

Conservation and Biodiversity

Utilization of Community Science Data to Explore Habitat Suitability of Basal Termite Genera

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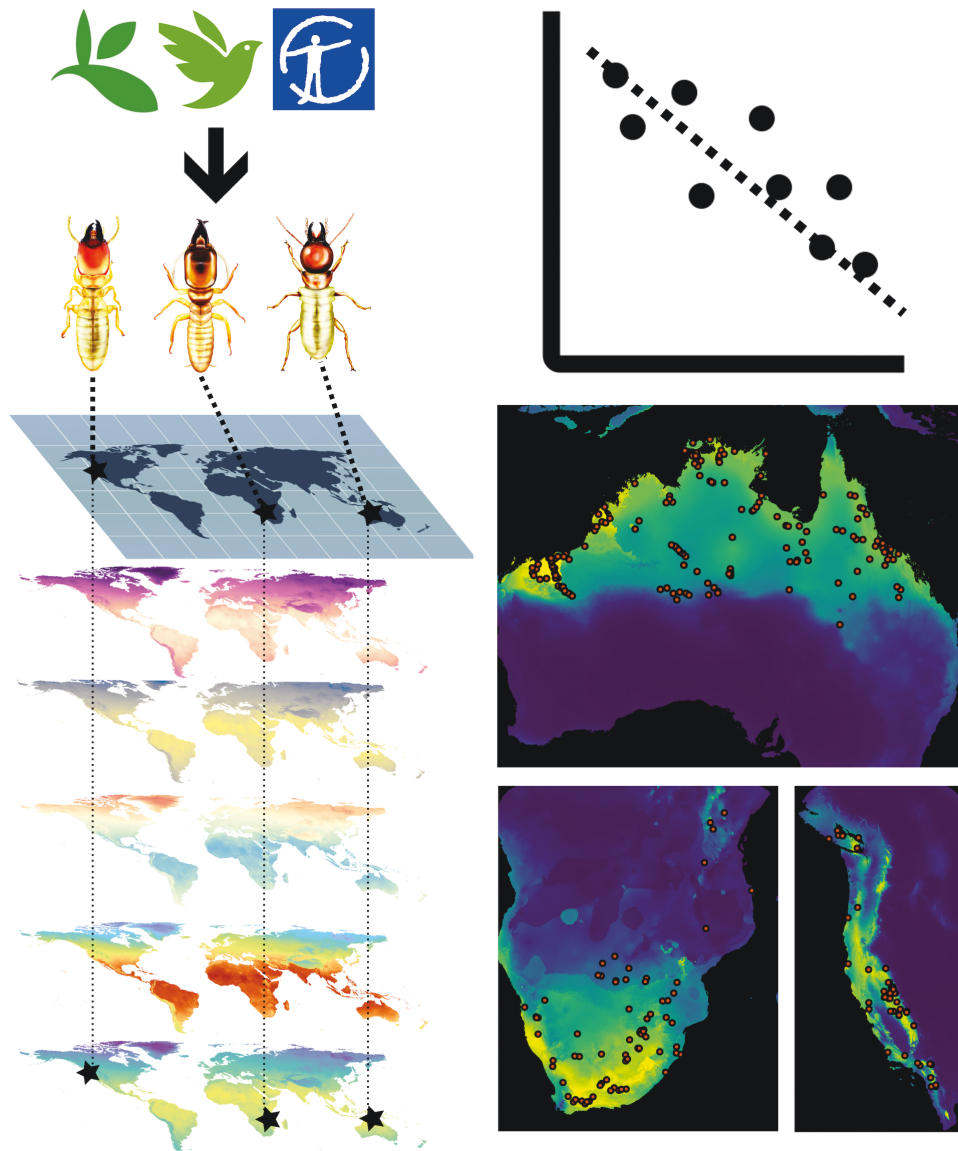
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Abstract

The advent of community-science databases in conjunction with museum specimen locality information has exponentially increased the power and accuracy of ecological niche modeling (ENM). Increased occurrence data has provided colossal potential to understand the distributions of lesser known or endangered species, including arthropods. Although niche modeling of termites has been conducted in the context of invasive and pest species, few studies have been performed to understand the distribution of basal termite genera. Using specimen records from the American Museum of Natural History (AMNH) as well as locality databases, we generated ecological niche models for 12 basal termite species belonging to six genera and three families. We extracted environmental data from the Worldclim 19 bioclimatic dataset v2, along with SoilGrids datasets and generated models using MaxEnt. We chose Optimal models based on partial Receiving Operating characteristic (pROC) and omission rate criterion and determined variable importance using permutation analysis. We also calculated response curves to understand changes in suitability with changes in environmental variables. Optimal models for our 12 termite species ranged in complexity, but no discernible pattern was noted among genera, families, or geographic range. Permutation analysis revealed that habitat suitability is affected predominantly by seasonal or monthly temperature and precipitation variation. Our findings not only highlight the efficacy of largely community-science and museum-based datasets, but our models provide a baseline for predictions of future abundance of lesser-known arthropod species in the face of habitat destruction and climate change.

Graphical Abstract



Key words: termite, maxent, niche modeling, temperature, precipitation

Termites (Blattodea), are social cockroaches that are ubiquitous globally. Termite taxonomic groups were historically defined by the presence or absence of certain gut endosymbionts; they were originally divided into the ‘higher termites’ (Termitidae), and the ‘lower termites’ (all other families) based on the endosymbiotic fauna in their hindguts, which are responsible for digestion of the cellulose in the wood termites consume. Flagellated protists, archaea, and bacteria are found in the hind guts of ‘lower termites’ inherited likely from nonsocial cockroach ancestors (Cleveland 1923, Brugerolle and Radek 2006, Engel et al. 2009, Dietrich et al. 2014, Poulsen 2015, Korb et al. 2019); ‘higher termites’ instead rely solely on bacteria and their host cellulases, or fungi, to digest cellulose (Brune and Ohkuma 2010, Poulsen 2015). Recent classification instead defines two major groups, the non-Neoisoptera and Neoisoptera (Engel et al. 2009); the Neoisoptera are a monophyletic group of termites which possess a fontanelle for

defense in the soldier caste, (comprising the ‘lower termite’ families Stylotermitidae, Serritermitidae, and Rhinotermitidae as well as the ‘higher termite’ Termitidae) include several common pest termites. The non-neoisopteran taxa form a paraphyletic assemblage, with the monophyletic family Kalotermitidae recovered as sister to the Neoisoptera. The Kalotermitidae were considered ‘lower termites’ based on their endosymbiotic fauna, and the family includes several hard wood feeding species that are economically important pests. By contrast, harvesters’ termites, which are non-Kalotermitidae, non-neoisopteran termites (including Stolotermitidae, Archotermopsidae, and Hodotermitidae) that form a taxonomic assemblage at the basal nodes of the termite tree of life are less well studied since few are structural pests, and they are far rarer in online databases of termite records (Fig. 1). Termite niches have not been well studied empirically, and here we use Ecological Niche Modeling to evaluate the climatic variables shaping termite distributions.

