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DECOMPOSITION

Termite sensitivity to temperature affects global wood decay rates

Amy E. Zanne^{1,2*}, Habacuc Flores-Moreno³, Jeff R. Powell⁴, William K. Cornwell⁵, James W. Dalling^{6,7}, Amy T. Austin⁸, Aimée T. Classen⁹, Paul Eggleton¹⁰, Kei-ichi Okada¹¹, Catherine L. Parr^{12,13,14}, E. Carol Adair¹⁵, Stephen Adu-Bredu^{16,17}, Md Azharul Alam¹⁸, Carolina Alvarez-Garzon¹⁹, Deborah Appau²⁰, Roxana Aragón²¹, Marcelo Ardon²², Stefan K. Arndt²³, Louise A. Ashton²⁴, Nicholas A. Barber²⁵, Jacques Beauchêne²⁶, Matty P. Berg^{27,28}, Jason Beringer²⁹, Matthias M. Boer⁴, José Antonio Bonet³⁰, Katherine Bunney¹³, Tynan J. Burkhardt³¹, Dulcinéia Carvalho³², Dennis Castillo-Figueroa^{33,34}, Lucas A. Cernusak³⁵, Alexander W. Cheesman³⁵, Tainá M. Cirne-Silva³², Jamie R. Cleverly³⁵, Johannes H. C. Cornelissen³⁶, Timothy J. Curran¹⁸, André M. D'Angioli³⁷, Caroline Dallstream³⁸, Nico Eisenhauer^{39,40}, Fidele Evouna Ondo⁴¹, Alex Fajardo⁴², Romina D. Fernandez²¹, Astrid Ferrer⁶, Marco A. L. Fontes³², Mark L. Galatowitsch⁴³, Grizelle González⁴⁴, Felix Gottschall⁴⁵, Peter R. Grace⁴⁶, Elena Grandá⁴⁷, Hannah M. Griffiths¹², Mariana Guerra Lara⁸, Motohiro Hasegawa⁴⁸, Mariet M. Hefting⁴⁹, Nina Hinko-Najera⁵⁰, Lindsay B. Hutley⁵¹, Jennifer Jones⁶, Anja Kahl⁵², Mirko Karan^{35,53}, Joost A. Keuskamp^{54,55}, Tim Lardner²⁹, Michael Liddell³⁵, Craig Macfarlane⁵⁶, Cate Macinnis-Ng³¹, Ravi F. Mariano³², M. Soledad Méndez⁸, Wayne S. Meyer⁵⁷, Akira S. Mori⁵⁸, Aloysio S. Moura³², Matthew Northwood⁵¹, Romã Ogaya⁵⁹, Rafael S. Oliveira⁶⁰, Alberto Orgiazzi⁶¹, Juliana Pardo⁶², Guille Peguero^{63*}, Josep Penuelas^{64,65}, Luis I. Perez⁸, Juan M. Posada⁶⁶, Cecilia M. Prada⁶⁷, Tomáš Přívětivý⁶⁷, Suzanne M. Prober^{56,68}, Jonathan Prunier⁶⁹, Gabriel W. Quansah⁷⁰, Víctor Resco de Dios^{71,72}, Ronny Richter^{52,73,74}, Mark P. Robertson¹³, Lucas F. Rocha³², Megan A. Rúa⁷⁵, Carolina Sarmiento^{7,76}, Richard P. Silberstein^{77,78}, Mateus C. Silva⁷⁹, Flávia Freire Siqueira³², Matthew Glenn Stillwagon²², Jacqui Stol⁸⁰, Melanie K. Taylor^{81,82}, François P. Teste⁸³, David Y. P. Tng²⁰, David Tucker⁴⁶, Manfred Türke^{39,40}, Michael D. Ulyshen⁸¹, Oscar J. Valverde-Barrantes⁸⁴, Eduardo van den Berg⁷⁹, Richard S. P. van Logtestijn⁸⁵, G. F. (Ciska) Veen⁸⁶, Jason G. Vogel⁸⁷, Timothy J. Wardlaw⁸⁸, Georg Wiehl⁵⁶, Christian Wirth^{52,73}, Michaela J. Woods⁷⁵, Paul-Camilo Zalamea^{7,76}

