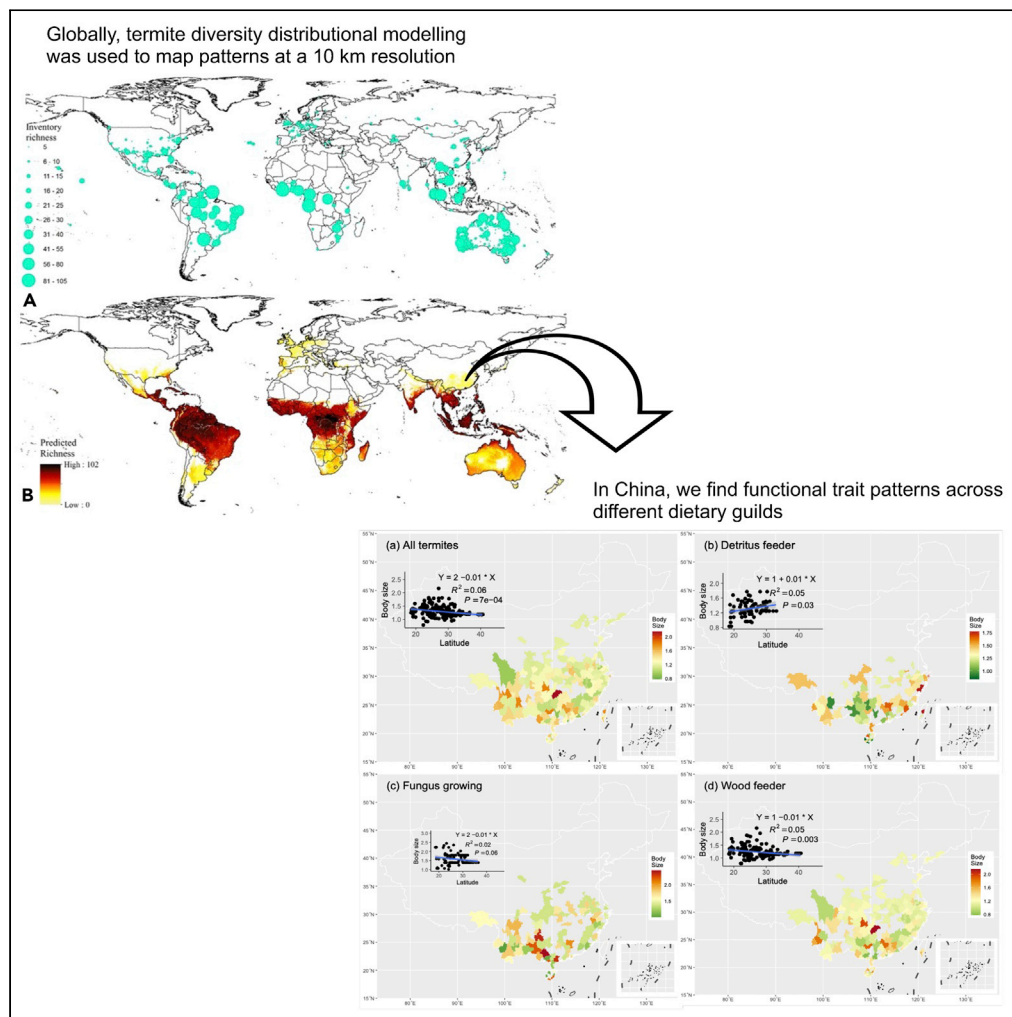


## Article

# Understanding global and regional patterns of termite diversity and regional functional traits



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## Highlights

Termite species diversity  
peaked in tropical regions  
with over 100 species

On average, termite  
species became bigger  
toward the tropics

Temperature, NDVI, water  
were major drivers  
controlling the termite  
richness

Temperature and soil  
were key factors driving  
termite body size

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## Article

## Understanding global and regional patterns of termite diversity and regional functional traits

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## SUMMARY

**Our understanding of broad-scale biodiversity and functional trait patterns is largely based on plants, and relatively little information is available on soil arthropods. Here, we investigated the distribution of termite diversity globally and morphological traits and diversity across China. Our analyses showed increasing termite species richness with decreasing latitude at both the globally, and within-China. In addition, we detected obvious latitudinal trends in the mean community value of termite morphological traits on average, with body size and leg length decreasing with increasing latitude. Furthermore, temperature, NDVI and water variables were the most important drivers controlling the variation in termite richness, and temperature and soil properties were key drivers of the geographic distribution of termite morphological traits. Our global termite richness map is one of the first high resolution maps for any arthropod group and especially given the functional importance of termites, our work provides a useful baseline for further ecological analysis.**

## INTRODUCTION

Understanding the broad-scale biogeographical patterns of species diversity and distributions are central to ecology.<sup>1</sup> However, biogeographical studies have mostly focused on vascular plants,<sup>2</sup> vertebrates<sup>3</sup> or above-ground insects,<sup>4</sup> leaving gaps for groups like soil organisms that comprise an appreciable component of terrestrial biodiversity. Recent efforts to understand global taxonomic diversity patterns of soil organisms have revealed different patterns compared to those observed in above-ground organisms.<sup>5,6</sup> For example, the diversity of earthworm and oribatid mite species increases from the boreal to the temperate region but not further to the tropics.<sup>5,6</sup> Therefore, understanding whether other soil organisms also demonstrate distinctive large-scale biogeographic patterns is a research priority, especially because of their various roles in ecosystem function such as decomposition, nutrient cycling, and so on.

