that were found across all sampling plots. The camera calibration was checked by pointing the camera at two surfaces with known temperatures: the surface of a pan of gently simmering water and a bowl of ice cubes. The camera we used provides accurate recordings within the range of air temperatures experienced at all our sites, and the effect of relative humidity is minor at imaging distances between camera and subject below 10 meters.[72] As such, no post-hoc image correction was necessary prior to analysis. We took all images between 11:00 and 13:00, as temperatures during the hottest part of the day are likely to have the strongest ecological filtering effects,[73,74] however it is worth noting that patterns reported here may be different for nocturnal species that do not shelter in the open during the day. Each photo was paired with an ambient temperature recording using a thermocouple held next to the camera at 1.2 m above the ground. Thermal imaging and ambient temperature recording were repeated for each plot on ad-hoc random days when the weather was neither raining, overcast nor completely clear from June – September 2017, leading to 17 x 3 samples (N = 51).

Thermal images were converted into data matrices with each pixel representing a numeric temperature recording. These matrices were cropped to the central 200 x 200 cells which matched the 50 x 50 cm subplot located in the centre of each image (Figure S1). This returned 4,000,000 pixels per plot per day, leading to a total of 204,000,000 temperature recordings. Cropped matrices from adjacent subplot images were joined into a single matrix covering the 5 × 5 m grid, and the spatial resolution was reduced by a factor of 10 using a nearest neighbour interpolation in the package 'raster'.[75] Reducing spatial resolution resulted in temperature measurements recorded at a resolution of 2.5 x 2.5 mm, which we considered relevant to the scale of small-bodied invertebrates.[76] While the relationship between surface temperatures and invertebrate thermal limits is likely to vary with behavioural and physiological traits, fine scale surface temperatures are likely to be more directly linked to the temperature experienced by many tropical invertebrates than ambient air temperatures,[24] which fail to capture the highly heterogenous microscale climate conditions available to these very small-bodied organisms.[33]

The resulting raster layers represent the 2D thermal landscape of 5 x 5 m of forest floor and ground layer vegetation at each plot. This is a simplification of the highly complex 3-dimensional habitat of the rainforest floor, but nonetheless represents an ecologically relevant space that is widely exploited by many invertebrate species, which in tropical forests are highly constrained to specific forest strata.[77,78] For each 5 x 5 m sampling plot we extracted mean surface temperature, maximum surface temperature, mean ambient temperature and maximum ambient temperature across all 100 images. Therefore the 'mean' temperature referred to here is the mean of temperatures recorded during the hottest period of the day rather than the overall mean. For maximum surface temperatures we used the mean of the top 1% of temperature measurements to protect against single pixel aberrations or extreme temperatures erroneously inflating values.

Simulated warming

No database of predicted future soil or leaf surface temperatures currently exists.[79,80] We therefore directly applied two potential warming scenarios of +1°C (moderate warming) and +3°C (severe warming) to surface temperatures at our sites (Below figure). Global analyses indicate that very small increases (less than 1°C) have already occurred under some tropical forest canopies,[20] and regional climate models suggest that the air temperature in Borneo is likely to increase by 3-3.5°C by 2100 under the most extreme emissions scenarios.[81] However, the relationship between air and surface temperatures may not be linear and is likely to depend heavily on biome characteristics.[79] For example, surface temperatures in grasslands are driven mostly by direct solar radiation,[82] whereas in forests they are driven by a complex relationship between radiative heating of the canopy, which in turn heats lower forest strata though convective heating of the sub-canopy air and direct conductance between touching substrates.[79,83] Plant leaves are also able to regulate their temperature, which can be highly heterogenous over the leaf surface.[84] The ability of plants to control leaf temperature can however be diminished by environmental stress such as reduced water availability,[70] adding further uncertainty to how surface temperatures in a forest may change along a gradient of disturbance in the future.



Example surfaces generated from thermal imaging and simulated warming

(A) The location and scale of the SAFE project experimental area in Sabah, Malaysian Borneo and (B) Example composite thermal images of surface temperatures within forest sites at 60%, 70%, 80%, and 90% canopy closure both in the present and (C) when severe warming scenario of +3°C had been applied.

Canopy cover

At each plot we expanded a 20 x 20 m grid around the 5 x 5 m thermal image grid and acquired hemispherical images through a digital camera equipped with a fisheye lens installed on a tripod at 1 m above ground looking vertically upward. Fifteen images were taken throughout each plot to encompass the area of canopy and sky that would influence the 5 x 5 m thermal image grid (Figure S2). Fisheye images were processed in MATLAB (v R2018b)[64] using algorithms developed by the Global LAI Project[66] (https://globallai.wordpress.com/publications/). Canopy cover was estimated from the processed fisheye images at plot level using the freeware CAN-EYE (v 6.3.8).[85] Repeated measures of canopy openness were taken at each microclimate grid on the same days that microclimate values were recorded (N = 51).

