

Temperature sensitivity of termites determines global wood decay rates

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Abstract

Animals, such as termites, have largely been overlooked as global-scale drivers of biogeochemical cycles^{1,2}, despite site-specific findings^{3,4}. Deadwood turnover, an important component of the carbon cycle, is driven by multiple decay agents. Studies have focused on temperate systems^{5,6}, where microbes dominate decay⁷. Microbial decay is sensitive to temperature, typically doubling per 10°C increase (decay effective $Q_{10} = \sim 2$)⁸⁻¹⁰. Termites are important decayers in tropical systems^{3,11-13} and differ from microbes in their population dynamics, dispersal, and substrate discovery¹⁴⁻¹⁶, meaning their climate sensitivities also differ. Using a network of 133 sites spanning 6 continents, we report the first global field-based quantification of temperature and precipitation sensitivities for termites and microbes, providing novel understandings of their response to changing climates. Temperature sensitivity of microbial decay was within previous estimates. Termite discovery and consumption were both much more sensitive to temperature (decay effective $Q_{10} = 6.53$), leading to striking differences in deadwood turnover in areas with and without termites. Termite impacts were greatest in tropical seasonal forests and savannas and subtropical deserts. With tropicalization¹⁷ (i.e., warming shifts to a tropical climate), the termite contribution to global wood decay will increase as more of the earth's surface becomes accessible to termites.

Main Text

Future terrestrial carbon (C) storage depends on rates of biogeochemical cycling determined by biotic drivers, including animals². Nonetheless, the role of the decomposer macrofauna such as termites, and their sensitivity to climate factors is largely overlooked^{1,2}. Forests contain ~676 Gt of biomass¹⁸⁻²⁰, with a large fraction of the C they contain immobilized for centuries in living and dead wood^{10,21}. With rapid climate shifts, the amount, quality and distribution of wood is changing across the planet²²⁻²⁴. Wood decomposition will also respond to these shifts, driven by wood-dwelling microbes around the world and wood-feeding termites in the subtropics and tropics^{3,4,11-13,25}. The sensitivities of these biotic decay agents to temperature and precipitation will play a key role in determining the C balance of terrestrial ecosystems, i.e., if C is stored or lost as the world warms.

Such decomposition sensitivities are critical parameters in global C models²⁶. Existing models that include wood decay are built on a soil microbial paradigm^{5,6,27} that is applied to deadwood, as most studies of deadwood turnover have been conducted in temperate or boreal forest systems where microbes dominate the decay trajectory^{28,29} and termites are sparse or absent^{7,16,30}. Regional-scale studies suggest that microbial decay approximately doubles with a 10°C temperature increase (decay effective $Q_{10} = \sim 2$) for soil, litter and wood⁸⁻¹⁰. However, in the subtropics and tropics where wood is an especially large C store³¹⁻³⁴, termites can be critical contributors to wood decay^{4,29,35}, but their role at global scales is largely overlooked¹.

Toward broadening our quantitative understanding of how these two biotic decay agents may respond to a warming world, e.g., 2°C increase by mid century (Paris Agreement, 2015), we developed predictions about microbe and termite temperature and precipitation sensitivities.

(1) *Temperature-sensitivity*: Microbial decay of wood occurs locally via extracellular enzymes, subject to temperature-dependent enzyme kinetics³⁶. We predicted that global rates of microbial decay will be in line with local estimates (decay effective $Q_{10} = \sim 2$)⁸⁻¹⁰. Termite decay of wood, depends on both discovery and consumption by searching ectothermic animals sensitive to temperature, followed by chemical decay by a cultivated set of symbionts. While we lack local decay effective Q_{10} estimates for termites, we predicted both discovery and decay by termites will depend on termite population dynamics (numbers and activity patterns) and enzyme kinetic responses to temperature.