As ecosystem engineers, termites provide a range of ecosystem services: Organic matter decomposition, nutrient re-cycling, and soil structuring, which in turn affect plant growth and diversity, and can even mitigate the negative effects of climatic oscillation.<sup>7</sup> Termites can dominate soil ecosystems as their biomass may represent up to 95% of the overall soil biota in some areas.<sup>8</sup> Although termites represent an ideal study system to examine broad-scale diversity patterns because of good knowledge of their taxonomy, morphological traits and variety of ecosystem functions, their broad-scale biogeographical patterns have yet to be extensively investigated.<sup>8</sup>

Functional trait data are becoming increasingly important especially under global change that may alter the composition of communities across the globe.<sup>9</sup> Functional traits provide valuable insights unavailable from taxonomy alone into the processes behind local community assembly.<sup>10</sup> From a functional biogeography perspective of soil fauna, very few studies have been conducted, yet also show intriguing patterns such as the increase in body size of ground-dwelling beetles along a latitudinal gradient.<sup>11</sup> Meanwhile, the body size of a single ant species (*Leptothorax acervorum*) from the boreal zone was 10% larger than from temperate regions.<sup>12</sup> Based on these lines of evidence, we predict that termite functional traits (body size and leg length) follow Bergmann's rule which states that organism body size increases with increasing latitude.<sup>13</sup>

Termite species feed on a wide range of material, including leaf-litter, dead wood, soil and grass, indicating that termite functional trophic groups may be influenced by varying environmental factors that affect their

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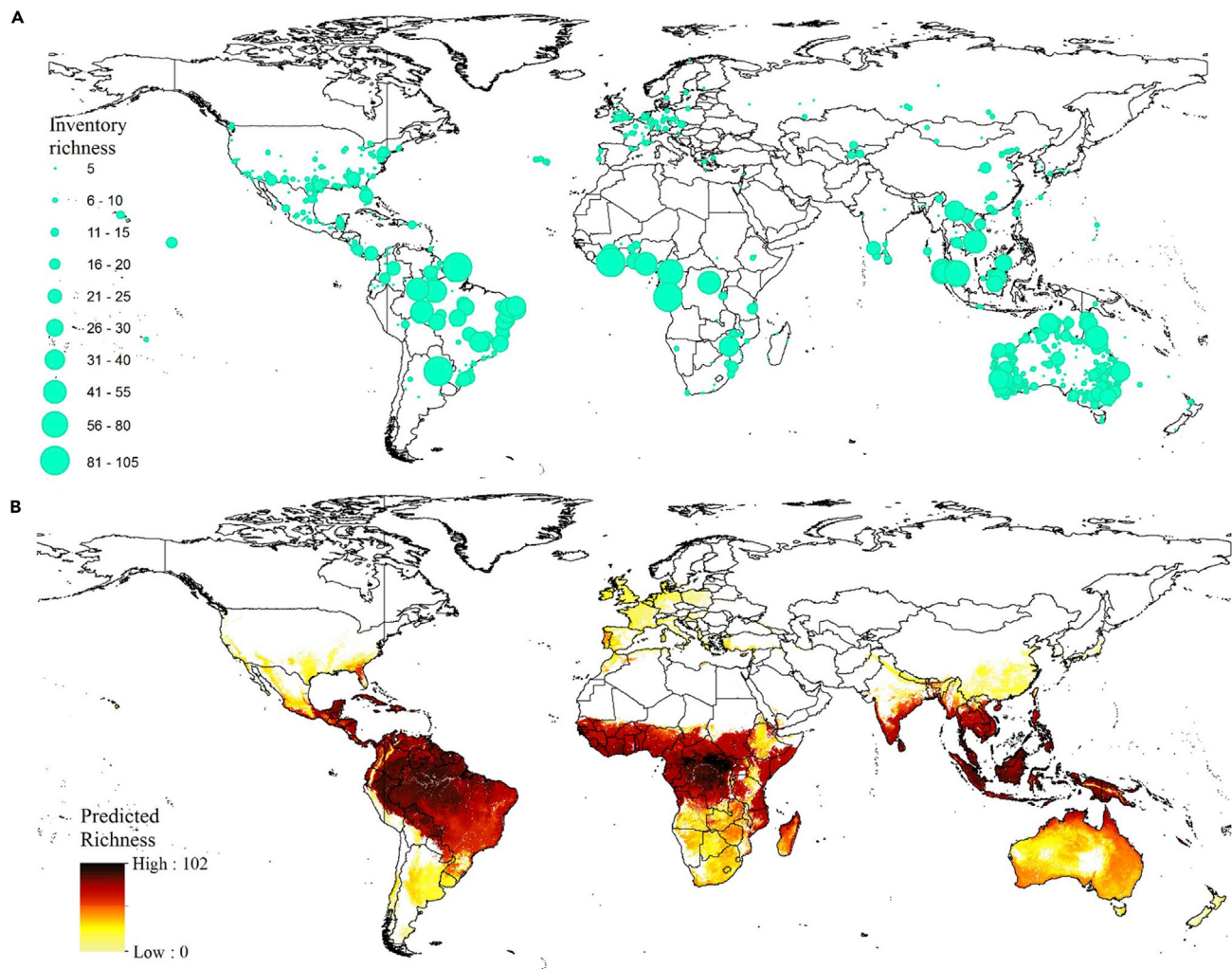
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**Figure 1. Global termite richness based on a global model of inventory data using Maxent**

Points show initial inventory data (A), whereas the color ramp projects the maxent projection of species diversity (B). White in panel B indicates no species.

food sources<sup>14</sup> According to their prevailing diet, termites can be assigned to three categories: Wood feeders, fungus growing and detritus feeders for functional biogeographic analyses.<sup>14</sup> To explore patterns in termite taxonomic richness and functional biogeography, we created a dataset of termite species and their functional traits together with environmental data. We explore patterns of termite taxonomic biogeography at the global scale. Because of a lack of functional trait data at the global scale, we explore the patterns of termite functional biogeography across China. At both the global and within-China scales, we determine what environmental factors explain termite taxonomic and functional biogeography, and how these compare between different scales. We expect that tropical regions will have higher termite diversity because high turnover of plant materials and diverse niche availability could potentially support high diversity.<sup>15</sup> Following Cerezer et al.,<sup>16</sup> we also expect that minimum temperature is the primary factor determining termite latitudinal diversity gradient at larger spatial scale as it may impose a limit to survivability in some regions, but different termite feeding groups may have different responses to the environmental factors.