Deadwood is a large global carbon store with its store size partially determined by biotic decay. Microbial wood decay rates are known to respond to changing temperature and precipitation. Termites are also important decomposers in the tropics but are less well studied. An understanding of their climate sensitivities is needed to estimate climate change effects on wood carbon pools. Using data from 133 sites spanning six continents, we found that termite wood discovery and consumption were highly sensitive to temperature (with decay increasing >6.8 times per 10°C increase in temperature)—even more so than microbes. Termite decay effects were greatest in tropical seasonal forests, tropical savannas, and subtropical deserts. With tropicalization (i.e., warming shifts to tropical climates), termite wood decay will likely increase as termites access more of Earth's surface.

Forested systems contain ~676 billion metric tons (Gt) of biomass (1), with a large fraction of their carbon immobilized for centuries in living wood and deadwood (2, 3). Carbon storage depends partly on decay rates of deadwood pools by organisms, which vary across climatic gradients (4, 5). Regional studies have suggested that wood decay by microbes approximately doubles with a 10°C temperature increase (decay effective $Q_{10} = \sim 2$, where Q_{10} is the increase in rate of a chemical reaction or biological process for each 10°C increase in temperature) (2, 6) driven, in part, by enzyme kinetics. Further, microbial decay occurs through extracellular enzymes, whose delivery is dependent on moisture (7, 8), which means that microbial wood decay should increase with humidity. Less is known about the climate sensitivities of important animal decayers, which also influence how climate change affects deadwood carbon stores.

Increasing evidence shows that termites are important decayers at local to regional scales (7, 9, 10). The abundance of wood-feeding termites across biomes is poorly understood (11), but decay by termites should be temperature sensitive. Termites increasingly contribute to wood decay in warm locations (12–14), with distributions set in part by ectothermic temperature tolerances (15). Termite wood decay depends on both discovery and consumption of wood by searching animals, followed by chemical decay through a cultivated set of microbial symbionts. Therefore, this symbiont chemical decay will also be shaped by temperature-dependent enzyme kinetics. In contrast to microbes, termites are likely less sensitive to moisture. Termites have a diversity of adaptations to conserve moisture, which presumably buffers their sensitivities to low precipitation (16–18). In other words, termite discovery and decay should continue with increasing aridity.

To test climate sensitivities of termite and microbial wood decay, we conducted a replicated experiment at 133 sites across extensive temperature and precipitation gradients representing most of the global bioregions (Fig. 1). At each site, researchers monitored decay of wood blocks for a common substrate, *Pinus radiata* [or, in a few cases, closely related *Pinus* species; (19)], for up to 48 months. All sites had harvests at ~12 months and most at ~24 months, with some sites including ~6-month, ~36-month, and/or ~48-month harvests. We allowed microbial access to all samples and manipulated termite access (“microbes” versus “microbes + termites” treatments); wood blocks were wrapped in fine mesh with or without larger holes to allow or exclude termites. At each site, researchers placed pairs of treatment blocks with the number of pairs equal to the number of harvests planned at each of 20 stations (a few sites placed fewer stations), which meant that each harvest from a site had 40 wood blocks [mean = 33.6 ± 14.2 (1 SD)] harvested at a given time point across both treatments. Stations were spaced at least 5 m apart (19) (table S11). A total of 8922 blocks were collected across all sites. Our focal species, *P. radiata*, was nonnative at all locations, which meant that no site decay agents evolved with it as a substrate.

Termite discovery (i.e., the estimated percentage of wood blocks with evidence of termites per year at a site) was greatest, but also highly variable, at low latitudes and elevations and where temperature and precipitation were high (Fig. 1, A and B; fig. S1; and table S1); low latitudes and elevations represent these warmer climates. High wood block discovery (>50%) occurred at temperatures above 21.33°C. In multivariate models, wood block discovery by termites rapidly increased with increasing temperatures (Fig. 2A and table S3), and temperature and precipitation significantly interacted (Fig. 1B, Fig. 2A, and table S3). Termite discovery was higher in warm tropical biomes in arid and semiarid sites (despite small sample sizes) compared with mesic and humid sites (at 25°C, discovery estimates at 250 mm were 1.4 times as high as those at 2000 mm and 1.9 times as high as those at 2700 mm), whereas in cool temperate biomes, the reverse patterns were observed (at 7°C, discovery estimates at 2700 mm were 4 times as high as those at 2000 mm and 150 times as high as those at 250 mm).