Invertebrate CT*max*

Live invertebrates (termites, leeches, dung beetles, ants, moths and non-coprophagic beetles) were collected from across the study area between 2014 – 2018, encompassing the same time-period during which microclimate and canopy measurements were taken. These taxa were chosen to represent a diversity of trophic levels and ecosystem functions. In 2016 there was a drought event in Borneo related to El Niño, during which the field station closed and therefore no thermal limit nor microclimate data were collected during this weather anomaly. The invertebrate groups in our study occur on the surfaces of the forest floor and understory vegetation during the day. Leeches were collected using manual searching, ants were collected from manual searching on the ground and understory vegetation layer and by using bait-cards, dung beetles were captured in pitfall traps baited with human dung, and moths and non-coprophagic beetles were captured using light traps. Dung beetles and leeches were identified to species,[49,86] ants and termites to genus,[10,87] moths to family, and non-coprophagic beetles were left unidentified. In total we included data from 5038 individual invertebrates from 129 individual taxa: 2359 ants (50 genera, mean = 47 individuals per genus), 1305 termites (15 genera, mean = 87 individuals per genus), 543 dung beetles (44 species, mean = 12 individuals per species), 39 leeches (2 species, mean = 20 individuals per species), 424 moths (17 families, mean = 26 individuals per family) and 368 non-coprophagic beetles (unknown number of species).

Ants were collected from across all forest types; termites, moths and non-coprophagic beetles were only collected from old growth forest sampling points; and dung-beetles and leeches were only collected from selectively logged and salvage logged forest sampling points. Our previous work indicates that forest microclimate predominantly alters invertebrate community composition at these sites via shifts in relative abundance rather than via changes in the presence and absence of taxa.[10,49] The degree of thermal plasticity within our sites is also expected to be small,[49] a pattern that is generalisable throughout ectotherms globally.[88] Therefore, while the mean assemblage CT*max* of species communities used here is likely to be representative across sites in the short term, it is possible that plasticity or thermal adaptation may moderately increase the resilience of native invertebrates over longer timescales.

We measured thermal limits using a ramping procedure. Individuals were placed in vials or Falcon tubes and submerged in a water bath (Grant TXF 200) set to 32°C. After a five-minute period to allow the air temperature in the vials to match that of the water, temperature was ramped upwards. The rate of ramping was 0.2°C per minute for ants, termites, moths, and non-coprophagic beetles, and 0.1°C per minute for leeches and dung beetles. The procedure started at 32°C as this was the common daytime temperature of the laboratory, and the slow ramping speed ensured that the temperature experienced within vials matched the temperature of the water, measured using a thermocouple placed within a vial during calibration runs. For all taxa, *CTmax* was defined as the temperature at which individuals lost the ability to respond to stimulus, assuming that an inability to move represented ecological death. For ants, beetles, termites, and moths the vial was manipulated to move the individual insect or turn it on its back. If no response of the invertebrate was detected after manipulation, the temperature was recorded as *CTmax*. A similar approach was taken for leeches, but instead of movement we monitored their ability to adhere to the inside of the vial. If the vial was turned and the leech was unable to adhere to the internal surface the temperature was recorded as CT*max.* Ramping procedures have been shown to give variable estimates of CT*max* depending on ramping speed,[89] with a 0.1°C per minute increase in ramping speed expected to increase CT*max* estimates by 0.3°C in tropical invertebrates.[63] In our study leeches and dung beetles have the lowest recorded CT*max* among groups and were both ramped at 0.1°C per minute slower rates. However, increasing their CT*max* by 0.3°C in line with the expected difference incurred from a faster ramping rate would still place these two groups as the most thermally sensitive, and such a change would not affect our results or conclusions.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were carried out in R version 3.4.1.[90] First, we rescaled our canopy closure variable to be centred around a mean of 0 and used linear mixed-effects regression (LMER) to test for differences in mean temperature generated from air or surface methods. We fitted two models, one including sampling method (air or surface) and canopy closure as interacting terms, and one without an interaction. We then compared these two models (with and without the interaction term) using likelihood-ratio tests to test for differences in the relationship between canopy closure and temperatures measured using air or surface methods. We included plot identity as a random effect to account for repeated measures from the same plots on different days. We repeated the above analysis using maximum temperatures. Maximum temperatures did not conform to assumptions of normality, and so we fitted generalized linear mixed-effects regression models (GLMER), specifying a Gamma error distribution and logarithmic link function.

For all models we extracted both conditional and marginal R^2 values to compare the relative variation explained by random and fixed effects.[91] For LMER the R^2 values were calculated using the delta method, and for GLMER we used trigamma estimation. All p values reported are from likelihood-ratio tests, and reported slopes and standard errors have been back transformed to the original scale of canopy closure (%).

Next, we examined the relationship between the spatial coverage of surface temperatures and CT*max* of invertebrate groups across the disturbance gradient. To calculate the amount of surface area exceeding CT*max* we generated kernel density estimations across all the surface temperature recordings from each 5 x 5 m plot. We then calculated the area under the curve (AUC) of the smoothed kernel plot corresponding to the temperatures exceeding the mean CT*max* for each group. We repeated this step using current surface temperatures and those predicted using future climate change scenarios. As such, one value was generated for each invertebrate taxon per 5 x 5m sampling plot, which can be interpreted as the percentage total surface area exceeding CT*max* within each 5 x 5m plot. Using these values as our response variable, we then fitted generalised additive mixed models (GAMM) to examine the relationship between canopy closure and the amount of surface area exceeding CT*max,* with plot identity included as a random effect. Three GAMMs were fitted for each invertebrate group, representing the time periods 2015, 2021-2040, 2061-80. To interpret these models, we calculated and compared first derivatives of the splines using the package derivatives.R,[92] estimating the 95% confidence interval around 200 segments of the predicted line. If the confidence interval at a given point overlapped with 0, that point on the line was considered non-significant; conversely if it did not overlap with 0 it was considered significant. Segments of the predicted lines that were significant therefore define the threshold of canopy cover beyond which temperatures were significantly likely to exceed CT*max* for each invertebrate group over more than 1 % of the recorded surface area.