## RESULTS

### Global termite richness pattern and driving environmental factors

Using Maxent, richness was projected globally (Figure 1). Highest richness was most challenging to predict because of the lack of large numbers of very high inventories, with the highest predicted richness for a

**Table 1. Variable contribution scores and permutation importance of each factor considered in global Maxent richness models at different termite richness levels**

Species richness	5	10	15	20	25	30	40	55	80	105
bio6 contribution	17.38	3.66	2.72	1.68	11.56	<b>50.35</b>	<b>51.17</b>	<b>50.20</b>	<b>33.87</b>	<b>25.63</b>
bio6 permutation	<b>27.33</b>	9.36	<b>37.39</b>	<b>28.28</b>	<b>34.39</b>	<b>62.05</b>	<b>41.53</b>	<b>87.84</b>	<b>37.90</b>	<b>29.85</b>
clay contribution	1.65	2.10	3.35	4.68	2.30	4.21	0.43	0.00	0.58	2.54
clay permutation	1.45	1.84	1.77	5.96	5.31	5.48	0.64	0.00	0.81	2.43
epca contribution	3.96	4.67	9.33	6.20	0.41	1.23	0.90	0.08	0.04	3.45
epca permutation	8.12	8.90	16.10	15.52	3.31	5.41	4.37	0.71	0.05	5.83
ndvi contribution	1.40	1.49	13.95	1.19	1.80	1.94	0.28	10.82	<b>29.99</b>	<b>19.46</b>
ndvi permutation	3.32	2.10	18.66	3.05	3.87	4.01	1.19	7.85	<b>49.26</b>	<b>25.27</b>
ph contribution	4.22	4.66	1.12	3.00	<b>20.85</b>	3.38	<b>28.17</b>	8.44	1.56	1.48
ph permutation	1.08	4.52	1.88	0.82	<b>23.71</b>	1.37	<b>45.57</b>	2.85	0.00	0.16
silt contribution	8.46	15.95	11.64	13.11	5.11	2.32	6.04	0.00	0.00	14.47
silt permutation	7.59	11.70	12.03	13.55	9.21	4.76	6.69	0.00	0.00	14.83
tpca contribution	<b>43.70</b>	<b>49.40</b>	<b>45.42</b>	<b>48.74</b>	<b>53.76</b>	<b>23.05</b>	13.01	30.47	<b>32.10</b>	<b>30.80</b>
tpca permutation	<b>28.81</b>	39.32	7.34	6.55	11.02	0.51	0.00	0.75	8.50	17.75
wPCA contribution	<b>19.24</b>	18.07	12.47	<b>21.40</b>	4.21	13.51	0.00	0.00	1.87	2.16
wPCA permutation	22.31	22.26	4.83	26.26	9.18	16.41	0.01	0.00	3.47	3.86

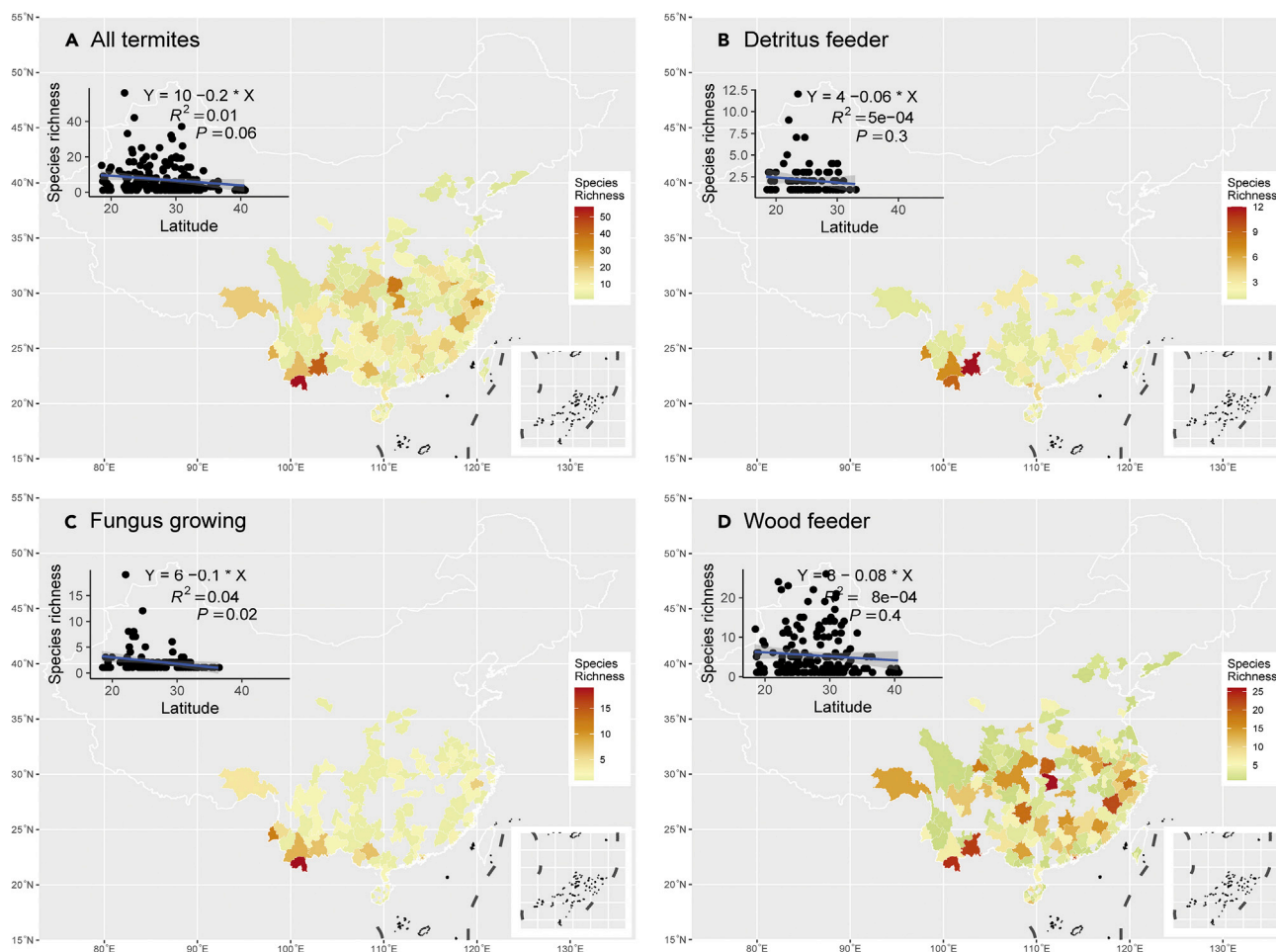
Bio6 = Min Temperature of Coldest Month. W-moisture related, T-temperature related, E-energy related, pca = Principal Component Analysis. Significant driving environmental factors are highlighted in bold font.

