RESEARCH ARTICLE | OPEN ACCESS

Biogeographical Variation in Termite Distributions Alters Global Deadwood Decay

Stephanie J. Law[1] | Habacuc Flores-Moreno[2] | Catherine L. Parr[3,4,5] | Stephen Adu-Bredu[6,7] | Katherine Bunney[4] | William K. Cornwell[8] | Fidèle Evouna Ondo[9] | Jeff R. Powell[10] | Gabriel W. Quansah[11] | Mark P. Robertson[4] | Amy E. Zanne[12] | Paul Eggleton[1]

[1]Life Sciences Department, The Natural History Museum, London, UK | [2]Department of Health and Biosecurity, CSIRO, Brisbane, Queensland, Australia | [3]School of Environmental Sciences, University of Liverpool, Liverpool, UK | [4]Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa | [5]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa | [6]Biodiversity Conservation and Ecosystem Services Division, Forestry Research Institute of Ghana, Council for Scientific and Industrial Research, Kumasi, Ghana | [7]Department of Natural Resources Management, CSIR College of Science and Technology, Kumasi, Ghana | [8]School of Biological, Earth & Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia | [9]Scientific Cell Department, National Agency for National Parks, Libreville, Gabon | [10]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia | [11]Soil Analytical Services, Soil Testing Laboratory, CSIR-Soil Research Institute, Kumasi, Ghana | [12]Department of Biology, University of Miami, Miami, Florida, USA

Correspondence: Stephanie J. Law (stephaniejanelaw@gmail.com)

ABSTRACT

Aim: Termites are a crucial group of macroinvertebrates regulating rates of deadwood decomposition across tropical and sub-tropical regions. When examining global patterns of deadwood decay, termites are treated as a homogenous group. There exist key biogeographical differences in termite distribution. One such clear distinction is the distribution of fungus-growing termites (FGT, subfamily Macrotermitinae). Considering that climate will have shaped termite distribution and ecosystem processes, we evaluate the roles of termite distribution (presence of FGT) and climate (aridity) on global patterns in deadwood decay.

Location: Between 46° N-43° S and 175° E-85° W.

Time Period: Present (between 2016 and 2021).

Major Taxa Studied: Termites (Blattodea: Termitoidae).

Methods: We add salient data to an existing global dataset on deadwood decomposition, including new data from five existing sites and seven additional African sites. We analyse a dataset spanning six continents, 16 countries and 102 experimental sites. Firstly, we evaluate climatic differences (mean annual temperature, mean annual precipitation and mean annual aridity) between sites with and without FGT. Secondly, using aridity as a single comparative climate metric between sites that accounts for temperature and precipitation differences, we examine the interaction between FGT and aridity on global patterns of termite deadwood discovery and decay through multivariate logistic and linear regressions.

Results: Termite-driven decay and wood discovery increased with aridity; however, responses differed between FGT and NFGT sites. Wood discovery increased with aridity in FGT sites only, suggesting a greater role of FGT to deadwood decay in arid

environments. On average, both termite discovery and decay of deadwood were approximately four times greater in regions with FGT compared with regions without FGT.

Main Conclusions: Termite discovery and decay of deadwood is climate dependent, and higher decay may be through greater discovery of deadwood in FGT sites. Inclusion of biogeographical differences in termite distribution could potentially alter current and future global estimates of deadwood turnover.

1 | Introduction

Termites are social insects that have a large global biomass, estimated at ca. 0.08 Gt C, approximately equivalent to the global biomass of livestock (Rosenberg et al. 2023) and are one of the world's most important ecosystem engineers (Jouquet et al. 2011). Research has increasingly highlighted the importance of termites for deadwood decomposition (Griffiths et al. 2019; Zanne et al. 2022), but little is known regarding the biogeographic variation in termite decomposition of deadwood and what might drive this variation.

One of the most obvious biogeographical patterns is the distribution of fungus-growing termites (FGT, family Termitidae, subfamily Macrotermitinae). These termites, which have an intimate mutualism with white-rot fungi of the basidiomycete genus *Termitomyces*, are found only in the old-world tropics (Africa, Asia, Madagascar, i.e., not in the Americas, Australasia or Europe) (Aanen and Eggleton 2005). Within this geographic distribution FGT are found across a range of ecosystems from rainforests to semi-desert biomes, although they are arguably most dominant in dry savannas (Aanen and Eggleton 2005; Jones and Eggleton 2011). In savannas, colony sizes of FGT are often larger than most other termite species present (in abundance and biomass), where a single colony can reach over a million individuals and over 7 kg of termites in dry weight (Darlington, Zimmerman, and Wandiga 1992; review by Van Thuyne and Verrecchia 2021). While in forests, biomass of FGT is often lower than that found in savannas and FGT biomass is instead comparable to other feeding groups (Eggleton et al. 1999).

FGT not only have a distinct biogeographical distribution but also have marked biological and behavioural differences from other termites. In the Macrotermitinae, the process of lignocellulose digestion is largely externalised to the mutualist fungus comb (within the termite nest) providing FGT extraordinary digestive efficiencies (da Costa et al. 2019). Accordingly, reported consumption rates by FGT are generally higher than other termites and can be up to a magnitude greater (Collins 1983; Meyer, Crewe, and Braack 2003; Wood and Sands 1978). Globally, FGT may account for 30% of all dead plant biomass consumed by termites (Seiler, Conrad, and Scharffe 1984). When present, FGT can play a dominant role in litter removal, and in some cases are responsible for over 90% of litter removed by termites (deadwood and leaf litter) (Buxton 1981; Collins 1983). Thus, FGT are considered to be major contributors and regulators of decomposition (Schuurman 2005). Even when the biomass of FGT is lower than other termite feeding groups in the community, their ecological impact with regards to carbon mineralisation through decomposition can be greater when respiration from their fungus combs is also considered (Wood and Sands 1978; Yamada et al. 2005). Discriminating termites into FGT and NFGT has also revealed

how behavioural adaptations between the two groups can have differential impacts on soil functioning, particularly in drier conditions (Jouquet et al. 2022).