(2) *Precipitation-sensitivity*: Microbial activity and substrate access are dependent on moisture³⁷⁻⁴⁰. We predicted microbial decomposition will be highest in humid locations. Termites have a range of adaptations to conserve moisture buffering termite decay responses to low precipitation⁴¹⁻⁴³. While termite abundance is known to be high in the humid tropics^{13,30}, little is known about wood feeding termite abundance across biomes⁴⁴. We predicted termite discovery and decay to be less sensitive to precipitation than wood-dwelling microbes.

To test sensitivities, we conducted a replicated wood decomposition experiment that allowed microbial access (=microbes) to all samples and manipulated termite access (=microbes+termites) at 133 sites across extensive temperature and precipitation gradients representing most bioregions globally (Figure 1). At each site, researchers typically placed 40 blocks (mean = 34.3 ± 14.6 (1SD)) with 20 per treatment per harvest at 20 stations with stations spaced ≥ 5 m apart (see Methods, Supplementary Table S1). In total, we monitored decay in 8,869 wood blocks of a common substrate, *Pinus radiata* (or in a few cases closely related *Pinus* species; see Methods), wrapped in fine mesh with and without larger holes to allow or exclude termites for up to 48 months. Our focal wood species, *P. radiata*, was novel at all locations allowing us to disentangle substrate-decay agent history³⁵.

Wood-feeding termites were largely, but not solely, a tropical phenomenon. Termite discovery (i.e., percentage of wood blocks with evidence of termites per site and time point) was greatest, but also highly variable, at low latitudes and elevations and where temperature and precipitation were high (Figure 1A, B, Extended Data Figure 1; Extended Data Table 1). Similarly, microbial decomposition was fastest at low latitudes and elevations and where temperature and precipitation were high, although latitude and precipitation were weaker predictors (Figure 1C, Extended Data Figure 2; Extended Data Table 2). When termites discovered wood, decomposition rates were higher at low elevations and where temperature was high (Figure 1C, Extended Data Figure 2; Extended Data Table 2). While past work found large local contributions of termites to wood decay^{3,4}, this is the first assessment of the impact of termite discovery and decay at global scales, revealing the responsiveness of wood-feeding termites to shifts in spatial locations and climatic conditions (Figure 1, Extended Data Figures 1-2, Extended Data Tables 1, 3).

Temperature sensitivity. Wood block discovery by termites rapidly increased with increasing temperatures (Figures 1B, 2A, Extended Data Table 3), with the greatest estimated shifts between 17°C (23% discovery) and 26°C (80% discovery) (Figure 2A); >50% of wood blocks were estimated to be discovered as temperatures increased above 21.3°C. For microbial decay, in the absence of discovery by termites, temperature sensitivity was in line with previous work (decay effective Q_{10} of 1.75; 95% CI: 1.46-2.11; Extended Data Table 4)⁸⁻¹⁰. When termites discovered a wood block, however, consumption increased rapidly with temperature (decay effective Q_{10} of 6.53; 95% CI: 4.53-9.40; Figure 2C, Extended Data Table 5). The high consumption rate by termites at warm sites may be related to large population numbers, high activities or both, but implies that the residence time of wood will be much shorter than expected due to termites in warm locations. The termite decay effective Q_{10} is much steeper than any previously recorded for microbes^{8-10,45}, suggesting a different mechanism determining termite versus microbial decay. Consequently, subtropical, tropical or global models using a single microbial-derived decay effective Q_{10} are likely to: (1) underpredict wood decomposition; (2) overpredict terrestrial C storage; and (3) underpredict temperature sensitivity. The use of a termite-corrected decay effective Q_{10} should improve the accuracy of modelled wood decomposition under current and future climate predictions.