10 km area reaching up to 105 species in parts of central Africa, global models performed the best for modeling because of a higher number of high inventories for modeling. Projected diversity peaked in the equatorial tropics in Africa, Central America and parts of India showing some of the highest levels of richness. As good lists of non-native species were not available for everywhere we model total richness of all termites present, and inventories were only removed when they clearly did not match those from surrounding areas and represented either a port, or in some cases major cities.

Patterns in the global model match those available for some parts of the world (i.e., Australia) and conform to the coarse-scale maps previously published. The AUC of the global map was on average 0.93 for testing and 0.9 for training, with the only richness level falling below 0.87 for testing being the highest diversity level (105) at 0.67. For these global models the main drivers of termite richness were the temperature sPCA layer followed by the water sPCA layer until a richness of 25 species based on variable contribution (Table 1), and up to 10 species based on permutation importance. In both cases this transitioned to minimum temperature as the main driver, highlighting the importance of factoring in ecophysiological limiting variables. NDVI was also a major driver based on both measures at richness levels of 80 and 105 species. Different regions largely showed similar drivers, but this may have changed if we had been able to run the separate guilds at a regional level. However, a relative consistency in patterns and processes at regional and global levels supports the patterns here, as significant divergence in any regions would have required further work to understand the discrepancy.

### Termite richness patterns of diet guilds within China and driving environmental factors

Guild and ecophysiological models were only run for China (National). We ran our analysis twice—once for all of China to determine the role of different environmental factors in the overall distribution of termites and identification of any ecophysiological limits. We ran it a second time just for areas with termites recorded to look at drivers across their range. The termite species richness in each prefectural-level city ranged from 1 to 56 species across China. Our results show notable latitudinal trends in termite diversity in all termites and the fungus growing group, with the highest richness in southern China (Figure 2). We used multimodel selection to identify the best model explaining termite diversity. The best model for overall richness included a number of variables relating to moisture (aridity), thermal stability, minimum temperature of the coldest month, thermicity, evapotranspiration, and variables based on nesting ability (variability in soil silt levels) and carbon availability (both above and below ground) ( $n = 322$ ,  $r^2$  Adj = 0.35, AICc: 2099.47). The top



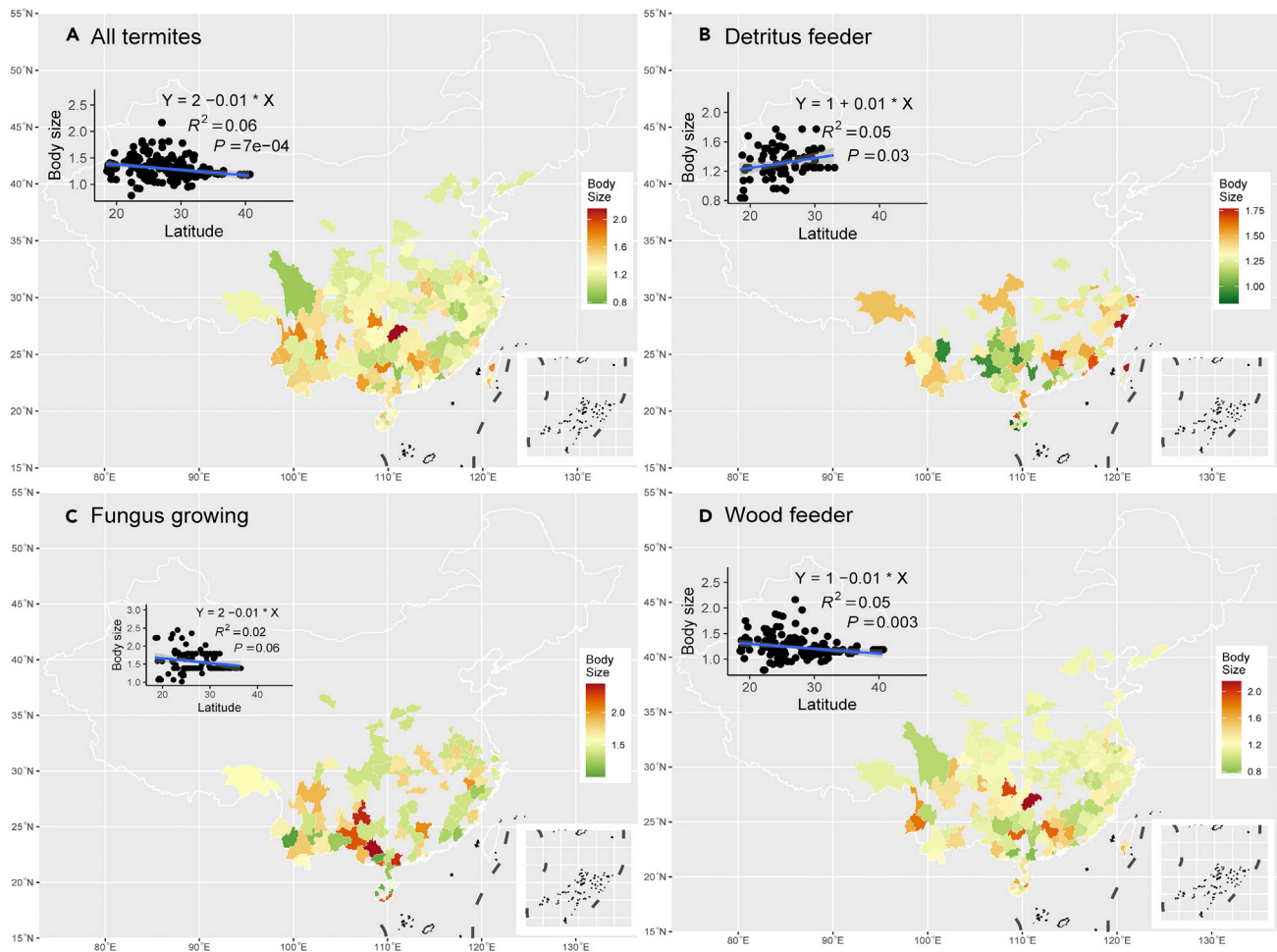
**Figure 2. Distribution map of termite species richness in China**  
(A) all termites, (B) detritus feeders, (C) fungus growing, (D) wood feeders.

variables were aridity (mean), silt (std), mean minimum temperature of the coldest month, temperature seasonality and isothermality, AGB (mean), Actual evapotranspiration (std) and precipitation of the driest month (mean), showing diversity was highest in warm areas which were not highly arid. Therefore, we also ran this analysis for just the part of China with termite populations, which highlighted the importance of above and belowground carbon, silt, clay, and aridity (in addition to minimum temperature ( $n = 239$ ,  $r^2$  Adj = 0.30, AICc: 1625.07).