Termite-driven decay of deadwood is sensitive to climate: on a global scale termites elevate decay most in tropical seasonal forests, tropical savannas and subtropical deserts (Zanne et al. 2022), biomes where FGT often thrive (Jones and Eggleton 2011). While climate (specifically differences in temperature and precipitation or humidity) shapes decay rates by impacting the decomposer community (reviewed by Griffiths et al. 2021), regional experiments have shown that the influence of FGT on decomposition rates can exceed that expected by climatic variables (Schuurman 2005; Veldhuis et al. 2017). Recent research examines global patterns in deadwood decay along temperature and precipitation gradients (Zanne et al. 2022). However, the aridity gradient may be a more useful metric when exploring the effects of termite distribution on deadwood decay for the following reasons: (1) aridity accounts for the interacting effects of temperature and precipitation and thus better captures water availability which is arguably biologically more meaningful than precipitation (Zomer, Xu, and Trabucco 2022); (2) termite distribution, in terms of richness, abundance, biomass and foraging activity, is influenced by aridity (Heděnec et al. 2022; Liu et al. 2022; Schuurman 2005) and (3) several studies indicate that termite contribution to litter decomposition (including deadwood), particularly the contribution made by FGT, increases with aridity (Heděnec et al. 2022; Schuurman 2005; Veldhuis et al. 2017).

The presence of FGT has long been considered a potential major factor in global termite ecology (Jones and Eggleton 2011; Wood and Sands 1978). It is therefore surprising that, despite the ecological dominance of FGT, there have been no studies to date exploring the relationship between global biogeographic variation in deadwood decomposition and the presence of FGT. Here, we use existing data from a global experiment on the decay of a common substrate (*Pinus radiata*) (Zanne et al. 2022) and include new data from additional sites in regions where FGT are present (Law et al. 2024). Termite contributions to the decay of deadwood can be assessed as a two-step process: first, termites must discover deadwood, shown by either termite presence or attack as defined by Zanne et al. (2022) and second, termites must consume deadwood (i.e., cause decay) (Law et al. 2023; Zanne et al. 2022). Specifically, we examine how termite discovery and termite-driven decay varies in regions where FGT are present and absent through the following hypotheses:

1. The impact of FGT on deadwood decomposition is greater than other termites leading to broad biogeographical differences in the decomposition of deadwood (across all biomes). This pattern is shown by higher termite discovery of

deadwood and greater decay rates of discovered deadwood in regions with FGT compared with regions without FGT.

2. There exist biogeographical differences in the response of termite-driven deadwood decay with aridity. Specifically, FGT will have a greater impact on decomposition processes in relatively arid areas such as savannas. This is evident by a greater increase in wood discovery and deadwood decay with aridity when FGT are present compared with their absence.

2 | Method

2.1 | Datasets

Experimental sites used in this dataset followed the same protocol for the deployment, harvest and evaluation of wood blocks as outlined in Zanne et al. (2022) with only minor differences among them (outlined below). As we were solely interested in exploring biogeographical patterns of termite-driven decay, we only used sites which indicated termite presence, this comprised 95 sites from Zanne et al. (2022); new data were added to increase the sample size for five of these original sites and seven new African sites were also added (Law et al. 2024). Sites were assigned as within the geographical distribution of FGT (subfamily Macrotermitinae) if they were in Afrotropical, Oriental or Malagasy realms (Aanen and Eggleton 2005; Jones and Eggleton 2011); this included 22% of sites (22/102) and 25% of countries (4/16) in the dataset (Table S1). Here on, we refer to sites as FGT sites (with fungus-growing termites) or NFGT sites (non-fungus-growing termites, i.e., without FGT). One site on Okinawa Island, Japan, was dropped from the Zanne et al. (2022) dataset, as although FGT are found on Okinawa, their distribution is limited (Hojo 2019) and we could not classify the site as FGT or NFGT with certainty.

Using latitude and longitude coordinates, mean annual aridity values for all sites were extracted from the Global-Aridity Index database (Zomer, Xu, and Trabucco 2022) at 30 arc-seconds spatial resolution (~1 km at the equator) (Law et al. 2024). The Aridity Index is unitless with values decreasing as aridity increases; it is measured as the ratio of mean annual precipitation over mean annual evapotranspiration. Additionally, values for mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) were extracted for new sites from the WorldClim dataset (Fick and Hijmans 2017) using the same spatial resolution of 2.5 arc-minutes (~5 km at the equator) as existing sites (Law et al. 2024). While FGT sites were nested within the range of aridity and MAP of NFGT sites, FGT sites occupied hotter regions with significantly greater MAT (Table 1, Figure S1). To account for climatic differences between NFGT and FGT sites we only included NFGT sites that fell within the same aridity range as FGT sites (0.284–1.642), this included 80% of NFGT sites (*n* = 64 sites) (Figure 1); 13 NFGT sites were more humid and only three were more arid than FGT sites (Figure S3.2). Thus, the final analysed dataset included 86 sites (22 FGT and 64 NFGT sites) and used 8306 wood blocks across six continents and 15 countries. We used aridity as a metric of spatial comparison in climate between NFGT and FGT sites as the Global-Aridity Index accounts for both temperature and precipitation as well as other climatic variables, such as humidity, wind speed and solar radiation (Zomer, Xu, and Trabucco 2022). Aridity better captures water availability than MAP and water availability can influence termite activity (Cheesman, Cernusak, and Zanne 2018). Furthermore, the Global-Aridity Index is used to classify drylands into four zones distinct from humid regions: ≤0.03 hyper-arid, 0.03–0.2 arid, 0.2–0.5 semi-arid, 0.5–0.65 dry sub-humid and >0.65 humid (UNEP 1997).