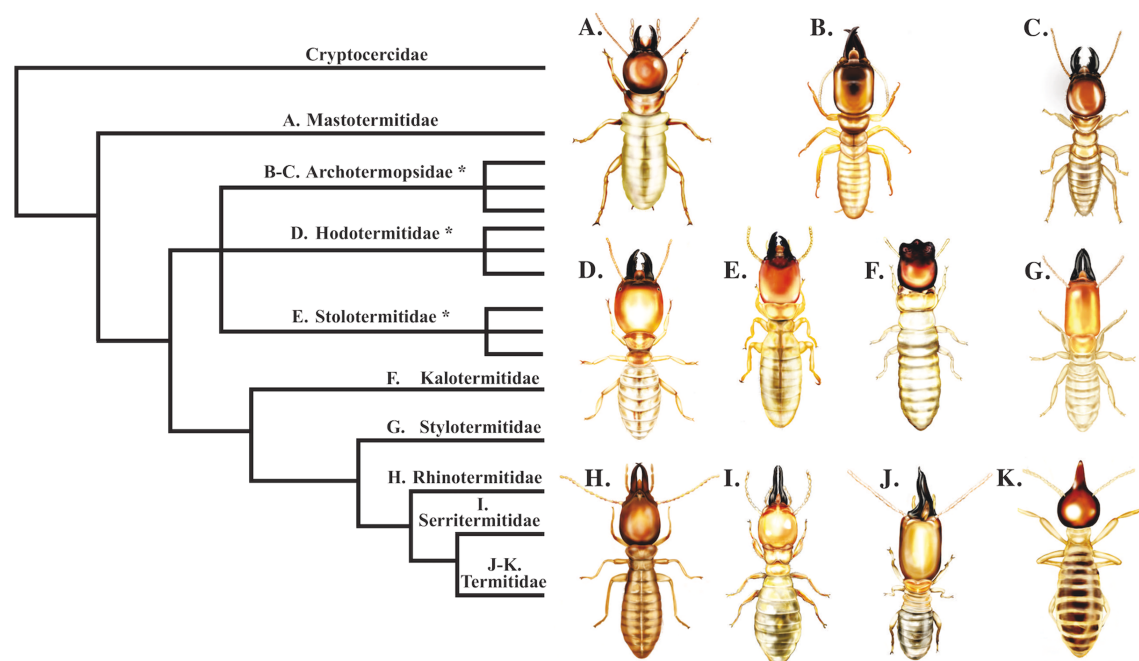


Fig. 1. Summary tree showing current state of termite phylogeny. Simplified schematic based on familial termite relationships recovered with high support in (Engel et al. 2009, Legendre et al. 2015). Stylotermitidae is placed in its current position based on (Bucek et al. 2019). Branches representing unresolved relationships (bootstrap values < 75) are indicated by *. The cockroach family Cryptocercidae was used as an outgroup, and soldier illustrations correlate with families used in summary tree. **A.** *Mastotermes* (Froggatt 1897, Blattodea Mastotermitidae), **B.** *Zootermopsis angusticollis* (Hagen 1858, Blattodea, Archotermopsidae), **C.** *Hodotermopsis sjostedi* (Holmgren 1911, Blattodea, Archotermopsidae), **D.** *Anacanthotermes ochraceus* (Burmeister 1839, Blattodea, Hodotermitidae), **E.** *Porotermes adamsoni* (Froggatt 1897, Blattodea, Stolotermitidae), **F.** *Cryptotermes brevis* (Walker 1853, Blattodea, Kalotermitidae), **G.** *Stylotermes halumicus* (Liang, et al. 2017, Blattodea, Stylotermitidae), **H.** *Coptotermes formosanus* (Shiraki 1909, Blattodea, Rhinotermitidae), **I.** *Serritermes serrifer* (Hagen and Bates, Blattodea, Serritermitidae), **J.** *Neocapritermes tarqua* (Krishna and Araujo 1968, Blattodea, Termitidae), **K.** *Nasutitermes corniger* (Motschulsky 1855, Blattodea, Termitidae)

Ecological Niche Modeling (ENM) is a ubiquitous technique utilized by ecologists to estimate the abiotic distribution of a species by correlating observational (occurrence) data with spatially explicit environmental data (Guisan and Zimmerman 2000, Guisan and Thuiller 2005). Occurrence data is commonly obtained from natural history collections, community science observations, or abundance data based on field sampling, while environmental data is typically derived as climate variables from field stations or remote sensing satellites. These models are generated and overlaid on a Geographical Information System (GIS) to visually interpret the factors which underlie the species' distribution. Such modeling has become an essential tool for addressing issues in ecology, evolution, biogeography, conservation biology, and climate change (Guisan and Zimmerman 2000; Guisan and Thuiller 2005; Pearman and Weber 2007; Pearman et al. 2008; Peterson 2011; Peterson et al. 2011; Anderson 2012, 2013).

To reduce spatial biases within modern-day ENMs, occurrence data must be sampled throughout the entire range of the taxon (Peterson 2011). Such information is crucial for assessing environmental suitability of regions or times of interest for species or genus-level niche characteristics. In recent years, the centralization of large biodiversity datasets (GBIF, iNaturalist) has allowed more accurate and large-scale modeling of species distributions where localities accrued from museum specimens are lacking. Such aggregated biodiversity datasets possess extreme potential for determining habitat suitability of endangered or lesser-known arthropod species. Although ENM has been used for several insect groups (Urbani et al. 2017, Kass et al. 2020, Lee et al. 2021), for the social cockroaches, commonly called termites, niche modeling has not been widely implemented beyond pest taxa and

invasive species (Tonini et al. 2014, Maynard et al. 2015, Cramer et al. 2017, Hyseni and Garrick 2019, Hochmair et al. 2020).

A recent review of available records noted that most termite observations seem to be available from Australia, where Stolotermitidae are most species rich (Hochmair et al. 2020), however, GBIF, iNaturalist and other databases have generally had far fewer records from the non-Kalotermitidae, non-Neoisopteran families and museums currently hold the bulk of geographic range information for these taxa. To date, no ecological niche modeling has been undertaken for a majority of such 'lower termites' including *Mastotermes* Froggatt 1897 (Mastotermitidae Desneux 1904), *Stylotermes* Hagen, 1858, *Porotermes* Hagen, 1858 (Stolotermitidae Holmgren 1910), *Hodotermes* Hagen 1853, *Zootermopsis* Emerson 1993, *Archotermopsis* Engel et al., 2009, *Hodotermopsis* Holmgren, 1911 (Archotermopsidae Engel et al., 2009). Ecological niche modeling has only been performed for *Microhodotermes* Sjöstedt (Hodotermitidae) (Cramer et al. 2017).

Non-Kalotermitidae, non-neoisopteran termites are generally found in the southern hemisphere, except for *Zootermopsis*, a genus distributed in the Southwestern United States including, Arizona, New Mexico, and Mexico, as well as the Pacific northwest coasts including California, Oregon, Washington, and Canada. Hodotermitidae include taxa from the Middle East, Africa, and Southwest Asia, while Stolotermitidae has a disjunct distribution extending through Eastern Australia & New Zealand, southern Africa, and South America. Archotermopsidae is similarly disjunct with representatives found in Africa, Asia, and North America. The family Mastotermitidae is the earliest branching lineage in the termite tree of life, but the sole living representative, *Mastotermes darwiniensis*,

currently restricted to Australia and New Zealand (but with a broader fossil distribution) is a highly apomorphic taxon (Nalepa and Jones 1991, Thorne and Carpenter 1992, Thorne et al. 2000, Zhao et al. 2019) (Fig. 1). The remaining extant families generally make small to moderate sized colonies (but these can be rather large in *Microhodotermes*), and only Hodotermitidae have true worker castes, with Stolotermitidae and Archotermopsidae instead having pseudergates (Legendre et al. 2015). Hodotermitidae are typical harvesters, feeding on grasses, twigs, bark, and laying pheromone trails (Krishna et al. 2013a). Archotermopsidae and Stolotermitidae include species which feed on rotting wood (Krishna et al. 2013a). In most of these non-Kalotermitidae non-neoisopteran taxa pair bonds are formed between male and female mates (Grasse 1947, Nalepa and Jones 1991).

Here, we used specimen records from the American Museum of Natural History (AMNH) termite collection, The Global Biodiversity Information Facility (GBIF.com), and iNaturalist to generate MaxEnt models for select species in the genera *Hodotermes*, *Mastotermes*, *Microhodotermes*, *Porotermes*, *Stolotermes*, and *Zootermopsis*. This project is the first to utilize community-science and museum biodiversity data to construct full-range habitat suitability models of non-Kalotermitidae, non-neoisopteran termites outside of a single study on *Microhodotermes* (Cramer et al. 2017). The aim of this project is to create ecological niche maps for these enigmatic 'lower termites', which we hope will be used by future studies as a baseline when making predictions. Additionally, given recent fires and ongoing anthropogenically driven habitat alteration, these models can be used by future studies to make predictions about potential shifts in the ranges of these species.