Microbial wood decay was fastest at low latitudes and elevations and where temperature and precipitation were high, although latitude and precipitation were weaker predictors than elevation and temperature (Fig. 1C, fig. S2, and table S2). Microbial temperature sensitivity was similar to that observed in regional studies [decay effective Q_{10} of 1.73; 95% confidence interval (CI), 1.44 to 2.09] (2, 6). In multivariate

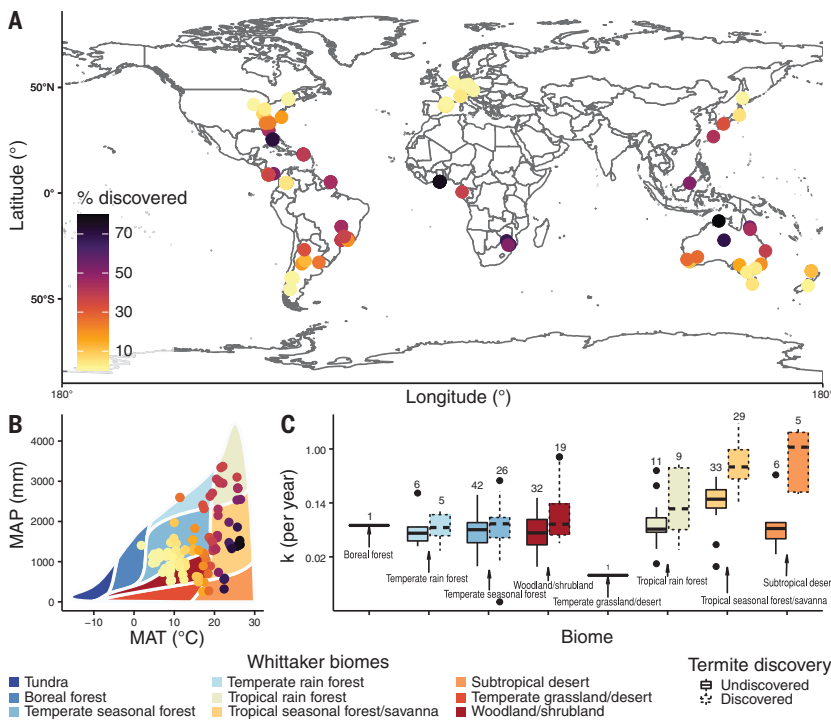


Fig. 1. Geographic, biome, and climatic distribution of experimental sites. (A) Dots denote the 133 study site locations. (B) Study site distribution across mean annual temperatures (MATs), mean annual precipitations (MAPs), and Whittaker biomes (24). In (A) and (B), the color of the dots represents termite discovery rate (i.e., estimated percentage of wood blocks with evidence of termites per year at a site). (C) Decay rate (k) estimates across Whittaker biomes [shown by arrows and colors matching the legend for (B)], with boxplots for each biome representing blocks discovered by termites (dashed boxplots on the right side of each pair) and blocks undiscovered by termites (solid boxplots on the left side of each pair) (examples of discovered blocks are given in fig. S3). The y axis is \ln -transformed, but tick labels represent untransformed values for decay. For the boxplots, center line indicates the median, box limits indicate upper and lower quartiles, whiskers indicate the 1.5 \times interquartile range, and points indicate outliers. Numbers on top of the solid boxplots indicate the total number of sites per biome, and numbers on top of the dashed boxplots indicate the number of sites where termite discovery occurred.