Wood blocks were deployed across all sites between 2016 and 2019, although most sites were established in 2017. All sites monitored wood blocks for at least 12 months and most for 24 months, with some sites including additional harvests at approximately six months, 36 months and 48 months. While all wood blocks were exposed to microbial decay, only some were exposed to termite decay; termite access was manipulated by enclosing wood blocks in fine 300 μm nylon or polyester mesh bags sealed with stainless steel staples. Wood blocks were deployed in pairs: one that allowed termites access through holes cut into the mesh and another that excluded termites (with no holes in the mesh) (see Zanne et al. 2022 for detailed method). The majority of sites (86% of sites, 74/86) used the common substrate *Pinus radiata* for all wood blocks; however, a few sites were unable to access *P. radiata* and instead used *P. taeda* (Brazil, *n* = 11 sites) or southern yellow pine (likely *P. echinata*) (Panama, *n* = 1 site). As most sites used a common substrate and other substrates were of the same genus, we did not include wood chemistry as part of the analysis (see supplementary in Zanne et al. [2022] for wood chemistry analysis).

TABLE 1 | Comparison of mean values and range of site characteristics for sites with fungus-growing termites (FGT) and sites without fungus-growing termites (NFGT). Aridity values decrease as aridity increases.

	Mean ± SD		Range	
	FGT sites	**NFGT sites**	**FGT sites**	**NFGT sites**
Aridity	0.95 ± 0.43	1.17 ± 0.58	0.284–1.642	0.107–2.660
MAT (°C)[a]	25.3 ± 1.70	16.4 ± 5.14	21.0–27.9	6.0–26.5
MAP (mm)	1398 ± 601	1546 ± 767	563–3102	256–3371
Richness of wood-feeding genera[a]	5.61 ± 1.19	2.70 ± 2.12	1.73–8.55	0.26–9.79
Richness of all termite genera[a]	12.3 ± 8.30	7.79 ± 5.70	1.46–38.60	0.98–27.20

[a]Indicates significant differences between means (non-parametric Wilcoxon tests). MAT (°C): $W = 131.5$, $p < 0.001$. Richness of wood feeders: $W = 193$, $p < 0.001$. Richness of all termite genera: $W = 547$, $p = 0.007$.
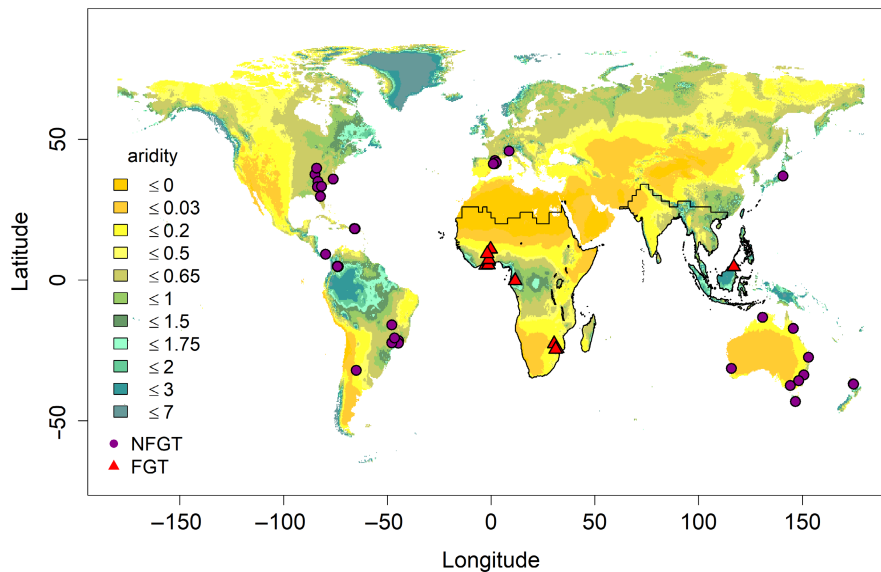
FIGURE 1 | Geographic location of the 86 study sites and estimated annual aridity values. Aridity values decrease as aridity increases. The following aridity ranges can be used as a general climate classification: ≤0.03 hyper-arid, 0.03–0.2 arid, 0.2–0.5 semi-arid, 0.5–0.65 dry sub-humid and >0.65 humid (UNEP 1997). Purple circles show sites with no fungus-growing termites (NFGT, $n = 64$) and red triangles sites with fungus-growing termites (Macrotermitinae) (FGT, $n = 22$). Black borders delineate the assumed geographic distribution of Macrotermitinae (Aanen and Eggleton 2005; Jones and Eggleton 2011).

All wood blocks within the Zanne et al. (2022) dataset were covered with 70% green shade cloth; however, no shade cloth was used for wood blocks at new sites in the additional data (all FGT sites) (8% of sites, 7/86). Shade cloth can alter the microenvironment and is recommended to protect mesh from UV degradation (Cheesman, Cernusak, and Zanne 2018), thus the presence (or absence) of shade cloth can influence decay rates. We therefore carried out additional analyses to test if the presence or absence of shade cloth significantly influenced our results on decay (see Supplementary Material S2 for details). We found no evidence that the inclusion of shade cloth changed our results significantly (Tables S6.1–S6.3) so we omitted shade cloth from our final analysis.