We used the machine learning algorithm Maxent v3.4.4. (Maximum entropy) (Phillips and Dudík 2008), which remains one of the top-performing algorithms for fitting presence-background SDMs (Valavi et al. 2021) in conjunction with the kuenm R package (Cobos et al. 2019). To evaluate models, we used the 'checkerboard' method of spatial partitioning in which a checkerboard grid is overlaid across our study extent, and localities are partitioned into two separate bins based on their placement (50% testing, and 50% training) (Radosavljevic and Anderson 2014). As the combination of two key complexity settings in Maxent models, feature classes and regularization multipliers, can strongly influence model outputs (Warren and Seifert 2011, Radosavljevic and Anderson 2014), we tuned model complexity to find optimal settings. This process consists of varying complexity settings, running models with combinations of these settings, and finally selecting optimal settings based on performance metrics. Feature classes determine the shape of the model fit, while regularization multipliers control how much complexity is penalized—this can result in predictor variable coefficients shrinking to 0 and thus dropping out of the model (Phillips and Dudík 2008). For tuning, in order of increasing complexity, we chose the feature classes linear (L), quadratic (Q), and hinge (H), as well as regularization multipliers 1 through 5 (higher numbers penalize complexity more). We excluded from consideration other available feature classes because of difficulties in interpretation and excessive complexity (product), and due to redundancy with existing classes (threshold) (Phillips et al. 2017). The regularization multiplier value range we chose includes the default value of 1, but also values higher than this to fit simpler models; this approximate range is typically used for studies with similar sample sizes (Moreno-Amat et al. 2015, Kass et al. 2020).

We assessed model performance through statistical significance of the partial Receiver Operating Characteristic (ROC) and omission rate, and chose the optimal model based on the Akaike Information

Criterion for low sample sizes (AICc) (Cobos et al. 2019). Within the kuenm R package, statistical significance among models is determined via bootstrap resampling of 50% of the testing data, with probability distributions assessed by direct count of the proportion of bootstrap replicates possessing an AUC value of ≤ 1.0 (Cobos et al. 2019). AUC ranges from 0 (no-better-than-random prediction) and 1 (perfect prediction) (Peterson et al. 2008, Peterson 2011). Model performance was measured via omission rate in which a threshold is applied to a continuous model prediction. Application of the threshold makes the model binary, in which points are categorized as either within or outside the prediction. We set our omission rate to 10% ($E = 10\%$) which excludes the lowest 10% of values of points within a prediction, making it the strictest of all binary predictor metrics for MaxEnt (Peterson and Soberón 2012, Kass et al. 2021). Model performance is assessed by AICc which indicates how well models fit into our data while penalizing complexity to favor simpler models (Warren and Seifert 2011). AICc is calculated by standardizing the raw scores of all Maxent models within geographic space to sum to one, then multiplying the suitability scores of each grid cell containing a presence. The number of parameters (nparam) is measured by counting all parameters with a nonzero lambda weight (Warren and Seifert 2011). Among models which were statistically significant, we selected the optimal model with the delta AICc ≤ 2 and had omission rates below 10%. In the event of multiple models possessing significance, we opted for simpler models (fewer features and regularization). We generated the final model using our thinned occurrence dataset with 10 bootstrap replicates with 'cloglog' outputs, and generated distribution predictions using each species' uncorrelated environmental dataset.

We documented variable importance and marginal response curves to better understand the modeled relationships between the predictor variables and our data for each final model. We recorded the permutation importance metric output by Maxent, which is calculated by randomly permuting the values of all environmental variables but one, building a new model, then calculating the difference between each model's training AUC and that of the empirical model (Phillips 2005). Marginal response curves are generated by constraining all predictor variables but one to their means, then making model predictions along the full range of the focal variable associated with the training data. These curves show the modeled relationship of each variable individually with the occurrence data when all other variables are held constant and are affected by the complexity of the model settings (Phillips et al. 2017).

Suitability predictions, permutation analyses, and response curves revealed differences in bioclimatic variable importance among termite genera despite geographic overlap. Predictions for *Microhodotermes viator* and *Porotermes planiceps* (Mastotermitidae) revealed high overlap in suitability within the southwest tip of South Africa, however suitability extends eastward along the coast of South Africa in *P. planiceps* (Fig. 2A and B). Permutation analyses revealed that Mean Diurnal Range (bio02), pH in H₂O, possessed high variable importance within optimal models of *M. viator* and *P. planiceps*, with both variables exhibiting negative linear response curves. Volumetric fraction of coarse particles, soil suborder and proportion of silt particles possessed high variable importance in *M. viator*, with response curves exhibiting positive quadratic, and positive and negative linear relationships with suitability. Furthermore, suitability was highest within cambisol, greysol, and plinthosol soils. Within *P. planiceps*, proportion of clay particles possessed high permutation importance, exhibiting a negative linear relationship with suitability (Table 3).

Hodotermes mossambicus also shared significant overlap in suitability with *M. viator* and *P. planiceps*, but suitability extends

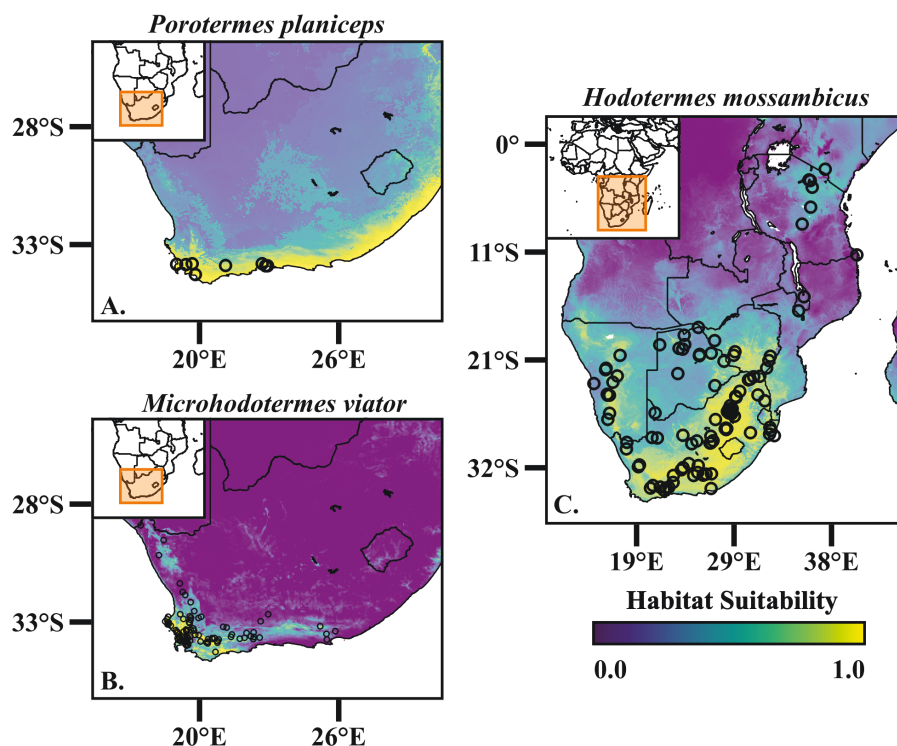


Fig. 2. Termite SDM predictions for species located within South Africa (top and bottom), and Argentina (right) for **A.** *Porotermes planiceps* (Stolotermitidae) **B.** *Microhodotermes viator* (Hodotermitidae), and **C.** *Porotermes quadricollis*. Final model predictions were generated using our thinned occurrence dataset and final set of uncorrelated environmental variables for each species, with 10 bootstrap replicates with 'cloglog' outputs in which raw values are converted to a range of 0–1 to approximate a probability of occurrence (Cobos et al. 2019). Brighter shades indicate areas of higher suitability (higher probability of occurrence), while darker shades indicate areas of lower suitability (lower probability of occurrence).

northward into Namibia, Botswana, Zimbabwe, and Mozambique (Fig. 2C). Precipitation of the wettest month (bio13), isothermality (bio03), pH in H2O, Proportion of silt particles, and maximum temperature of the warmest month (bio05) possessed the highest permutation importance, with response curves exhibiting predominantly negative linear, or positive hinge relationships (Table 3).