Precipitation sensitivity. Termite discovery was influenced by the interaction between temperature and precipitation (Figures 1B, 2A, Extended Data Table 3). In warm tropical biomes, termite discovery was higher in arid and semi-arid deserts and seasonal forests and savannas as compared to more mesic and humid sites (at 25°C, discovery estimates at 250 mm were 1.4× higher than at 2000 mm and 1.9× higher than at 2700 mm). In contrast, in cool and cold temperate biomes the reverse pattern was observed (at 7°C, discovery estimates at 2700 mm were 3.6× higher than at 2000 mm and 153.4× higher than at 250 mm). This interactive climate effect on discovery may be mediated by more frequent extreme low temperatures in dry and cold climates compared to humid and cold climates and/or the dual metabolic challenges of coping with both dry and cold simultaneously.

Even though microbial and termite decomposition increased in warm locations (Figures 1C, 2B,C, Extended Data Tables 4-5), they differed in their response to precipitation.

Microbial decomposition increased with increasing precipitation, but this effect was weak and did not interact with temperature (Figure 2B, Extended Data Table 4). In contrast, precipitation was not a significant predictor of termite decomposition (Figure 2C, Extended Data Table 5). These results suggest that while precipitation shapes the discovery phase, it does not affect the decay phase of termite decomposition; however, the strong temperature and precipitation interaction effect on discovery means that termites increase overall decay most in tropical seasonal forests and savannas and subtropical deserts (Figure 1C). Further, even though microbial abundance is highly sensitive to precipitation³⁷⁻⁴⁰, temperature was a stronger driver than precipitation of microbial-driven decay, perhaps mediated through its effects on enzyme kinetics³⁶.

Termite contributions to wood decay will increase with tropicalization. Given the extreme sensitivity of both termite discovery and decay to temperature, a warming world will likely lead to an expansion of termites globally with important consequences for C cycling. Termites today have the potential to decompose >50% of deadwood in 28.8% of the land surface (Figure 3). With middle of the road climate warming estimates, by midcentury, we predict an expansion of high termite discovery into subtropical regions representing a 14.2% increase in land surface with high termite activity globally (from 39 to 45 million km²). (Figure 3. Tropicalization (i.e., warming shifts to a tropical climate) is occurring in many ecosystems around the world¹⁷. The temperature sensitivity demonstrated in this study suggests the huge termite contribution to wood decay will expand both within and beyond the tropics, consistent with widespread tropicalization in other ecosystems.

Conclusions. Until now, we lacked the global quantitative context of how microbial and termite decay are differentially sensitive to important climate drivers – temperature and precipitation and how these variables interact with one another. Previous work showed that downed deadwood decomposition is slow at high latitudes where termites are absent and microbial decay is slow, with the converse thought to be true in the humid tropics^{12,13}. Instead, we found that wood was most damaged by termites in tropical seasonal forests and savannas and subtropical deserts (Figure 1), with termites accelerating decay up to 3.71× above background microbial decay. Such findings were only possible with a well replicated globally distributed experiment – in this case, a grassroots effort with no centralized funding, meaning the project integrated research programs of all scales across country borders. This large termite contribution has been underappreciated; not only is the termite effect large and expected to increase (Figure 3), but it also has a different functional form than microbial decay. It has a clear two-step process: 1) discovery, which can be highly variable, and 2) decomposition. The high temperature sensitivity of termites will mean that any global estimates of wood C storage and turnover that ignore termite discovery and decay will mispredict C cycling, over-estimating C storage in large regions of the world.

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Methods

In this study, 8923 wood blocks were deployed across 133 sites in 20 countries and all continents except Antarctica (Figure 1A, Supplementary Information Table S1). The majority of sites were established in 2017, with 6 sites established in 2018 in Puerto Rico with the delay following Hurricane Maria. Untreated wood was sourced within countries or regions (i.e., Europe) and followed protocols established in Cheesman *et al.*⁴³. Most locations used *Pinus radiata*, but a few study sites were unable to access *P.*

radiata; they instead used *P. taeda* (Brazil), *P. ellioti* (French Guiana), and southern yellow pine (likely *P. echinata*) (Panama). We accounted for these differences based on wood chemistry (see below). Here, we targeted wood-dwelling microbes and wood-feeding termites as these are the two primary biotic wood decay agents globally⁷.