Although it was not possible to determine which termite species were responsible for deadwood decay at each site, the presence of Macrotermitinae in FGT sites was checked by examining available termite survey data and the presence of sheeting on wood blocks. Although sheeting is formed by a range of termite taxa, sheeting is best studied and most recorded for FGT (Harit et al. 2017). The use of sheeting as an indicator of FGT decay is a method previously used in published work (Veldhuis et al. 2017). Macrotermitinae presence was confirmed at 86% of FGT sites (18/21; one FGT site reported an absence of all termites) and accounted for 64% of termite encounters in transect surveys (mean 63.7% ± SD 33.1) (Table S1). All FGT sites without available data on termite species composition were in Ghana ($n = 3$ sites). However, Macrotermitinae are widely distributed and dominant across Ghana, in both forested and savanna biomes (Wagner, Cobbinah, and Bosu 2008), demonstrated by the high encounter rate of Macrotermitinae across the nine other Ghanaian sites in this study (mean 75.8% ± SD 15.5) (Table S1). We therefore assume, and it is highly likely, that Macrotermitinae was present in all Ghanaian sites in this study. Furthermore, significantly more wood blocks recorded

the presence of sheeting in FGT sites compared with NFGT sites (Figure S1). Using available transect data (see Table S1), we found that decay rates of deadwood in FGT sites increased significantly with higher encounter rates of FGT ($p < 0.001$, Figure S1, Table S2.1), implying that FGT are largely responsible for deadwood decay in FGT sites, particularly for African FGT sites. For these reasons, we are confident that the effects on discovery and decay of deadwood in FGT sites are primarily attributed to Macrotermitinae.

Throughout we use the term termite-driven decay when referring to the decay of discovered wood blocks (i.e., wood with termites present or signs of termite attack), akin to the definition provided by Law et al. (2023). We acknowledge that microbial decay processes will have occurred in both discovered and undiscovered wood blocks and that the microbial decay process is likely to have interacted with that of termites. However, in this experimental design, we are unable to detect or tease apart such interactions. To verify that differences in decay rates between FGT and NFGT sites can be attributed primarily to differences in termite-driven decay rather than microbial we tested for biogeographical differences in decay of undiscovered blocks (see outlined below).

2.2 | Statistical Analysis

To calculate discovery rates, we only used data from wood blocks that allowed termites access. Termite discovery was coded as a binary variable, with wood samples categorised as discovered or undiscovered. Wood blocks were considered discovered by termites when termite-driven decay of blocks had been noted visually. We ran a multivariate logistic regression (using the 'glm' function in R) at the wood block level (using all wood blocks that allowed termite access including

discovered and undiscovered) to examine how aridity and the presence of FGT estimated the probability of termite discovery. We also included an interaction between predictors to test if any influence of FGT on discovery rates differed according to aridity. To account for variation in deployment length of wood blocks, we included an offset in the model for time since deployment.

To test the effects of aridity and the presence of FGT on termite-driven decay rates, we first calculated a mean k-value (decay rate) of termite-discovered wood blocks for each site. All k-values for wood blocks had been estimated using a negative exponential model of decay (i.e., $k = -$ ($\log_e$(final mass/initial mass))/deployment length). We then fitted log-transformed k-values to a linear regression using the same predictors as the discovery model. After inspecting the data, we checked for any curvature in the relationship between decay rates and aridity by fitting a second order polynomial and compared models using Akaike Information Criterion (AIC) values. However, the best model did not include a polynomial function and the interaction between aridity and the presence of FGT was insignificant and dropped from the model. To help balance out the impact of large differences in sample size among sites, sites with higher sample sizes (i.e., number of discovered wood blocks) were given greater weight in the regression. We also modelled decay using an unweighted regression and model outcomes did not significantly change (Table S5.2).

To assess whether biogeographical differences in decay of discovered blocks (between FGT and NFGT sites) can be attributed to termites, rather than differences between the locations in microbial decay, decay predictors were also examined for undiscovered blocks (see Supplementary Material S3). While microbial decay (decay of undiscovered blocks) is greater in FGT sites compared with NFGT sites ($\beta = 0.800$, $t = 5.774$, $p < 0.001$, Table S3), the difference in mean decay rates between NFGT and FGT sites was small (difference in $k = 0.08$) compared with discovered blocks (difference in $k = 0.87$) (Figure S3.1). This small effect of microbial decay cannot sufficiently explain observed differences between decay in FGT and NFGT sites.

Additionally, we used the full dataset available, including all FGT and NFGT sites ($n = 102$ sites rather than 86), to test for any effect of MAT and MAP (including an interaction) on termite discovery or on termite-driven decay of deadwood, akin to Zanne et al. (2022). For termite discovery, we used a multivariate logistic regression with the binary response of termite discovery at the wood block level. For termite-driven decay, we ran a multivariate linear regression using mean k (decay rates) for discovered blocks at the site level (see Supplementary Material S5). For each site, we also extracted richness values for all termite genera and for wood-feeding termite genera (which includes FGT) from Woon (2022). Using separate bivariate linear regressions, we tested if aridity had any effect on either metric of termite richness or if richness of wood-feeding genera influenced mean decay rates of discovered blocks (see Supplementary Material S4).

Details and results of extra analyses can be found in the Supplementary Material. All data manipulation and analyses were carried out using R version 4.3.1; models were fitted using the R functions 'lm' or 'glm' (R Core Team 2023). Interactions in models were visualised and pairwise comparisons of estimated marginal means carried out in the 'emmeans' package (Lenth 2023) using the functions 'emmip', 'emmeans' and 'emtrends' with proportional averaging and Tukey HSD or Sidak corrections for multiple comparisons. Model predictions were made using the function 'ggpredict' in the package 'ggeffects' (Ludecke 2018) and all plots were made using the package 'ggplot2' (Wickham 2016). Variables from model predictions were back transformed to original values for decay rate (k) for all plots. Figure 1 map was produced using the following R packages 'geodat' (RS-eco. 2022), 'raster' (Hijmans 2023) and 'sf' (Pebesma and Bivand 2023), using aridity values from the Global-Aridity Index (Zomer, Xu, and Trabucco 2022).