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models, precipitation was not a significant predictor of microbial decay (Fig. 2B and table S4). When termites discovered wood, decay rates were higher at low elevations and where temperature was high (Fig. 1C, fig. S2, and table S2). Further, decay rates in termite-discovered wood were more sensitive to changes in temperature (decay effective Q_{10} of 6.85; 95% CI, 4.73 to 9.92) compared with decay rates in undiscovered wood, where microbes dominated decay. In multivariate models, precipitation was not

a significant predictor of decay for termite-discovered wood (Fig. 2C and table S5).

The termite-discovered wood decay effective Q_{10} is much steeper than any previously recorded for microbes (2, 6), which suggests that a different mechanism determines termite versus microbial wood decay. The observed high consumption rate by termites at warm sites may be related to termite assemblage composition, large population numbers, high activity, or some combination of these mech-

anisms. Consequently, subtropical, tropical, or global models using a single microbial-derived decay effective Q_{10} are likely to (i) underpredict wood decay, (ii) overpredict terrestrial carbon storage (all else being equal—e.g., inputs into deadwood pools), and (iii) underpredict temperature sensitivity of decay. Use of termite-corrected decay effective Q_{10} values, which may vary on the basis of termite assemblage composition, location, and/or wood substrate, should improve the accuracy of modeled wood decay under current and future climate predictions. Such model modifications can capitalize on empirical measures in the literature, such as ours for termites and (20) for insects more broadly. Our results suggest that precipitation variation influences the discovery, but not the decay, phase of termite wood decay. However, strong temperature and precipitation interaction influences on discovery mean that termites increased overall decay most in subtropical deserts and tropical seasonal forests and savannas (Fig. 1C). Further, even though microbial abundance is sensitive to precipitation (4, 5), temperature was a stronger driver than precipitation for microbial-driven decay, perhaps mediated through effects on enzyme kinetics (21). Differences in decay sensitivity to precipitation were small, with only microbial-mediated wood decay weakly sensitive to precipitation; microbial decay largely occurs through the release of moisture-sensitive extracellular enzymes (7, 8), whereas termites can conserve moisture, buffering aridity effects (16–18). Although low termite discovery in warm humid locations remains surprising, competitive interactions among decayers (11, 13), biome-specific adaptations to moisture, variation in resource availability affecting foraging behavior, etc., may reduce discovery.

Given the high sensitivities of both termite wood discovery and decay to temperature, termites will likely expand their range in a warming world, with important consequences for carbon cycling. Using data-driven estimates of temperature and precipitation effects on termite discovery (table S3), we estimated discovery rates across the globe, restricting predictions to the range in mean annual precipitation covered by our sites $\pm 10\%$. Termites today have the potential to discover large amounts of deadwood (>50%) at sites across 30.2% of the land surface (assuming our estimated discovery rates apply across wood and termite species; Fig. 3). To bracket potential climate change effects on discovery, we used our estimated climate relationships with all available midcentury Coupled Model Intercomparison Project 6 (CMIP6) climate models for shared socioeconomic pathway (SSP) scenarios 1-2.6 and 5-8.5 (22). All scenarios predicted an expansion of termite discovery in tropical and subtropical regions, with the degree of expansion depending strongly