Predictions for *P. quadricollis* revealed high suitability within northwest Argentina (Fig. 3A). Isothermality (bio03), and Soil suborder possessed the highest permutation importance with response curves exhibiting positive linear relationships with suitability; suitability was highest within cambisol soil (Table 3).

Predictions for *S. ruficeps* revealed high suitability along the northeastern coasts of the southern island of New Zealand, with additional areas of high suitability within the southern interior of the southern island (Fig. 3B). Soil suborder possessed the highest permutation importance, with suitability being highest within cambisol soils.

Predictions for *S. brunneicornis* revealed high suitability throughout Tasmania (Fig. 3C), with mean diurnal range (bio02), minimum temperature of the coldest month (bio06), isothermality (bio03), proportion of clay particles, and precipitation of the driest month (bio14) possessing the highest permutation importance. Response curves revealed positive and negative linear relationships with suitability.

Predictions of *Z. angusticollis* and *Z. nevadensis* (Stolotermitidae) possessed substantial overlap in suitability along the coasts of northwest California, Oregon, Washington, and British Columbia (Fig. 4A and B). Annual mean temperature (bio01), and soil suborder possessed high permutation importance within optimal models of both species, with response curves exhibiting positive linear relationships.

Zootermopsis angusticollis possessed high variability in soil suborder, with suitability being highest within Calcicols, Histols, Lixisols, Luvisols, Phaeozems, and Planosols, while suitability was highest in leptosols for *Z. nevadensis*. Mean diurnal range (bio02), precipitation of the driest month (bio14), and pH in H2O, also possessed the high permutation importance within *Z. angusticollis*, with response curves exhibiting positive and negative linear relationships. Precipitation of the wettest month (bio13), and precipitation seasonality (bio15) possessed high permutation importance within *Z. nevadensis*, with response curves exhibiting positive and weak negative linear relationships with suitability (Table 3).

Predictions for *Z. laticeps* revealed high suitability within southern Arizona, New Mexico, and northern Mexico (Fig. 4C). Soil pH, soil suborder, volumetric fraction of coarse particles, precipitation of the driest month (bio14), and isothermality (bio03) possessed the highest permutation importance, with response curves exhibiting positive and negative linear relationships; suitability was highest within Gleysol and Podzol soils (Table 3).

Predictions of *P. adamsoni* and *S. victoriensis* (Mastotermitidae) possessed significant overlap in suitability along southeast Australia, and Tasmania (overlapping with *S. brunneicornis*) (Fig. 5A and B). Mean diurnal range possessed high permutation importance within both species' optimal models, with response curves exhibiting a negative linear relationship with suitability. Precipitation of the driest month (bio14), proportion of silt particles, pH in H2O, minimum temperature of the coldest month (bio06), and volumetric fraction of coarse particles possessed high permutation importance within *P. adamsoni*, with response curves exhibiting positive quadratic, and negative hinge relationships with suitability (Table 3). Precipitation of the driest month (bio14), proportion of clay

Table 1. Termite species chosen for analysis, with sample size of occurrence localities before and after spatial thinning by 5 km, and geographic range of species

Species	No. occurrences	Thinned occurrences	Countries
Archotermopsidae			
<i>Hodotermes mossambicus</i>	139	108	South Africa, Namibia, Botswana, Angola, Zimbabwe, Mozambique
Hodotermitidae			
<i>Mastotermes darwiniensis</i>	277	173	Northern Territory, Queensland, Western Australia
Mastotermitidae			
<i>Microhodotermes viator</i>	203	89	South Africa
<i>Porotermes adamsoni</i>	147	98	New South Wales, Victoria, Queensland
<i>Porotermes planiceps</i>	15	8	South Africa
<i>Porotermes quadricollis</i>	14	10	Chile, Argentina
<i>Stolotermes brunneicornis</i>	51	28	Tazmania
<i>Stolotermes ruficeps</i>	23	14	New Zealand
<i>Stolotermes victoriensis</i>	45	31	Victoria, New South Wales, Queensland
Stolotermitidae			
<i>Zootermopsis angusticollis</i>	466	234	Baja, California, Oregon, Washington, British Columbia
<i>Zootermopsis laticeps</i>	92	27	Arizona, New Mexico, Chihuahua
<i>Zootermopsis nevadensis</i>	56	50	Baja, California, Oregon, Washington, British Columbia

particles, soil suborder, and isothermality (bio03) possessed high permutation importance within *S. victoriensis*, with response curves exhibiting positive quadratic and negative linear relationships with suitability; suitability was highest within cambisol soils (Table 3).

Finally, Predictions for *M. darwiniensis* (Hodotermitidae) revealed high suitability within northern Australia (Fig. 5C). Precipitation seasonality (bio15), proportion of silt particles, isothermality (bio03), proportion of clay particles, and annual mean temperature (bio01), possessed the highest permutation importance, with response curves exhibiting positive quadratic, and positive and negative linear relationships with suitability (Table 3).

Although the data for some species is presently limited due to lack of occurrences, the results were generally robust, with most species possessing at least 0.70 AUC_{test} , and 10% omission less than 0.1. Species which possessed low AUC_{test} (<0.70) include *S. ruficeps*, and *Z. laticeps*. Even though the true geographic extent of *S. ruficeps* is well known (i.e., it is endemic to New Zealand), occurrences were low for this species ($n = 8$), and there was unequal sampling across both islands, which may explain why the model possesses an omission rate equal to zero. *Zootermopsis laticeps* possessed higher occurrence records ($n = 27$), however, the lack of knowledge about the true geographic range of the species potentially resulted in an underfit model, explaining the low AUC_{test} and no 10% omission; the same can be said for *P. quadricollis*. Omission rates fluctuate more readily in low occurrence models since fewer data points can dictate the 10% threshold of omission regardless of the spatial partition involved (Radosavljevic and Anderson 2014). Preliminary data in which occurrence points for *S. ruficeps*, *Z. laticeps*, and *P. quadricollis* were partitioned using the 'jackknife' method revealed more complex models and 10% omission rates closer to 0.1, suggesting our models are overfitting due to the lack of knowledge about the species' ranges or lack of occurrence records. In general, these species are not common in collections, but if collection information from multiple museums were incorporated this could potentially be overcome if that data was accessible. A potential pitfall for termite species is the lack of taxonomic knowledge for proper

species identification by community scientists, as well as spatial uncertainty of occurrences, which may slow down the accumulation of research grade occurrences (Araújo et al. 2019).