3 | Results

Termite discovery of deadwood and decay rates of discovered blocks were greater in regions where FGT were present (Odds ratio $= 38.90$, $z = 18.11$, $p < 0.001$ and $\beta = 1.38$, $t = 6.35$, $p < 0.001$ for discovery and decay, respectively) (Tables S4.1 and S5.1). Mean discovery (probability $0.71 \pm SE\ 0.06$ vs. $0.16 \pm SE\ 0.05$) and mean decay rates ($1.16 \pm SE\ 0.16$ vs. $0.29 \pm SE\ 0.05$) were approximately four times greater in FGT sites than NFGT sites (Figures 2a and 3a). Examination of the significant interaction between aridity and the presence of FGT in termite discovery (Odds ratio $= 0.29$, $z = -6.02$, $p < 0.001$, Table S4.1) revealed that termite discovery increased with aridity but only for FGT sites (trend $= -1.22$, $z = -8.80$, $p < 0.001$ vs. trend $= 0.02$, $z = 0.15$, $p = 0.885$ for FGT and NFGT sites, respectively; Figure 2b). Decay rates of discovered deadwood increased with aridity for both FGT and NFGT sites ($\beta = -0.82$, $t = -2.74$, $p = 0.008$) (Figure 3b). These results indicate that for a given aridity, termite discovery and termite-driven decay of deadwood was greater in FGT sites compared with NFGT sites. Furthermore, differences in termite discovery between FGT and NFGT sites was greater as aridity increased.

Using the complete data set available (i.e., without restricting sites to the same climatic envelope), as expected (and in line with Zanne et al. 2022), we found the greatest termite discovery in hot sites with low precipitation (Figure S5a and Table S8.1). However, with the inclusion of additional data, decay of discovered blocks increased not only with greater MAT ($\beta = 1.31$, $t = 16.17$, $p < 0.001$) (as found in Zanne et al. [2022]) but also with lower MAP ($\beta = -0.55$, $t = -6.50$, $p < 0.001$) (Figure S5 and Table S8.2). While we found no relationship between aridity and the generic richness of wood feeders, generic richness of all termites did decrease for aridity corresponding with drylands (values <0.65) (Figure S4, Tables S7.2 and S7.3).

4 | Discussion

Our findings are the first to demonstrate that biogeographical patterns in global deadwood decay can be linked to termite distribution, specifically the presence of FGT where rates of termite discovery and termite-driven decay of deadwood increased on average fourfold when compared with regions without FGT (within the same aridity range). In line with Zanne et al. (2022),
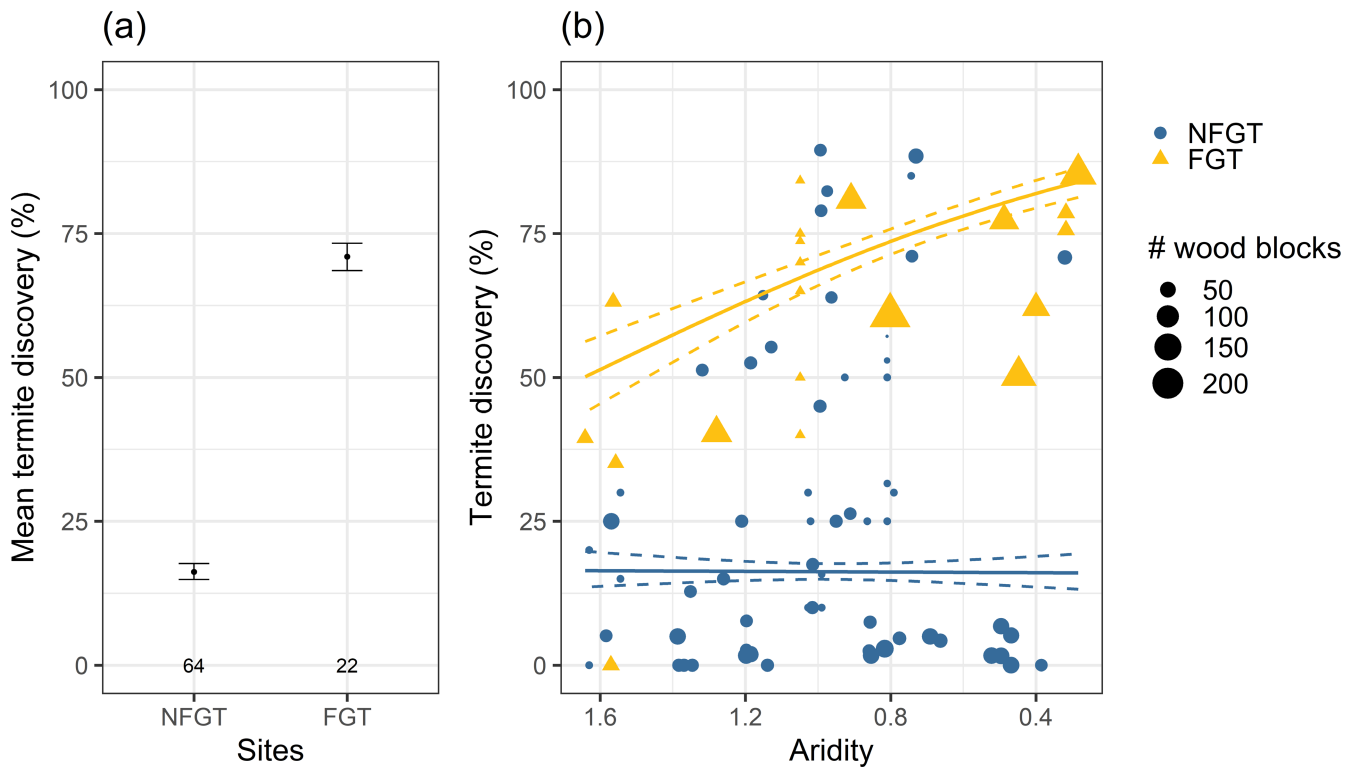
FIGURE 2 | Plots show model predictions for termite discovery of deadwood. Panel (a) shows marginal mean estimates (with 95% confidence intervals) for termite discovery of deadwood in sites with non-fungus-growing termites (NFGT) and sites with fungus-growing termites (FGT), figures at the bottom indicate number of sites. Panel (b) shows termite discovery by mean annual aridity for NFGT sites (blue circles) and FGT sites (orange triangles). Lower aridity values indicate more arid regions. Points show the percentage of wood blocks discovered at each site ($n = 86$) and are scaled in size by the number of wood blocks that allowed termite access. Solid lines indicate predictions for termite discovery across aridity values from logistic regression, for NFGT sites (blue) and for FGT sites (orange). Dashed lines represent 95% confidence intervals around predictions.