Richness for all three termite diet types is highest in Yunnan (Figure 2). Species with fungal diets were limited to the tropics. The best model for wood diets for the whole of China used six variables ( $n = 322$ ,  $r^2$  Adj = 0.27, AICc = 1872.72), which are silt (mean and standard deviation), potential evapotranspiration, above ground carbon biomass and mean NDVI as well as aridity. For the wood diet, the best model included a combination of productivity variables (NDVI mean, as well as above and below ground biomass) ( $n = 239$ ,  $r^2$  Adj = 0.23, AICc = 1452.02), silt, and wilting point.

For a national fungal diet, the best model had nine variables ( $n = 322$ ,  $r^2$  Adj = 0.40, AICc = 1135.98), these included both above and below ground mean biomass, mean NDVI, standard deviation in tree density and above ground biomass, actual evapotranspiration and like many others was limited by minimum temperature. Of interest, at the country level, no other soil variables were listed. The best model for fungal diets used six variables, below ground biomass, aridity, maximum and minimum temperature, growing degree days, wilting point, annual precipitation, percentage clay in soil and tree density, indicating such species are more common in hot, forested areas ( $n = 239$ ,  $r^2$  Adj = 0.18, AICc: 971.92).





**Figure 3. Distribution map of termite body size in China**  
 (A) all termites, (B) detritus feeders, (C) fungus growing, (D) wood feeders.

National detritus diet was largely driven by carbon (above and below ground biomass, soil carbon) and included nine variables in the final model ( $n = 322$ ,  $r^2 \text{ Adj} = 0.41$ , AICc: 952.58). Thermicity and several measures of temperature stability were also influential as well as soil silt content. Detritus diet used seven variables in the best model ( $n = 239$ ,  $r^2 \text{ Adj} = 0.41$ , AICc: 768.43). These included two soil variables (mean silt and standard deviation in wilting point), above and below ground carbon biomass, thermicity and mean annual temperature.

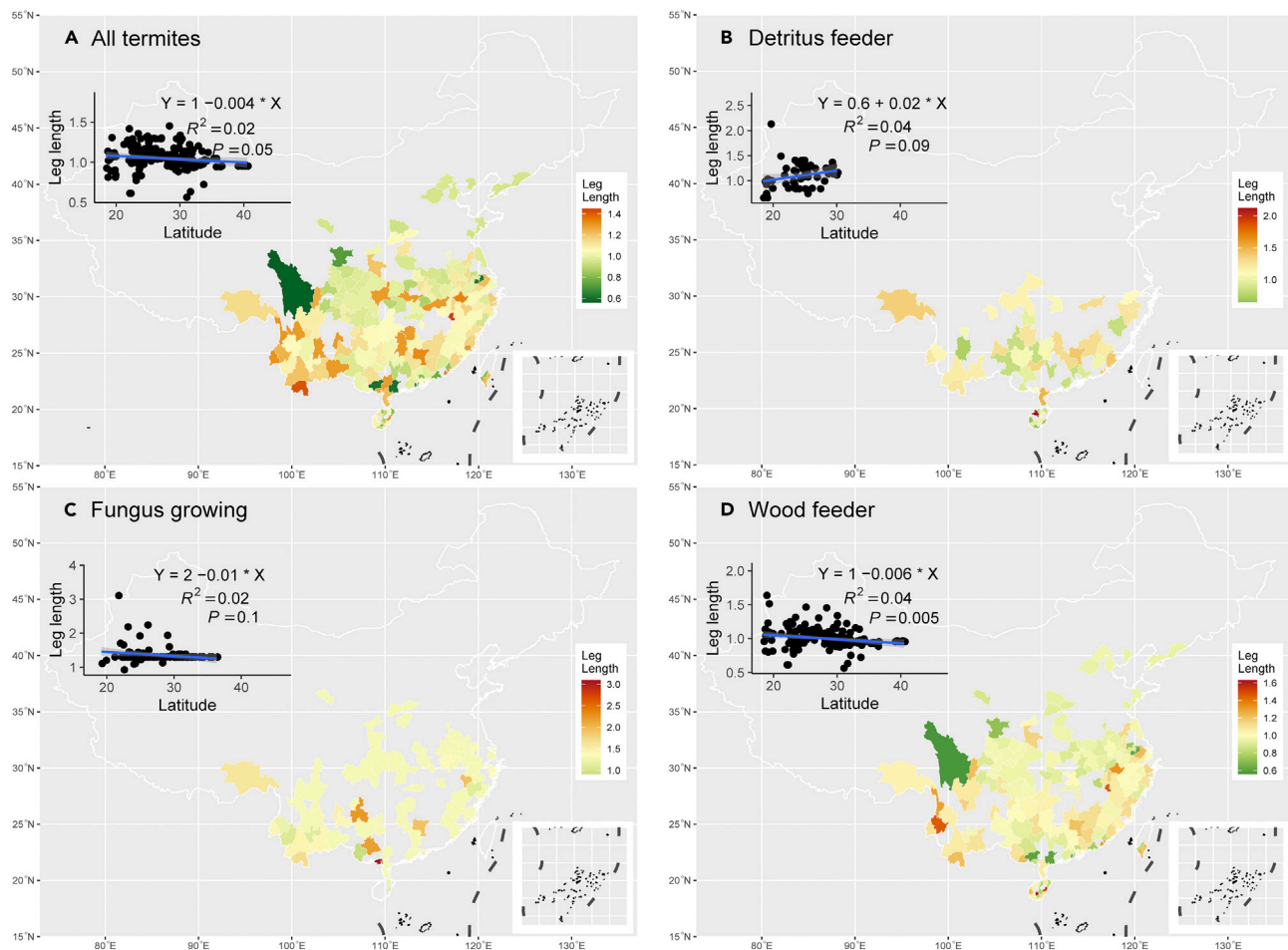
### The geographic distribution of termite morphological traits in China