The presence of simple feature classes, combined with high AICc values suggests underfitting of several species' models (Phillips and Dudík 2008, Warren and Seifert 2011, Radosavljevic and Anderson 2014). Optimal models for *H. mossambicus*, *P. adamsoni*, *Z. angusticollis*, and *Z. nevadensis* were explained by either linear or hinge feature classes and high degrees of regularization suggesting heavy penalization on overcomplexity, combined with high AICc values indicates overly simple models (Warren and Seifert 2011). Overfitting is also apparent within the models for *S. ruficeps*, *Z. laticeps*, *P. quadricollis*, and *P. planiceps*. Even though the AICc values for the three species are minimal (163 - 590), this may be an artifact due to the small sample sizes of occurrence data. Furthermore, all three species models are explained by simple feature classes and high regularization, but low numbers of coefficients (1–8 parameters) (Table 2). High numbers of coefficients in a model suggest high degrees of variable contribution among multiple variables resulting in high regularization to reduce the noise of multiple variables (Phillips and Dudík 2008, Warren and Seifert 2011, Radosavljevic and Anderson 2014). However, fewer coefficients and high regularization results in a handful of variables dictating the model, increasing chances for overfitting. Underfitting is further supported by the prediction rasters produced. Predictions for *H. mossambicus*, *S. ruficeps*, *Z. laticeps*, *P. quadricollis*, and *P. planiceps* possess large areas of intermediate suitability, with minimal areas of distinct high or low suitability indicative of a generalist model (Phillips and Dudík 2008, Warren and Seifert 2011, Radosavljevic and Anderson 2014) (Figs. 2A, C, 3A,B, and 4C). Optimal models for *S. brunneicornis* are explained by simple linear or hinge feature classes, however, their AICc values and coefficients are very low, suggesting less overfitting (Warren and Seifert 2011). Predictions for *S. brunneicornis* possess more distinct boundaries of areas of high or lower suitability (Fig. 3C). Finally, optimal models for *M. darwiniensis*, *M. viator*, and *S. victoriensis*, possess linear quadratic feature classes, low degrees of

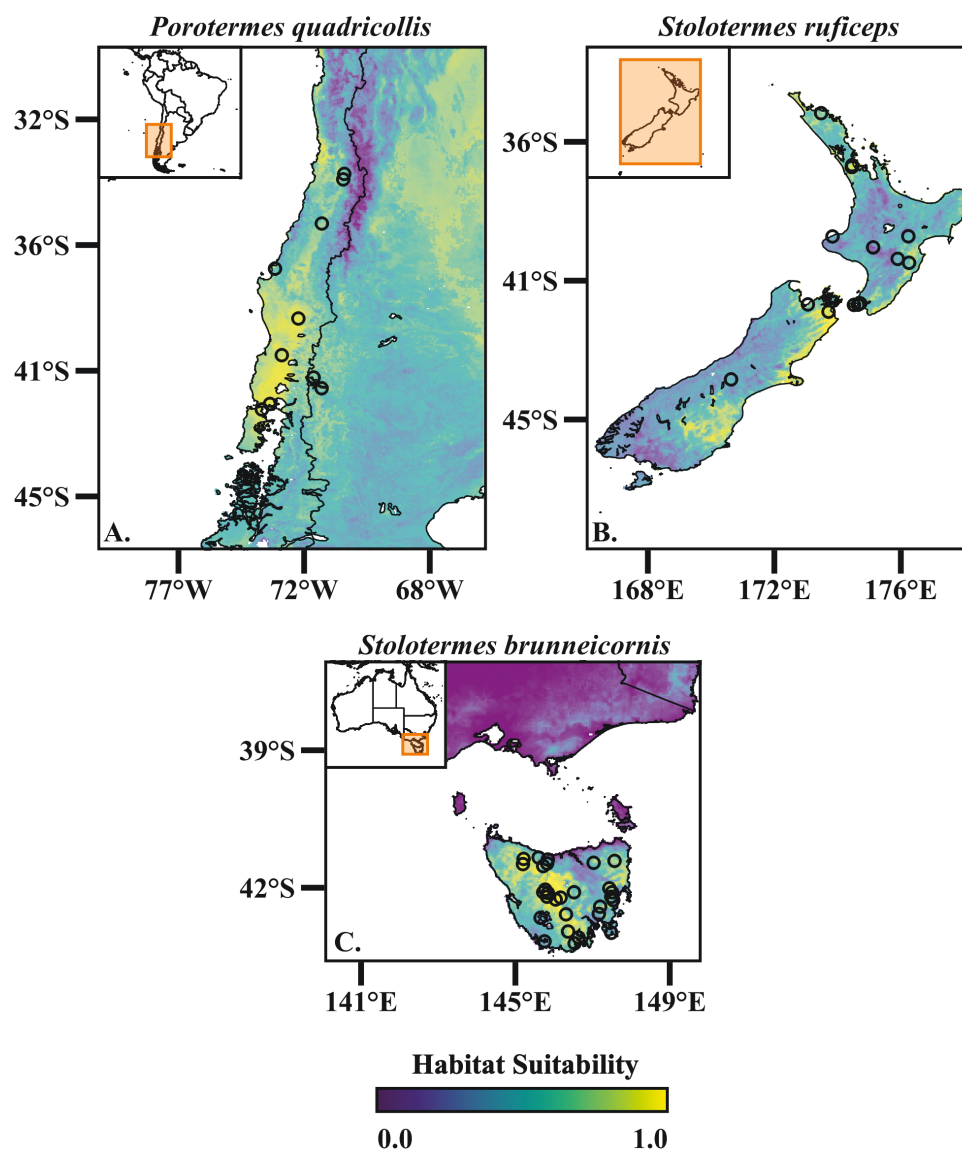


Fig. 3. Termite SDM predictions for species located within Argentina and Chile (top left), New Zealand (top right), and Tasmania (bottom) for **A.** *Porotermes quadricollis* (Stolotermitidae) and **B.** *Stolotermes ruficeps*, and **C.** *Stolotermes brunneicornis*. Final model predictions were generated using our thinned occurrence dataset and final set of uncorrelated environmental variables for each species, with 10 bootstrap replicates with 'cloglog' outputs in which raw values are converted to a range of 0–1 to approximate a probability of occurrence (Cobos et al. 2019). Brighter colors indicate areas of higher suitability (higher probability of occurrence), while darker colors indicate areas of lower suitability (lower probability of occurrence).

regularization, and high parameters, and intermediate AICc values suggesting a balance between over and underfitting.

Termite niche modeling suggested interesting drivers of habitat suitability, including temperature. Temperature is hypothesized to be a main factor driving termite distributions (Cancello et al. 2014), and has been hypothesized as the main driver for their distribution being purely restricted to the tropics and subtropics (Eggleton et al. 1994, Eggleton 2000, Cerezer et al. 2020). Furthermore, current research suggests that increases in termite species richness towards the equator are the result of increases in average and extreme temperature gradients (Cerezer et al. 2020). Response curves from our analyses seem to partly support previous research in which habitat suitability for some termite species increased with increases in temperature variables which exhibited high importance in modeling, however other species sampled expressed negative relationships in suitability with temperature fluctuations and extremes. Even though

termite species exhibited a litany of environmental variables which exhibited high permutation importance within modeling, the most common temperature variables present were annual mean temperature (bio01), mean diurnal range (bio02), and isothermality (bio03). All species which possessed mean annual temperature as a variable of high importance (*M. darwiniensis*, *Z. angusticollis*, *Z. nevadensis*) expressed positive linear relationships with suitability. *Stolotermes brunneicornis* also expressed negative relationships with minimum temperature of the coldest month (bio06) suggesting that yearly and monthly temperatures were associated with increased suitability. The only species which expressed negative relationships with increasing temperature was *H. mossambicus*, in which suitability decreased with increases in temperature of the warmest month (bio05). Since occurrences for *H. mossambicus* extend over 30°C latitude, we hypothesize that temperature of the warmest month might have inflated permutation importance due to