Wood was cut into blocks at volume of $\sim 403 \text{ cm}^3$; blocks were dried at 120°C to constant mass and weighed for initial dry mass. Wood blocks were divided into two treatments; all treatments allowed wood-dwelling microbe access with half the blocks excluding (=microbes) and the other half including (=microbes+termites) wood-feeding termites. Wood blocks in all treatments were wrapped with $300 \mu\text{m}$ nylon or polyester mesh bags sealed with stainless-steel staples. Bags in the microbes+termites treatment had 10 holes ($\sim 5 \text{ mm}$ diameter) punched into the mesh on the underside of the mesh bag to allow termite access. In our statistical analyses (see below), holes did not alter wood decay rates e.g., through altered microclimate.

Most sites deployed 20 wood blocks per treatment (microbes and microbes+termites) replicated for each harvest at 20 stations (Supplementary Information Table S1). 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 (Supplementary Information Table S1). Stations were spaced $\geq 5 \text{ m}$ apart and $\geq 0.5 \text{ m}$ away from existing large deadwood, termite mounds, exposed rocks or substantial water flow paths. All wood blocks were covered with 70% green shade cloth to reduce solar radiation degradation of the mesh bags.

For each lot of initial wood samples, 3-5 blocks were sent to the University of Illinois. Sawdust samples were ground and analyzed for % nitrogen (N) and C content from individual blocks using an elemental analyzer (Costech, Valencia, CA, USA) (Supplementary Information Table S1). Average elemental %N and %C per lot were used to represent variation within and across wood species as wood chemistry typically is a strong predictor of decomposition rates^{47,48} (Extended Data Tables 6-10).

Wood blocks were harvested at ~ 6 months ($n = 739$), ~ 12 months ($n = 4517$), ~ 24 months ($n = 3488$), ~ 36 months ($n = 125$) and ~ 48 months ($n = 54$) after deployment. Once collected, wood blocks were assessed for termites. We assessed termite discovery and decay following a two step method. First, we filtered to those sites where site researchers recorded termite presence. Second, for those sites with termites, we recorded blocks as discovered when they were noted as having termites, mudding (i.e., imported soil), and/or damage (e.g., internal chambering, external surface scoring, or removal) in wood blocks (Extended Data Figure 3). When wood blocks were found to be damaged but this damage was not attributable to termites (e.g., small holes, non-termite larvae, etc.), these blocks were recorded as undiscovered by termites; few blocks had macrofauna damage not attributable to termites (termite discovery was $2.7\times$ higher than discovery by other macrofauna), supporting the importance of termites as the main macrofauna decaying wood. After termite discovery assessment, wood blocks were dried at 100°C for 72 hrs, before reweighing for final mass.

Using site latitude and longitude, we obtained elevation (m) and climate variables from Fick and Hijmans⁴⁹, including both mean annual temperature (MAT; °C) and mean annual precipitation (MAP; mm) at 0.5° resolution; climate data were summarized over the window over which the blocks were deployed at field sites. Whittaker's biomes were obtained from Ricklefs⁴⁶. We used "raster" and "plotbiomes" packages in R (v4.04).

Analyses

Discovery - Termite discovery was calculated as the percentage of wood blocks with evidence of termites per site and time point. We ran two sets of two-tailed analyses to understand how wood block discovery by termites varied across geographic and climatic space. First, we ran a series of bivariate logistic regressions, examining how individual spatial (Absolute (Latitude) and elevation) and climatic (MAT and MAP) predictors estimated discovery. Second, we ran a multivariate logistic regression including MAT, MAP and their interaction, to explore the climatic sensitivity of discovery. In both models, we used an offset for time since deployment to account for variation in deployment length.