Whilst most traits showed a generally negative relationship with latitude (particularly body size), most traits showed a major decrease in size at the tropical to temperate transition and then largely plateaued (Figures 3 and 4, supporting information Appendix2-Figures S1–S3). Once Hainan Island is excluded (as the area is a diverse island with many endemic species and may skew patterns) all traits show a weak negative correlation, showing that most components of body traits appear to get smaller at higher latitudes (linear regression models for each trait: Body size  $\hat{y} = 2 - 0.01X$ , leg length  $\hat{y} = 1 - 0.004X$ , mandible length  $\hat{y} = 1 - 0.007X$ ) (Figures 3 and 4, supporting information Appendix2-Figure S1). It should also be noted that pronotum variables showed a much less consistent response than other traits (supporting information Appendix2-Figures S2 and S3).

## DISCUSSION

### The geographic distribution pattern of termite diversity

Our findings are in general agreement with geographic distribution pattern of many aboveground organisms, such as vascular plants,<sup>2</sup> mammals,<sup>3</sup> and birds<sup>17</sup> and belowground organisms, such as soil fungi,<sup>5</sup>



**Figure 4. Distribution map of termite leg length in China**  
(A) all termites, (B) detritus feeders, (C) fungus growing, (D) wood feeders.

which found that average species diversity decreased with increasing latitude. This has also been found in many regional studies.<sup>8</sup> In contrast, topsoil bacteria<sup>18</sup> and earthworms<sup>6</sup> show the opposite pattern that higher species diversity was found at temperate region at global scale. However, our results are consistent with previous termite work, which shows decreased termite diversity away from the tropics,<sup>19</sup> and our work highlights the strong influence of minimum temperature as a major factor both at national, regional and global scales.

NDVI and plant biomass was shown to be a major driver for the highest levels of global richness, which indicated that termite diversity is supported by available food resources in areas where the minimum temperature is not too low, and despite known evolutionary differences between regions<sup>19</sup> these universal trends persist. Because higher net primary production will lead to higher amounts of wood fall, leaf-litter and grass which are major food sources for termites,<sup>20</sup> therefore, NPP can influence the termite richness by changing energy availability. Our analysis highlighted that whilst soil parameters were important, the ecophysiological limitation of minimum temperatures, and the need for available food resources were the major drivers at all levels. However, it should be noted that differing pressures will exist in each region as in addition to different resources and pressures there have been different selective pressures across their evolutionary history.<sup>21</sup>

### The geographic distribution of termite morphological traits

Our analysis revealed that the whole community mean value of termite morphological traits generally does differ across different prefectural-level city ranges in China. Furthermore, the correlation analysis revealed that termite body sizes tend to increase as they approach the equator. Bergmann's rule states that organism

body size increases with increasing latitude gradient,<sup>13</sup> yet no consistent patterns along latitude have emerged for a range of arthropods studied. For example, Heinze et al.<sup>12</sup> found that the body size of an ant species (*L. acervorum*) follow Bergmann's rule; Classen et al.<sup>22</sup> demonstrated that bee species show the opposite pattern at the community level; and Haga and Rossi<sup>23</sup> show no relationship between body size of seed-feeding beetle with latitude gradient. Thermoregulatory or heat conservation hypothesis, large organisms with lower surface-to-volume ratio are better enabled to conserve heat in cold regions, proposed to explain Bergmann's patterns,<sup>13</sup> yet how this rule can be usefully applied to ectotherms requires further study. It should also be emphasized that other factors besides temperature, for instance food resources, predation, habitat heterogeneity, may covary along latitude, and are possible to impose selective pressure on morphological traits.<sup>9</sup> For example, food availability decreased with increasing latitudinal gradient and has been proposed as the determinant of beetle size latitude gradients.<sup>11</sup> Reduced habitat complexity selected for ants with longer legs, which provides important benefits (higher motility) in simpler ground surface.<sup>24</sup> Therefore, morphological trait variation across altitude gradients largely reflect historical patterns of speciation within and between taxa in each biogeographical region.<sup>9</sup> This is a key point as more diverse communities are more likely to have a diversity of traits, whereas as diversity declines at high latitudes this variation may also be reduced. In addition, soil-dwelling organisms such as termites may expect to experience thermal buffering, meaning they are less exposed to extreme temperatures unless the soil either dries out, or freezes, and thus traits that vary in species above ground may be of less relevance to subterranean species.

### The relationships between functional traits of termite and environmental factors

In our study, soil properties were the most important driver of termite body size, with a largely negative effect. Negative correlations between soil properties and termite body size occur as a result of soil heterogeneity distribution in China. Our data reveal large termite body sizes in the southern China, and these regions have low soil organic carbon density,<sup>25</sup> which could supply basic resources for termites and drive bigger body sizes.<sup>26</sup> Meanwhile, termite species specialized toward foraging sites rich in soil organic matter to enhance nutrient intake,<sup>27</sup> which probably explains why soil factors influence termite body size.

Our results also showed that temperature factors are the major predictor of termite body size across China, especially for detritus feeders and wood feeders. For many species, temperature is likely to affect metabolism, development and growth, which can influence species body size.<sup>28</sup> In addition, termite morphological traits (such as leg length and mandible length) may also be affected by predation pressure and physical structure of the habitat floor since these traits are related to foraging behavior and defense.<sup>29</sup>

This is first study to quantitatively model termite diversity and functional traits at large scales. We mapped out global patterns of termite richness, showing some differences in driver importance in some regions, and a strong latitudinal diversity gradient with diversity declining away from the tropics. This same latitude pattern was also shown in China, which is unsurprising as China marks the northern distribution of termite distributions in Asia. Moreover, our datashow the soil and temperature was the most important driver controlling the variation in the geographic distribution of termite functional traits. Mapping the distribution of functional traits is central to the quantification of ecosystem functioning because functional biogeography links species functions to their environment. Our analysis shows the complementarity between analysis conducted at two different scales, and showed consistent drivers and patterns in both Chinese and global analysis. Access to resources combined with ecophysiological limits impact both overall diversity and functional traits, and thus provide a fundamental basis for understanding the diversity of termites across scales.