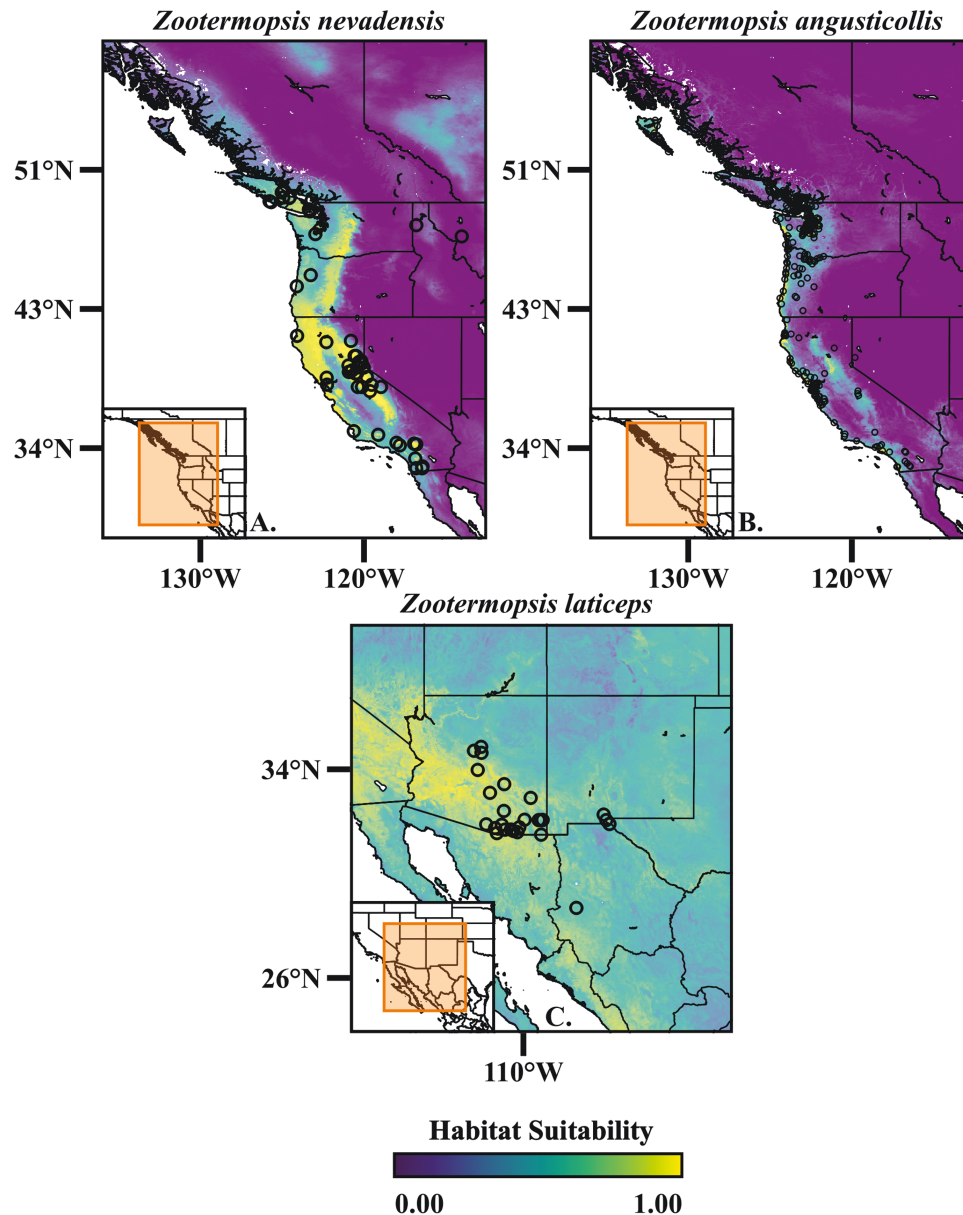


Fig. 4. Termite SDM predictions for species located within Eastern United States and Canada for **A.** *Zootermopsis nevadensis* (Stolotermitidae)(left) **B.** *Zootermopsis angusticollis* (right), and **C.** *Zootermopsis laticeps* (bottom). Final model predictions were generated using our thinned occurrence dataset and final set of uncorrelated environmental variables for each species, with 10 bootstrap replicates with ‘cloglog’ outputs in which raw values are converted to a range of 0 - 1 to approximate a probability of occurrence (Cobos et al. 2019). Brighter colors indicate areas of higher suitability (higher probability of occurrence), while darker colors indicate areas of lower suitability (lower probability of occurrence).

occurrences closer to the tropics possessing less temperature fluctuation than South Africa.

It is interesting that all species which had mean diurnal range as a predictor expressed negative relationships with suitability, while isothermality expressed both positive and linear relationships with suitability across taxa. Annual mean diurnal range is a metric for determining relevance of temperature fluctuation on a species by determining the average range of temperature across months (monthly maximum temperature—monthly minimum temperature) (O'Donnell and Ignizio 2012). Isothermality determines if species distribution is affected by fluctuations within a month relative to a year by quantifying how large day-to-night temperatures differ relative to summer-to-winter temperatures. Isothermal values close to 100 indicate daily temperature ranges match annual temperature

ranges (O'Donnell and Ignizio 2012). Species models which possessed isothermality exhibited negative linear relationships with suitability include *H. mossambicus*, *M. darwiniensis*, and *S. victoriensis*, while *P. quadricollis* and *S. brunneicornis* expressed positive linear relationships. We hypothesize that our termite species exhibit higher suitability for lower monthly temperature extremes but express plasticity in resilience to large yearly temperature fluctuations. Previous research has suggested that termites possess narrower thermal niches within the tropics (Cerezer et al. 2020). However, no discernable patterns of variable importance pertaining to temperature are shared among related species (i.e., among the species of *Zootermopsis*), or species sharing geographic overlap (i.e., Australian species of *Stolotermes* and *Porotermes*), suggesting temperature thresholds and suitability are species specific. A caveat to this hypothesis is

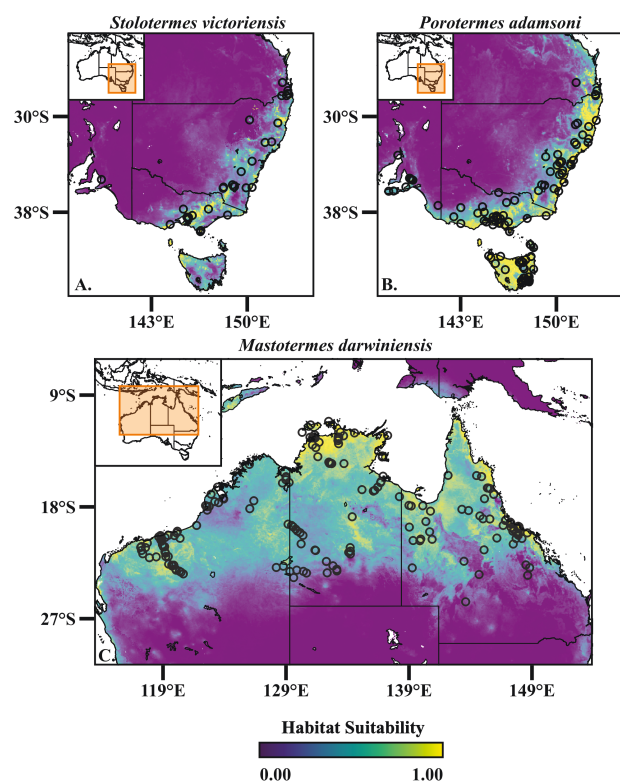


Fig. 5. Termite SDM predictions for species located within Southern Australia for **A.** *Porotermes adamsoni* (Stolotermitidae) (left) and **B.** *Stolotermes victoriensis* (right), and **C.** *Mastotermes darwiniensis* (Mastotermitidae). Final model predictions were generated using our thinned occurrence dataset and final set of uncorrelated environmental variables for each species, with 10 bootstrap replicates with 'cloglog' outputs in which raw values are converted to a range of 0 - 1 to approximate a probability of occurrence (Cobos et al. 2018). Brighter colors indicate areas of higher suitability (higher probability of occurrence), while darker colors indicate areas of lower suitability (lower probability of occurrence)..

that these variables are for the land surface. Since termite mounds constructed by species *Microhodotermes* and *Hodotermes* possess constant temperature and circulation for optimal thermoregulation (Korb 2003), further research is required to understand the degree of temperature fluctuation above and below ground.