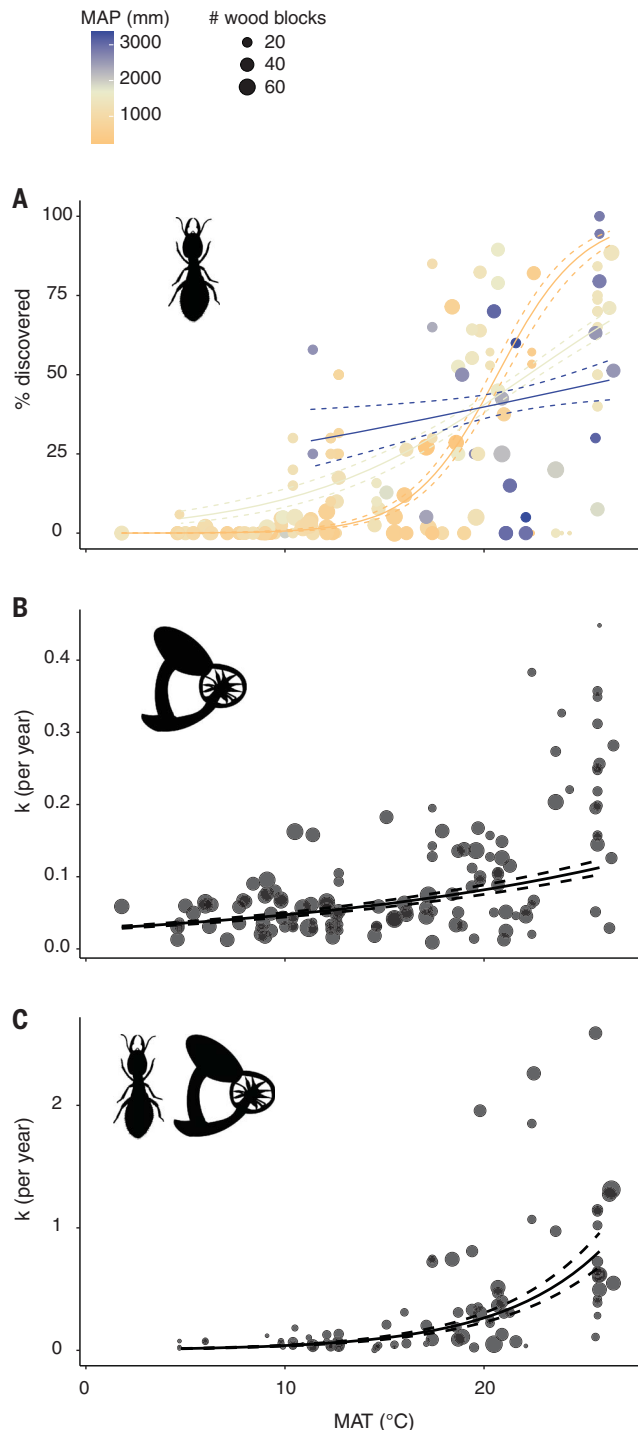
Fig. 2. Discovery and decay of wood based on significant climatic predictors. See tables S3 to S5 for full models.

(A) Termite discovery rate;

the estimated percentage of wood blocks in the microbes + termites treatment across all sites with evidence of termites per year, across MAT and MAP. (B) Decay rates of termite-undiscovered wood across MAT.

(C) Decay rates of termite-discovered wood across MAT (note, MAP was not a significant predictor of termite-undiscovered or -discovered wood decay). Dot size represents

number of wood blocks. Symbols in the upper left corner of each plot denote the role of wood-feeding termites and/or wood-dwelling microbes. Solid lines represent logistic (A) or linear [(B) and (C)] regression predictions and [for (A)] those at 250-mm MAP (orange; representative of mean desert and savanna biomes), 2000-mm MAP (cream; representative of mean temperate biomes), and 2700-mm MAP (blue; representative of mean tropical and temperate humid biomes). Dashed lines represent 95% CIs around predictions. The y axes for (B) and (C) are ln-transformed, but tick labels represent untransformed values for decay.