### Limitations of the study

Given the lack of accurate trait data for termites globally we were unable to project differing global distributions for the different diet and nesting guilds, and thus had to assume similar ratios in each group and similar drivers overall. In addition, we acknowledge that some parts of the world have less data, and thus our analysis assumes that by using a large global database we can capture representative global patterns, and whilst these patterns are independently compared and assessed, countering a lack of data is challenging. Future work should explicitly and representatively work to fill such gaps.

### STAR★METHODS

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

- [KEY RESOURCES TABLE](#)



- **RESOURCE AVAILABILITY**
  - Lead contact
  - Materials availability
  - Data and code availability
- **METHOD DETAILS**
  - Global species distributional modelling
  - Modelling distributions globally
  - China termite species richness data
  - Morphological trait data for China
  - Environmental data
- **QUANTIFICATION AND STATISTICAL ANALYSIS**

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.105538>.

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## AUTHOR CONTRIBUTIONS

S.L., S.X., and X.Y. conceived the experiment. S.L., S.X., and A.C.H. conducted the experiments, collected and analyzed data. All authors wrote the manuscript, reviewed and commented on the manuscript.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
<b>Deposited data</b>		
Global termite richness inventory dataset	termite database records and GBIF records	<a href="https://www.termitediversity.org/">https://www.termitediversity.org/</a> <a href="https://doi.org/10.15468/dl.yd4edv">https://doi.org/10.15468/dl.yd4edv</a>
Termite morphological trait data in China	Zhang Guangyue, 2000. Fauna Sinica Insecta, Vol.14 Homoptera.	<a href="https://figshare.com/s/ed5fb4688a5b7d3ddd4f">https://figshare.com/s/ed5fb4688a5b7d3ddd4f</a>
<b>Software and algorithms</b>		
Maxent	American Museum of Natural History	<a href="https://biodiversityinformatics.amnh.org/open_source/maxent">https://biodiversityinformatics.amnh.org/open_source/maxent</a>
ArcGIS	ESRI	<a href="http://www.arcgis.com">www.arcgis.com</a>
R	Statistical software for data science	<a href="https://www.r-project.org">https://www.r-project.org</a>

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources should be directed to the lead contact: Shengjie Liu ([liushengjie@xtbg.ac.cn](mailto:liushengjie@xtbg.ac.cn)).

#### Materials availability

This study did not generate new unique reagents.

#### Data and code availability

- Relevant data in our study are available in the data repository <https://figshare.com/s/ed5fb4688a5b7d3ddd4f>, <https://www.termitediversity.org/>, <https://doi.org/10.15468/dl.yd4edv>
- This study does not generate original code and the R code is available from the supplementary file [Data S1](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

### METHOD DETAILS

Analyses were conducted globally using inventory data from plots across the planet combined with predictive analyses, and at a national scale for China using detailed guild-based data. These are detailed in sections below.

#### Global species distributional modelling

##### *Global termite data aggregation*

To generate a dataset of termite species richness across the globe, we aggregated data on termite species distributions and inventories of species richness. We combined inventory data based on datasets from Li et al.,<sup>30,31</sup> Liu et al.,<sup>29</sup> Cerezer et al.,<sup>16</sup> termite database records (<https://www.termitediversity.org/>) and GBIF records (<https://doi.org/10.15468/dl.yd4edv>) which included over 148151 additional records, almost entirely collated since 2000. After removing any duplicate records (same species at same latitude and longitude) this provided a total dataset of 2503 inventories, with a reasonable coverage across most termite-occupied parts of the planet. Termite inventories of richness were developed by creating 10 km grids and inventorying the number of species recorded (from a minimum of 50 records) using the “extract values to points” function in ArcMap 10.3 followed by using summary statistics to count the number of species recorded within each 10 km grid. This termite layer was then scrutinized to remove erroneous records. For example, ports often had high numbers of records which were clearly not representative of the taxa within the rest of the country and were probably due to alien species being imported on wood, but could

not be easily filtered out because of a lack of complete checklists. These were noted when certain areas within a country had disproportionately higher richness than anywhere else. In these cases, species lists were examined, and if large numbers appeared to be non-native (at least 3x higher than anywhere else in the country [region for Europe], or if they were the sole record for the country the adjacent countries, based on searches of species listed) to the region the area was removed due to likely non-representative listings. In these cases, we looked at the inventory to determine the presence of species not listed as native, and if it corresponded with a city or port, it was removed (all flagged cases corresponded with this).

### Modelling distributions globally

To model species richness patterns on a global basis, we combined three spatial layers representing patterns of water availability, energy and temperature variation with inventories of termite diversity (supporting information Appendix2-Table S3, which axis each variable was considered in is noted as E, T or W; layers within these were processed in ArcMap 10.3 and the first layer retained). Spatial Principal Component Analysis (sPCA) was used to create three sPCA layers (reflecting water, energy and temperature, based on analysis of layers within those categories) that were used in analysis as these contained the maximum amount of variability, but would not reflect the changes in ecophysiology and regional patterns which are likely to persist in some parts of the world, which is why some more specific environmental variables were not included. These three types of layers followed the approach using the principal components tool in ArcMap 10.3<sup>32</sup> to create one sPCA representing energy likely to be directly available to species (solar, net primary productivity etc.). These variables will impact energy availability, and also have direct ecophysiological implications for the species. Additional variables were added including minimum temperature (this was shown by the Chinese analysis (see later text) as being critically important to determining species survival), NDVI (representing net primary productivity), and soil pH, clay and silt (based on the Chinese models, outlined later in text) to represent key soil variables in addition to resources directly available, but some guilds in different parts of the world may be more dependent on them so generalizing globally might be misleading. These variables were included because they improved model performance (based on AUC) and because of their known ecophysiological significance. Furthermore, we aimed capture the overall variability in patterns through the sPCA and capture any ecophysiological limits and thresholds (also highlighted in the China specific analysis). Analysis showed that there is a threshold effect for minimum temperature, and so it should be included, but to ensure all patterns were captured in the sPCA (which collapses out variation onto a minimal number of axes) it was added in both. It is also likely that whilst small differences in temperature are important in all areas with a moderate temperature range, minimum temperature becomes increasingly important at the edges of the range close to species thermal tolerance limit, thus this approach is likely to more accurately represent patterns. Environmental factors were chosen as variables which may either directly impact species survival or control their access to resources, these factors and the categories they represent are provided in supporting information Appendix2-Table S3. Whilst factors related to soil (etc.) are not captured by these layers, given the lack of detailed data in many parts of the world and differences in regional traits as a consequence of biogeography or adaptation could lead to biases in the model if run with these more ecophysiology-specific types of layer.