Precipitation is also hypothesized to affect termite community composition, diversity, and distribution, with termite species richness increasing with increasing rainfall (Eggleton et al. 1994, Eggleton 2000, Gathorne-Hardy and Eggleton 2001, Davies et al. 2015, Korb et al. 2019, Clement et al. 2021). Buxton (1981) found that African termite foraging behavior was most common during rainy seasons; since foraging behavior involves termites leaving their colonies to search for food in their habitat, this behavior results in termites being observed by humans and collected for databases such as those used here. This response to rainfall may not be universal across the taxon, however, by contrast, recent work by (Clement et al. 2021) suggests that rainfall does not shape species richness for Australian termites; this study only included Neoisopteran taxa, however, and none of the species included in the present study were evaluated in their work. Permutation analyses revealed that precipitation variables pertaining to moisture (i.e., wettest and driest) possessed the highest importance in species maxent models across regions. Most of the species possessed bioclimatic variables 13 and 14 (precipitation of the wettest and driest months respectively) as a variable of high

importance. *Porotermes mossambicus* possessed positive relationships with precipitation of the wettest month while *Z. nevadensis* expressed a negative relationship. *Stolotermes victoriensis* expressed a positive quadratic relationship with precipitation of the driest month while *S. brunneicornis*, *Z. angusticollis*, and *Z. laticeps* expressed negative linear relationships. Precipitation seasonality (bio15) also expressed a positive quadratic relationship within *M. darwiniensis*, and a positive relationship within *Z. nevadensis*. Due to the lack of discernible patterns of precipitation variables among taxa sampled, we hypothesize that precipitation extremes and variability is more species specific.

Previous research has suggested that termite abundance and habitat suitability are highest within tropical dry ecosystems as opposed to tropical rainforests within Australia (Davies et al. 2013, Clement et al. 2021). Studies have indicated that termite abundance in Queensland across a precipitation gradient increases at savanna sites, coining an Australian termite diversity anomaly (Clement et al. 2021), which is part of the global termite functional diversity anomaly. Response curves for Australian termite species (*M. darwiniensis*, *S. victoriensis*) indicated increased suitability with increases in precipitation. *Stolotermes brunneicornis* also expressed decreased suitability with increases in precipitation of the driest month, supporting the hypothesis that Southern Australian termite species prefer drier climates at least for three of the four Australian species sampled. Even though distributions for *M. darwiniensis* overlap with termite species collected within (Clement et al. 2021), *M. darwiniensis* was not sampled within their analysis. Furthermore, (Clement et al. 2021) sampled the feeding guild which was not a variable considered within our analysis. Habitat suitability modeling of more Australian termite species is required to support or refute the Australian termite diversity anomaly.

Termites spend much of their lifetime burrowing, tunneling, foraging, and in some families eating soil; combined with their high abundance makes them one of the main animals influencing soil chemical, physical, and biological function (Wood 1988, Holt and Lepage 2000). Conversely, the properties of soil could also drastically affect the distribution of termite species (Calaby and Gay 1959). Soil properties including class, moisture, particle size, nutrient availability, and amount of clay have been extensively studied in subterranean and soil-consuming termites within the family Rhinotermitidae, and Termitidae (Fall et al. 2001; Jouquet et al. 2002; Cornelius and Osbrink 2010, 2011; Wang and Henderson 2014; Bourguignon et al. 2015). Among the species sampled, no overall patterns of soil type in regard to silt, sand, or clay proportions were discovered, suggesting soil preference is species specific, yet parsing affinity to soil as opposed to vegetation within termites is an area of little study (Calaby and Gay 1959).

Studies of soil preferences on 'lower' Australian termites such as *Porotermes*, *Stolotermes*, and *Mastotermes* are sparser, restricted to a few dissertations and natural history observations (Mensa-Bonsu 1976, Nkunya 1988). In our analyses, the optimal model for *M. darwiniensis* expressed positive quadratic relationships with the proportions of silt and clay particles suggesting an optimal proportion of water retention and porosity when it comes to soil suitability. *M. darwiniensis* are most found within dead logs but possess runaway tunnels to and from foraging sites which may be affected by soil type (Hill 1942). *Stolotermes victoriensis* displayed the highest suitability within Cambisol soils which are classified as having high sand and silt content, which may explain why *S. victoriensis* also displayed negative relationships with proportion of clay particles. Interestingly, *S. brunneicornis* expressed the opposite pattern in which suitability increased with increases in the proportion of clay. Although the

Table 2. SDM Model performance and parameters chosen as optimal for each termite species. Settings shown are the p -value for the partial Receiver Operating Characteristic (pROC), feature classes, and regularization (rm). Statistics show are AUC of testing data (AUC_{test}), omission rate for 10 percentile training values, number of nonzero coefficients (parameters), and Akaike criterion for small sample sizes (AICc) and delta AICc

Species	p -value (ROC)	Feature	rm	AUC _{test}	delta.AICc	AICc	Omission (10%)	Parameters (nparam)
Archotermopsidae								
<i>Hodotermes mossambicus</i>	0	H	5	0.81	0	4117.7	0.04	24
Hodotermitidae								
<i>Mastotermes darwiniensis</i>	0	LQ	1	0.82	0	2666.2	0.09	15
Mastotermitidae								
<i>Microhodotermes viator</i>	0	LQ	1	0.95	0	1562.30	0.08	18
<i>Porotermes planiceps</i>	0	H	5	0.76	0	163.10	0.00	3
<i>Porotermes quadricollis</i>	0	Q	5	0.67	0	219.30	0.33	2
<i>Stolotermes brunneicornis</i>	0	L	4	0.86	0	485.01	0.06	6
<i>Stolotermes ruficeps</i>	0	L	3	0.69	0	274.50	0.00	1
<i>Stolotermes victoriensis</i>	0	LQ	1	0.94	0	629.50	0.10	9
<i>Porotermes adamsoni</i>	0	H	4	0.91	0	2037.70	0.10	24
Stolotermitidae								
<i>Zootermopsis angusticollis</i>	0	L	1	0.94	0	4482.80	0.09	22
<i>Zootermopsis laticeps</i>	0	L	4	0.62	0	590.80	0.00	8
<i>Zootermopsis nevadensis</i>	0	H	5	0.89	0	1082.60	0.09	20

biology of *S. victoriensis* and *S. africanus* overlap (Coaton 1949, Coaton and Sheasby 1979), no studies explore habitat preferences of *S. brunneicornis*. *Porotermes adamsoni* expressed a positive quadratic relationship to the proportion of silt particles and soil pH. Despite their overlap in substrate type (decaying logs on the forest floor) both species expressed differences in soil importance. We hypothesize these differences could be due to *P. adamsoni* being an invasive species and possessing physiological differences to soil type (Evans et al. 2013).

Although the North American ‘lower’ termite genera *Zootermopsis* feeds on unhealthy trees and dead branches, recent studies noted soil particles in their hindguts suggesting a closer association with soil microbial communities than previously thought (Mullins et al. 2021). Within our studies, *Z. angusticollis*, and *Z. laticeps*, and *Z. nevadensis* expressed different correlations with soil type with *Z. angusticollis* exhibiting highest suitability for 6 soil suborders. *Zootermopsis angusticollis* is an invasive species, which may explain their generalist preferences for soil type (Evans et al. 2013). *Zootermopsis laticeps* expressed positive relationships with volumetric fraction of coarse particles suggesting more coarse-grained soils correlate with suitability, indicative of the arid and desert regions it inhabits.

Substrate use of southern African species of termites differs greatly, ranging from above ground mounds (Heuveltijes) within *Microhodotermes*, to underground colonies in the northern Savannahs within *Hodotermes*. *Microhodotermes viator* and *H. mossambicus* prefer rainfall between 125 - 750 mm explaining their increases in suitability with increases in the proportion of silt, due to silt soils not retaining water (Coaton 1949). Furthermore, *M. viator* expressed a positive quadratic relationship with the volumetric fraction of coarse particles. Since *M. viator* do not build nests in soils of higher rock content (Coaton and Sheasby 1979), the species might possess an optimal soil grain size for colony establishment.