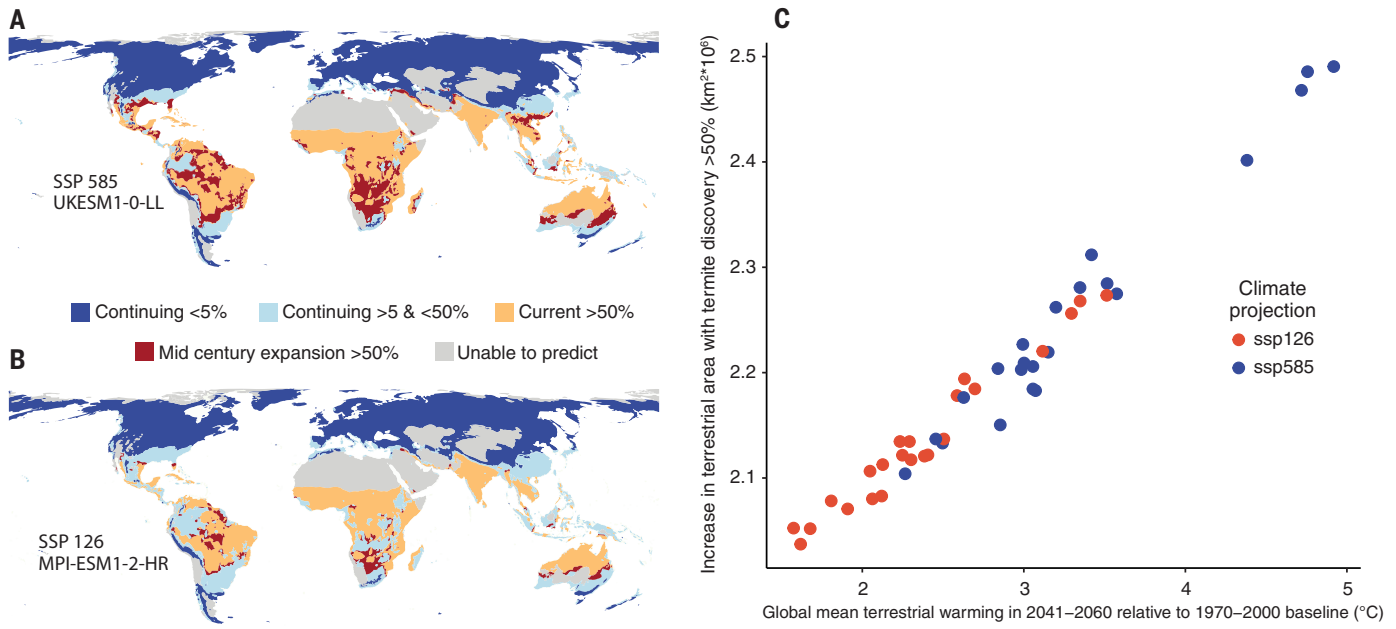


Fig. 3. Predicted termite discovery by midcentury under different climate projections. Global maps showing minimum and maximum termite expansion scenarios based on the model in table S3 and CMIP6 forecasts for 2041 to 2060. (A and B) Stronger climate change scenarios (SSP 5-8.5 UKESM1-0-LL) had the largest expansion in discovery rates (A), and weaker climate change scenarios (SSP 1-2.6 MPI-ESM1-2-HR) had the smallest (B). Termite discovery categories were rare (<5%, blue), continuing low (>5% and <50%, light blue), current high (>50%, orange), midcentury expansion to high (>50%, red), and unable to

predict (gray), restricting predictions to the range in MAP covered by our sites ($\pm 10\%$). We did not model the transitions from rare (<5%, blue) to continuing low (>5% and <50%, light blue) discovery. (C) Forecast increases in terrestrial area (in square kilometers) with discovery >50% by midcentury versus forecast mean terrestrial warming relative to a historical baseline. Each point denotes a forecast based on one individual CMIP6 SSP 5-8.5 (blue) or SSP 1-2.6 (red) climate model. The x axis of (C) is the mean forecast of 2041 to 2060 warming above the 1970 to 2000 baseline for terrestrial areas only.

on the extent of global terrestrial warming (Fig. 3). Warming shifts to more tropical climates are occurring in many ecosystems (23), and temperature sensitivities demonstrated in this study suggest that termite contributions to wood decay will expand both within and beyond the tropics with such tropicalization. Our estimates may even underpredict termite effects in areas where fungus-growing termites occur (i.e., Africa and Asia) (12, 16), which merits future research. The impact of termites on wood decay is both large and expected to increase (Fig. 3), and it also has a different functional form than microbial decay, with a clear two-step process—discovery and decay.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Figs. S1 to S4

Tables S1 to S12

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Termite sensitivity to temperature affects global wood decay rates

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Heat-dependent wood decay

Decomposition rates vary with temperature and precipitation, in part because of the effects of climate on decomposer organisms. Although microbes are widely recognized as decomposers, animals such as insects also play a key role in tropical systems. Zanne *et al.* replicated an experiment at 133 global sites to quantify climate-related variation in wood decomposition by both microbes and termites. Climate influenced both microbial and termite decomposition, but termite presence and activity were more sensitive to temperature. Termites may thus play a larger role in global wood decomposition as the climate warms. —BEL

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