Decay - We calculated proportion mass loss (ML) for a given time window = $1 - (\text{Initial mass} - \text{Final mass}) / (\text{Initial mass} * \text{Time})$. Microbial-driven ML was calculated for blocks in the microbes treatment, while microbial and termite-driven ML was calculated for blocks that were discovered by termites. Additionally, decomposition was calculated assuming an exponential steady-state of decay using percentage mass loss and time since deployment (i.e. $k = -\log(\text{Final mass}/\text{Initial mass})/\text{time}$). Data were weighted by the number of wood blocks in each discovery category (discovered and not discovered by termites) at each site as appropriate. Similar to the discovery models, we ran two sets of two-tailed analyses to understand how both microbes only and termite discovered decomposition rates (k) varied across geographic and climatic space. First, we ran a series of bivariate regressions, examining how individual spatial (Absolute (Latitude) and elevation) and climatic (MAT and MAP) predictors estimated k for each treatment. Second, we ran a multivariate regression including MAT, MAP and their interaction, to explore the climatic sensitivity of decay for each treatment. In discovery and decay models, when we included initial wood %N and %C to account for pine species, both variables were significant but otherwise had little effect on the models (Extended Data Tables 6-10); weak effects of latitude and precipitation became not significant in microbes decay models (Extended Data Tables 2, 7). Holes in the mesh did not alter decay rates (e.g., due to altered microclimate) when we analyzed the effect of treatment (holes/no holes) using a two-tailed test for all blocks undiscovered by termites (main effect and all interactions involving that treatment $P > 0.5$). For analyses, we used the "lubridate", "boot", "report", "see", "correlation", "modelbased", "effectsize", "parameters", "performance", "bayestestR", "datawizard", "insight", "easystats", "lme4", "patchwork", "ggeffects", "forcats", "stringr", "dplyr", "purrr", "readr", "tidyr", "tibble", "ggplot2", "tidyverse" packages in R (v4.04).

Termite discovery land surface area estimations - To explore the amount of land surface area impacted by high termite discovery, we first estimated from our model where high termite discovery ($\Rightarrow >50\%$) should be expected based on the macroclimate: this resulted in a threshold of MAT $>21.3^\circ\text{C}$. To estimate how

this threshold is expected to change in space, we estimated the land area predicted to have high discovery by mid century based on an ensemble of 8 future climate models (BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0), which were downscaled to 2.5 minute resolution and bias corrected using WorldClim v2.1. We used SSPs (middle of the road) 2-4.5 that predicts a global average 2°C warming by midcentury (2041-2060). Finally, we estimated percentage land area that does not currently and is not expected to have high termite discovery rates (= <50%), as well as percentage land area for warm sites (>21.3°C, either now or in mid-century) that are drier than any sites in the current study, meaning we are unable to estimate and predict termite discovery rates.

Data availability. Data used in this publication will be available at <https://github.com/Zanne-Lab/XXX>.

Computer code. Computer code used in this publication will be available at <https://github.com/Zanne-Lab/XXX>.

Methods References

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Declarations

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Competing Interests. The authors confirm there are no competing interests.

Supplementary Information is available for this paper.

Materials & correspondences. All correspondence and material requests should be sent to Amy Zanne (aezanne@gmail.com).

Figures

Figure 1

Geographic, biome and climatic distribution of experimental sites. A. Dots represent the 133 study site locations. Colour of the dots represents termite discovery (i.e., percentage of wood blocks with evidence of termites per site and time point). B Study site distribution across mean annual temperatures (MAT), mean annual precipitations (MAP) and Whittaker biomes. Colour of the points represents termite

discovery. C Decay rate (k) estimates across Whittaker⁴⁶ biomes (shown by arrows and colors matching legend in 1B), with boxplots for each biome representing blocks discovered by termites (dashed boxplots on right of pair) and blocks undiscovered by termites (solid boxplots on left of pair; examples of discovered blocks in Extended Data Figure 3). For boxplots, center line, median; box limits, upper and lower quartiles; whiskers, 1.5× interquartile range; points, outliers. Numbers on top of solid boxplots on left of pair indicate total number of sites per biome; numbers on top of dashed box plots on right of pair indicate number of sites where termite discovery occurred.