we also find that termite discovery and termite-driven decay of deadwood have a climate sensitive response and are greater in arid environments. However, our results indicate that greater termite discovery in arid environments is correlated to the presence of FGT as increases in discovery were only found in FGT sites. It is possible that greater discovery of deadwood with increasing aridity was mediated by all termites within FGT sites (both fungus growing and non-fungus growing). However, while individual species responses to aridity are likely to differ, we have no reason to believe that broad patterns for NFGT should differ greatly between realms. We propose that the most likely explanation for greater discovery of deadwood with aridity in FGT sites is primarily due to an increase in contribution by FGT. This hypothesis is supported by a significant increase in encounter rates of FGT in termite transects with aridity in FGT sites (Figure S1, Table S2.3), indicating greater representation of FGT in termite communities with increasing aridity. Furthermore, several studies across Africa and Asia report that while species richness (of all termite feeding groups) decreases with aridity, the relative abundance of FGT or density of FGT mounds increases (Collins 1983; Dosso et al. 2010; Shanbhag et al. 2017); thus, accounting for the increase in relative contribution of FGT to decomposition with aridity (Schuurman 2005; Veldhuis et al. 2017). Although we do not have data on the relative abundance of FGT, we also found a lower richness of all termite genera with aridity (Figure S4a) but an increase in encounter rate with FGT (Figure S1).

With the addition of new data, we find that termite-driven decay is predicted not only by an increase in temperature (as found by Zanne et al. [2022]) but also by a decrease in precipitation (see Supplementary Material S5). This finding contrasts with previous studies reporting positive effects of precipitation on all insect and termite-driven deadwood decay (Seibold et al. 2021; Wang et al. 2024). Conflicting results are likely influenced by site selection and the range of MAP; here we include only sites where termites are present and more arid sites in Africa with low precipitation thus shifting the range of MAP to include fewer wet sites and more dry sites with high rates of termite-driven decay. Our findings support and strengthen previous work highlighting the importance of termites, and particularly of FGT, to deadwood decay in arid environments (Schuurman 2005; Veldhuis et al. 2017; Zanne et al. 2022).

Although termites are vulnerable to desiccation, counterintuitively termite abundance, biomass and richness of wood-feeding termites are sometimes higher in arid environments (Clement et al. 2021; Heděnec et al. 2022). Behavioural strategies enable termites to persist where moisture is low (Jouquet et al. 2011), increasing their importance to decomposition and enhancing ecosystem resilience to drought (Ashton et al. 2019), this is particularly true for FGT. Without additional field data from these experimental sites, we surmise that elevated termite discovery and termite-driven decay of deadwood in FGT sites is indicative of greater abundance of
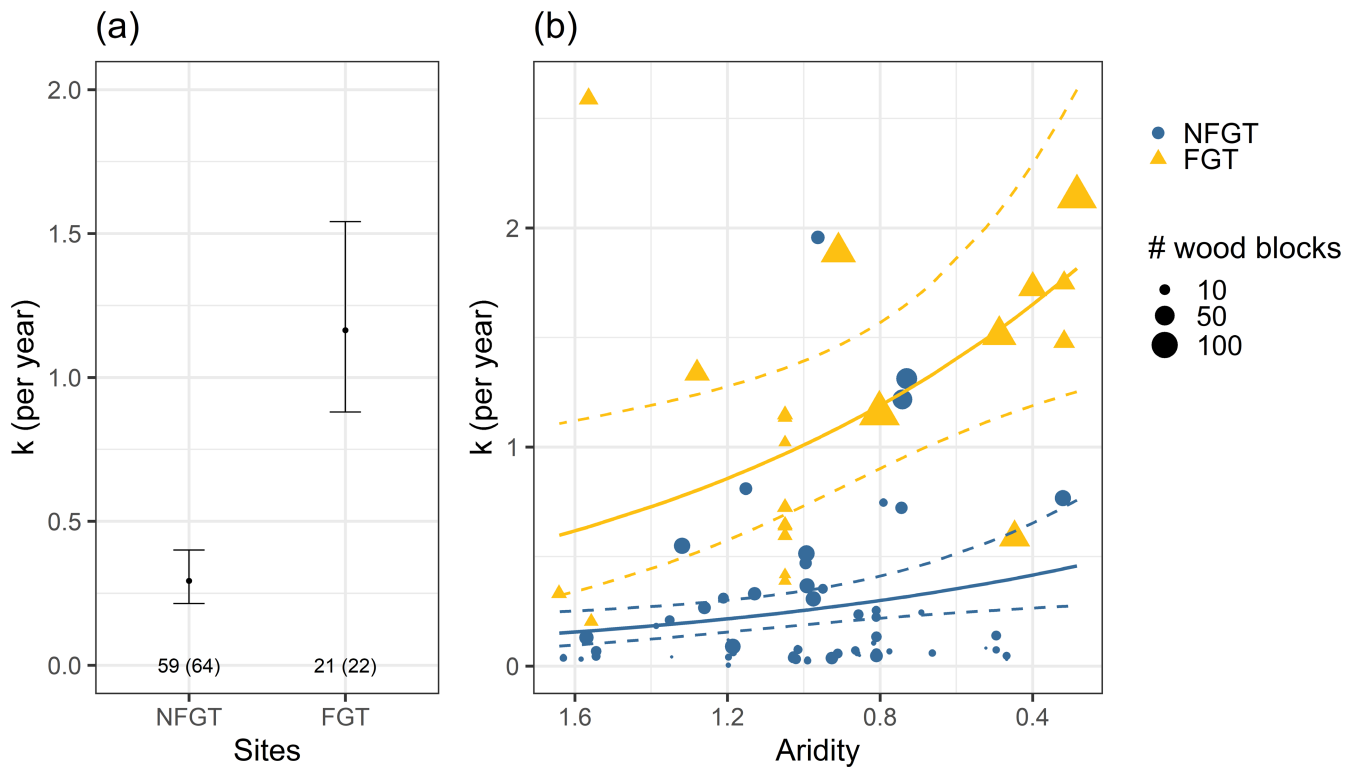
FIGURE 3 | Plots show model predictions for decay rates of discovered deadwood. Panel (a) shows marginal mean estimates (with 95% confidence intervals) for termite-driven decay in sites with non-fungus-growing termites (NFGT) and sites with fungus-growing termites (FGT); figures at the bottom indicate number of sites. No wood blocks were discovered in six sites where wood blocks were deployed (five NFGT sites and one FGT site), thus the total number of sites with discovered deadwood is 80. Panel (b) shows termite-driven decay rates by mean annual aridity for NFGT sites (blue circles) and FGT sites (orange triangles). Lower aridity values indicate more arid regions. Points represent sites ($n = 80$), scaled in size by number of wood blocks discovered at each site. Solid lines indicate predictions for decay rates from multivariate linear regression for NFGT sites (blue) and for FGT sites (orange). Dashed lines represent 95% confidence intervals around predictions.