sPCA layers were also created for the four regions (Americas, Europe-Africa, Asia and Australia), models were both run for regions independently and combined, and the best model was then selected based on concurrence with observation data. This was done to understand different global and regional drivers, the final models were best when using the global model (likely because of sample size, as some regions had less data) and so whilst we discuss regional differences in drivers, the map results are from the global model.

Richness classes based on these inventories were then grouped into divisions (of 5 up to 30, then richness values of 40, 55, 80 and 105) and Maxent was used to model richness based on the association between species richness based on the approach used by Orr et al.<sup>32</sup> These categorical richness levels were used because there would be too few samples if each inventory value was run independently, and because inventories are unlikely to be complete. Maxent was used based on default settings, with the ten-percentile training presence (as threshold as a baseline for unsuitable), and three replicates were run to remove stochasticity from models.

In addition to a global model, models were run separately for the Americas, Europe-Africa, Asia and Australia. Above this baseline value, the probability of occurrence was split into equal divisions to match the original values as similar to probability of occurrence. For example those with a value of 5 were classed to have 6 values, with those below the cumulative logistic threshold as 0 and equal divisions of 1–5 above this. Higher value areas likely supported more species. Reclassified model outputs were then combined in ArcMap (10.3, ESRI) using the Mosaic function and specifying the maximum value from overlapping reclassified layers to give the maximum number of species the area was suitable for based on all models together.

### China termite species richness data

Our termite species distribution data in China were primarily extracted from the book, *Fauna Sinica Insecta Vol.14 Isoptera*<sup>33</sup> and supplemented with other papers on Chinese termites (supporting information Appendix 1). Our database included in total 473 termite species belonging to 41 genera and 5 families across 182 prefectural-level cities of the 293 prefectural-level cities spanning latitudinal and longitudinal gradients across China. The remaining 111 cities were not included due to insufficient data on termite species present.

After data had been formatted to connect species level data to prefectures, analysis on drivers could be conducted. First some data standardization was needed, as in some cases data was listed at a county level, and these areas were too small for standard analysis (some counties didn't have any species data and were much smaller than most counties), thus counties were merged with adjacent counties to form three regions. Counties with no species records, but with counties with attributes on all sides, were removed from analysis, as they were likely to represent incomplete inventories rather than species-poor regions. In addition, we separated the regions of China with species recorded, and buffered them with one county to the side (included adjacent states in analysis to account for missing data) to explore drivers of variation other than not being able to survive below certain temperatures.

### Morphological trait data for China

Our functional traits were based on four morphological traits and diet characterizations. We summarized data on four morphological traits measured in the soldier caste of all termite species: (i) head width, as an indicator of overall body size; (ii) leg length, right tibia length as a surrogate measurement of leg length which is related to motion behaviour; (iii) mandible length, which play crucial roles in defence; (iv) pronotum length and width, the pronotum trait is related to foraging behavior and defence.<sup>29</sup> According to their prevailing diet and microhabitat type where they were observed, termites were assigned to three categories: wood feeders, fungus growing and detritus feeders.<sup>14</sup> Wood feeding termites primarily excavate and feed on fallen wood, and the fungus growing group of termites cultivate fungi to help them degrade complex lignin and cellulose, and detritus feeders which primary feed on leaf litter.<sup>14,34</sup>

As species distributions were listed to prefectural or county level the centroids of the area were used for analysis. Species-level average measurements for each trait were associated with distribution data using the joins and relates function in ArcMap 10.3, then the maximum, minimum and mean latitude of occurrence extracted using summary statistics, and these were cross-compared with the environmental conditions in these areas (see section 2.3). We used only species-level averages in traits and did not have sufficient data to assess intraspecific trait variation. For species with a total latitudinal range of under 5°, and not distributed exclusively on Hainan (as a tropical island species limited here are biogeographically restricted, and may be subject to pressures which are less relevant to mainland patterns) species were categorized into eight categories of latitudinal distribution limits based on their ranges and evidence of latitudinal shifts in traits explored using a simple linear regression. The termite mean trait value of at the prefectural-level cities were independent variable and the latitude of each prefectural-level city were response variable in the linear regression model.

### Environmental data

Variables included a range of variables related to climate, soil dimensions which may impact on food resources or nesting ability, carbon related variables and productivity variables, such as annual mean temperature, soil carbon content, NDVI (Normalized Difference Vegetation Index), above-and below ground biomass etc. (see more detail and data source in supporting information Appendix2-Table S1). The average and the standard deviation of each variable was extracted for each administrative region using the zonal statistics function. These were then collated into a table and joined to the shapefile of data



complete with the species attributions (richness and feeding and nesting habits). This shapefile was then exported and explored using the software Spatial Analysis for Macroecology (SAM) (<https://ecoevol.ufg.br/sam/>). GLMs with a Gaussian distribution were then used to assess the relationship between each variable and richness, then the top 14 variables analyzed in multimodel selection based on AIC to understand the most appropriate variable combination to explain richness patterns for each trait under examination (supporting information Appendix2-Table S2). Initially models were selected based on regressions between richness and each variable independently, the fourteen top variables were then used in a GLM, though for variables found to show high collinearity (as noted in model outputs) only the one with the highest independent regression score was retained. AIC shows model performance, and SAM will try all model combinations and derive an AIC and R for each. From each stage we used the top performing model and if it had under 14 variables we reran with the next highest variable, until model performance ceased to improve. The most effective model and most important drivers detailed in results.

### QUANTIFICATION AND STATISTICAL ANALYSIS

All results were repeatedly performed and confirmed by supplemental file Sets. Quantification and statistical analysis are presented in [method details](#).