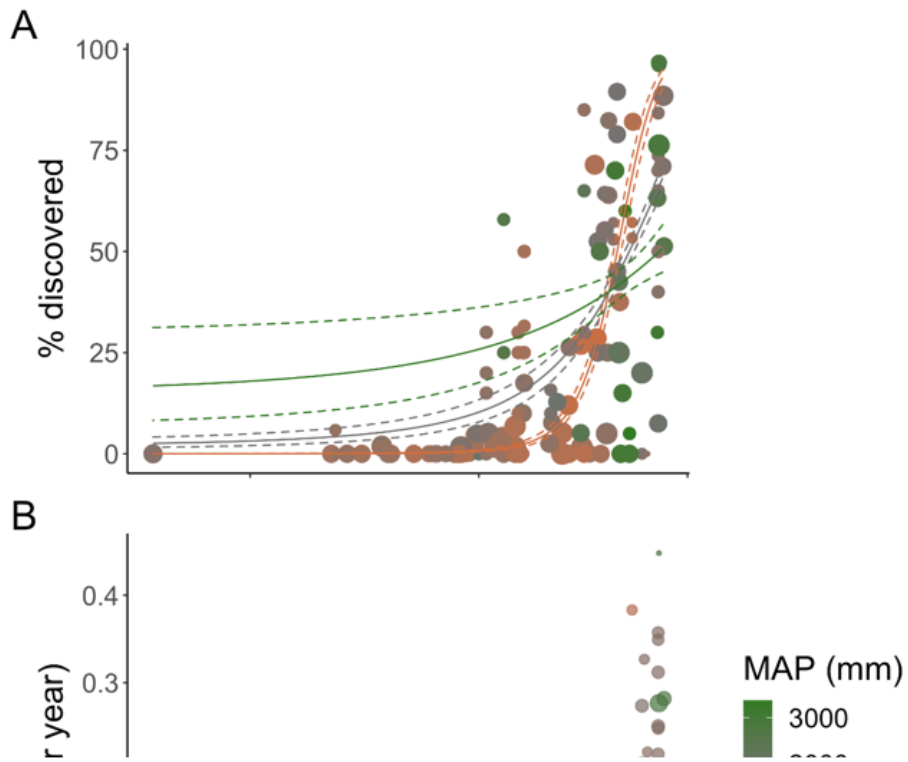


Figure 2

Discovery and decay of wood based on significant (Extended Data Tables 3-5) climatic predictors. A) Termite discovery (i.e., percentage of wood blocks with evidence of termites per site and time point) across mean annual temperature (MAT) and mean annual precipitation (MAP), B) Decay rates (k) of microbes across MAT and MAP, and C) Decay rates (k) of termite discovered wood across MAT (Note: MAP was not a significant predictor of termite discovered wood blocks). Solid lines represent logistic regression predictions at 250 mm MAP (orange; representative of mean desert/savanna biomes), 2000 mm MAP (gray; representative of mean temperate biomes) and 2700 mm MAP (green; representative of mean tropical/temperate humid biomes). Dashed lines represent 95% confidence intervals around predictions. The x-axis has been \log_{10} transformed for visualization.

Figure 3

Predicted termite discovery around the world by mid-century with tropicalization. Global map showing current >50% discovery = 39,186,249 km² (28.8% of land surface area), mid-century predictions of expansion to >50% discovery = 5,557,360 km² (4.1% of land surface area) and mid-century continuing <50% discovery = 73,794,138 km² (54.1% of land surface area) and areas where we were unable to predict as conditions were drier than the boundaries of the current study = 17,447,992 km² (12.8% of land surface area).

Supplementary Files

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- [Extendeddata.docx](#)