FGT, known to have large colony sizes and high consumption rates (Buxton 1981; Collins 1983). Fundamental biological and behavioural differences between FGT and NFGT may explain the contrasting patterns found in termite discovery of deadwood with aridity between FGT and NFGT sites. First, unlike NFGT, FGT maintain a fungus comb that has a higher metabolic rate than the termite and is highly efficient at breaking down deadwood (da Costa et al. 2019), it is this selection pressure that drives the higher consumption rate of deadwood by FGT. Second, FGT are better able to conserve moisture and water than most NFGT by foraging under sheeting and protecting the substrate from desiccation (Harit et al. 2017). These results are also supported by regional experiments, which showed that the presence of FGT promote decay rates of deadwood and that their effect is strongest under water-limited conditions (Schuurman 2005; Veldhuis et al. 2017).

Our data have two key limitations. The first, as already mentioned, is that we do not know which species of termite were responsible for decay of wood blocks at each experimental site. The stochastic nature of termite attack, alongside that most wood decay is likely to be from foraging termites rather than nesting termites due to the small size of the wood block, made it difficult to obtain direct samples of termites for identification. Instead, we are confident that FGT were present on the experimental sites and are highly likely to have contributed to the

decay process of deadwood (see Supplementary Material S1). Our findings provide indirect evidence that when present, FGT drive higher rates of discovery and termite-driven decay of deadwood with increasing aridity, at least in Africa. However, further research on the taxonomic composition of termites decaying deadwood is required to truly attribute differences in discovery and decay to specific termite groups.

The second limitation regards the distribution of experimental sites. While our sites cover a variety of biomes (see Zanne et al. [2022] for details) and a wide range of climatic values (Figure S1) that should capture global patterns, only one experimental site is present in Asia (Figure 1). With the exception of *Hypotermes*, which only occurs in Asia, Asian FGT genera are the same (but fewer) than African FGT genera (Aanen and Eggleton 2005), thus we may expect a similar response of Asian FGT to aridity. Still, key differences in ecological strategies exist between some Asian and African FGT species, that may drive differing responses to aridity, chiefly the subterranean nests of many Asian *Hypotermes* species (Thakur 1983) versus the large epigeal mounds of some African *Macrotermes* species. However, regardless of nesting strategy, the efficiency of the fungus comb, driving the high consumption rate of FGT, remains the same across African and Asian genera (Yamada et al. 2005) as does behavioural strategies to withstand desiccation (e.g., foraging under sheeting) (Harit et al. 2017). For these reasons, we

hypothesise that the increased contribution of FGT to deadwood decay with aridity will hold true across Asia. Yet while the importance of termites to deadwood decomposition across Asia is widely reported (Griffiths et al. 2019; Wu et al. 2021), further research across this region is needed to truly discriminate between the role of FGT and NFGT along aridity gradients.

Notably, as we compared FGT sites with NFGT sites that occupied the same aridity range, the lowest aridity value is 0.28 which falls within the classification of semi-arid (UNEP 1997) thus we do not test the most arid regions within FGT realms (Figures 1 and S1). Within more arid drylands such as deserts, it may be that either (1) termite-driven decay does not continue to increase and/or, (2) FGT no longer enhance discovery or decay above that of NFGT (see conceptual diagram in Figure 4a). When we examined all NFGT sites and thus a wider range of aridity values (0.107–2.660 vs. 0.284–1.640), we found no sign that termite-driven decay starts to decline in more arid regions; however this analysis includes only three more sites that are more arid than FGT sites (Figure S3.2).

While the ecological success of FGT in semi-arid savannas has partly been attributed to their climatically buffered mounds (Aanen and Eggleton 2005), in more extreme arid conditions, it is likely more difficult for FGT to maintain optimal climates for their fungal symbiont, which requires a narrow temperature range and high humidity (Korb 2011). Thus, under extreme aridity we may expect the influence of FGT on decomposition to wane. Rather, in desert biomes, termite-driven decay may remain high due to subterranean termites, which avoid inhospitable climatic conditions through underground nests and by approaching food from subterranean foraging tunnels. In arid and hyper-arid environments, specialist termites (nearly all formerly placed in the family Rhinotermitidae) have been identified as important decomposers of deadwood across biogeographic realms including *Gnathamitermes* and *Heterotermes* in Nearctic deserts and xeric shrublands (Haverty and Nutting 1975; Jones

and Eggleton 2011); *Psammotermes* in Afrotropical deserts (Juergens, Groengroeft, and Gunter 2023); and *Coptotermes* and *Heterotermes* in arid savanna and Australasian deserts (Jones and Eggleton 2011). While termites are perhaps the most important decomposers of wood in desert ecosystems (Whitford, Ludwig, and Noble 1992), further research on rates of termite-driven deadwood decay and the relative role of FGT is needed to verify if patterns described here continue into the most arid environments.

Global terrestrial aridity is projected to increase over the coming years under climate change scenarios and may cover more than half of the land area by 2100; however, regional predictions can vary considerably (Mirzabaev et al. 2022). Correspondingly, we may predict an increase in termite discovery and termite-driven decay of deadwood in regions where aridity increases and drylands are expected to expand, particularly between the dry sub-humid and semi-arid boundary (rather than in hyper-arid regions, which are not tested here). Such general predictions are made under the assumption that all termites will be able to expand into new habitable areas and do not consider differential responses of key termite groups to changes in climate or their impacts on decay. For example, our results indicate that should FGT be able to colonise new habitats they could have a greater impact on deadwood decomposition than colonisation by other termite species. Yet this may not be true for hyper-arid regions, indeed the future distribution of some African FGT species is predicted to be constrained by changes in precipitation with a range contraction projected for some species (Seymour et al. 2023). In such cases where the distribution of FGT is predicted to reduce, we may then expect to see a coinciding reduction in deadwood decomposition.

5 | Conclusions

The fate of deadwood under climate change scenarios will depend on the response of the biotic decomposer community. Our
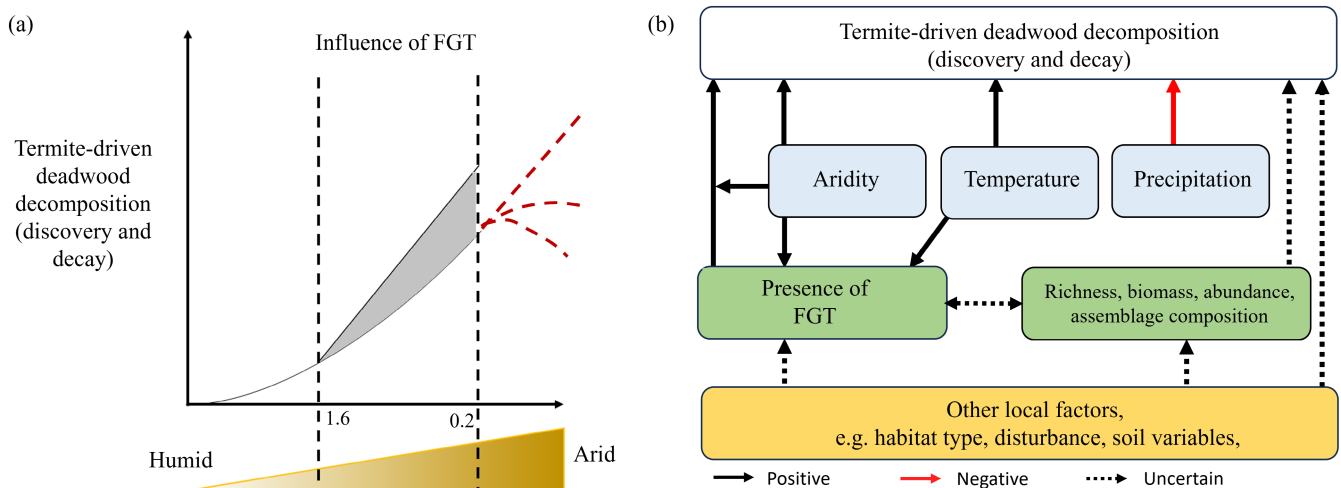

FIGURE 4 | Conceptual diagrams showing in panel (a) the role of aridity on termite-driven decay of deadwood and where fungus-growing termites (FGT) have the greatest influence on deadwood decay (shaded in grey). Vertical dashed lines indicate the range of aridity considered in this analysis and red dashed lines indicate possible trajectories for more arid environments. Panel (b) illustrates the dynamic pathways between climatic (blue) and biogeographical variables regarding termite distribution (green) influencing termite-driven decay of deadwood. Positive associations are indicated in black, negative in red and uncertain associations as dashed arrows.

study builds on previous findings on the climatic sensitivities of termite-driven decay of deadwood, highlighting the importance of aridity. We show for the first time that biogeographical patterns in deadwood decomposition can be attributed to continental differences in termite distribution. We therefore recommend that predictions for termite-driven decay responses considers the dynamic interactions between climatic controls (such as MAT, MAP and aridity) and biogeographical variation in termite distribution, particularly for key groups such as FGT (Macrotermitinae) (Figure 4b).

Author Contributions

The study was conceived and designed by P.E. and S.J.L. Data was obtained from H.F.-M., C.L.P., S.A.-B., K.B., W.K.C., F.E.O., J.R.P., G.W.Q., M.P.R., A.E.Z. and P.E., and collated and cleaned by S.J.L. Data analysis was conducted by S.J.L. with input from H.F.-M., A.E.Z. and P.E., S.J.L. wrote the manuscript with significant input from P.E., H.F.-M., A.E.Z. and K.B. All authors provided intellectual input and edited the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data produced from this study and the R-code to reproduce the analyses and figures are archived on the Dryad Digital Repository at https://doi.org/10.5061/dryad.wwpzgmssd.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.