Materials and Methods

Occurrence Records

We acquired occurrence records of non-Kalotermitidae non-neoisopteran species from the GBIF and iNaturalist. Recently, colleagues assessed the suitability of iNaturalist termite records for MaxEnt analyses for the over 6,000 records of termites in their database (Hochmair et al. 2020), finding that the records plus museum data can provide useful insights for geographic range studies. We selected occurrences possessing preserved museum samples and research grade observations which are occurrences possessing verified latitude and longitude coordinates, a photograph of the sighting, date, and 2/3 agreement on species identification by the community. Further occurrence filtering consisted of removing sightings with erroneous localities (middle of the ocean, locations of large museums). Additional localities were acquired from uncatalogued specimens of species housed within the AMNH termite collection. We used gazetteers to acquire coordinates for museum specimens lacking latitude and longitude data but specific enough locality information. In total, 12 species were selected for species distribution modeling; these had sufficient ($n > 5$) (Raxworthy et al. 2007) and verifiable (research grade) occurrence records and were in the genera *Hodotermes*, *Mastotermes*, *Microhodotermes*, *Porotermes*, *Stolotermes*, and *Zootermopsis* (Table 1). These taxa span several continents in their combined geographic ranges. Briefly, *Hodotermes* has an African distribution, *Mastotermes* an Australian distribution, *Microhodotermes* has an African distribution, *Porotermes* has an African, Australian, and Neotropical distribution, *Stolotermes* has an African and Australian distribution, and *Zootermopsis* has a Nearctic distribution.

Environmental Data

All modeling and environmental raster collection was conducted using the statistical program R v. 4.0 with the packages ENMeval

Table 3. Species used in maxent modeling, environmental variables which expressed the top five highest permutation importance within each species' optimal maxent model, permutation importance of each environmental variable, and the resultant response curve behavior expressed with that variable in relation to suitability, or soil type which expressed the highest suitability. Maxent calculates permutation importance by changing the values of each environmental variable at random, then calculating the difference using the AUC from the 'training data'. The values of each environmental variable are randomly permuted within the training presence and background data, the resultant drop in training AUC is calculated, then normalized to percentages. Response curves show how each environmental variable individually affects the maxent prediction in terms of increasing or decreasing suitability. Behavior of response curve is dictated by model complexity (feature classes and regularization multipliers). Variables follow Worldclim v2

Species	Environmental variable	Permutation (%)	Response behavior/Soil suborder
Archotermopsidae			
<i>Hodotermes mossambicus</i>	Precipitation of Wettest Month (bio13)	34.1	Negative linear
	isothermality (bio03)	31	Negative linear
	pH in H2O	16.6	Positive hinge
	Proportion of silt particles	8.2	Positive hinge
	Max Temperature of Warmest Month (bio05)	4.2	Negative linear
Hodotermitidae			
<i>Mastotermes darwiniensis</i>	Precipitation Seasonality (bio15)	64.3	Positive quadratic
	Proportion of silt particles	9.6	Positive quadratic
	isothermality (bio03)	9.4	Negative linear
	Proportion of clay particles	7.5	Positive quadratic
	Annual Mean Temperature (bio01)	2.9	Positive linear
<i>Microhodotermes viator</i>	Volumetric fraction of coarse particles	63.1	Positive quadratic
	Mean Diurnal Range (bio02)	27	Negative linear
	Soil suborder	8.4	Cambisols, greysols, plinthosols
	pH in H2O	5.8	Negative linear
	Proportion of silt particles	5.3	Positive linear
<i>Porotermes planiceps</i>	Mean Diurnal Range (bio02)	98.5	Negative linear
	Proportion of clay particles	1.2	Negative linear
	pH in H2O	0.3	Negative linear
<i>Porotermes quadricollis</i>	isothermality (bio03)	64.4	Positive linear
	Soil suborder	35.6	Cambisol
<i>Stolotermes brunneicornis</i>	Mean Diurnal Range (bio02)	50.5	Negative linear
	Min Temperature of Coldest Month (bio06)	24.1	Negative linear
	isothermality (bio03)	21	Positive linear
	Proportion of clay particles	2.8	Positive linear
	Precipitation of Driest Month (bio14)	1.6	Negative linear
<i>Stolotermes ruficeps</i>	Soil suborder	100	Cambisol
<i>Stolotermes victoriensis</i>	Precipitation of Driest Month (bio14)	82.6	Positive quadratic
	Mean Diurnal Range (bio02)	5.5	Negative linear
	Proportion of clay particles	4.4	Negative linear
	Soil suborder	3.8	Cambisol
	isothermality (bio03)	3.7	Negative linear
<i>Porotermes adamsoni</i>	Mean Diurnal Range (bio02)	92	Negative linear
	Proportion of silt particles	3.9	Positive quadratic
	pH in H2O	1.5	Positive quadratic
	Min Temperature of Coldest Month (bio06)	0.8	Negative Hinge
	Volumetric fraction of coarse particles	0.6	Negative Hinge

Table 3. Continued

Species	Environmental variable	Permutation (%)	Response behavior/Soil suborder
<i>Stolotermitidae</i>	<i>Zootermopsis angusticollis</i>		
	Annual Mean Temperature (bio01)	45	Positive linear
	Mean Diurnal Range (bio02)	18.6	Negative linear
	Precipitation of Driest Month (bio14)	13.9	Negative linear
	pH in H ₂ O	13.3	Negative linear
	Soil suborder	2.8	Calcicols, Histols, Lixisols, Luvisols, Phaeozems, Planosols
	<i>Zootermopsis laticeps</i>		
	pH in H ₂ O	28.9	Negative linear
	Soil suborder	26	Gleysols, Podzols
	Volumetric fraction of coarse particles	22.9	Positive linear
	Precipitation of Driest Month (bio14)	16.6	Negative linear
	isothermality (bio03)	4.3	Negative linear
	<i>Zootermopsis nevadensis</i>		
	Precipitation of Wettest Month (bio13)	41.3	Positive linear
	Precipitation Seasonality (bio15)	33	Positive linear
	Soil suborder	14.7	Leptosols
	Annual Mean Temperature (bio01)	7.7	Positive linear
	Proportion of clay particles	3.3	Weak negative linear

v2.0 (Kass et al. 2021) and Wallace v.1.9. (Kass et al. 2018). We acquired environmental rasters at 2.5 arc-second resolution (~5 km at the equator) from the WorldClim 2.0 database (Fick and Hijmans 2017). We downloaded the long-term bioclimatic dataset (1970–2000) consisting of 19 bioclimatic variables extrapolated from monthly Min and Max temperature, humidity, mean, and coefficient of variation of annual solar radiation. Variables follow Worldclim v2: BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (maximum temperature—minimum temperature)), BIO3 = Isothermality (BIO2/BIO7) ($\times 100$), BIO4 = Temperature Seasonality (standard deviation $\times 100$), BIO5 = Maximum Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range (BIO5–BIO6), BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO16 = Precipitation of Wettest Quarter, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter, BIO19 = Precipitation of Coldest Quarter. Although occurrence records for termite species range from the past 100 yr, we considered the broad patterns observed within these long-term datasets as sufficient to accurately represent the environmental conditions for the termite taxa. We omitted four layers from the bioclimatic variables (bio08, bio09, bio18, bio19) due to their known spatial artifacts (Moo-Llanes et al. 2021). We also acquired environmental variables from the Global Soil Information Facilities (GSIF) SoilGrids database at 250 m resolution at 0–5 cm (Hengl et al. 2017). We included soil pH in H₂O, proportion of sand (>0.05 mm), silt (≥ 0.002 mm and ≤ 0.05 mm), and clay (<0.002 mm) particles in the fine earth fraction (g/100 g), Volumetric fraction of coarse fragments (>2.0 mm)($\text{cm}^3/100 \text{ cm}^3$ (vol%)), and a categorical raster of the United States Department of Agriculture (USDA) Soil Taxonomy Suborders (67 soil classes). Species in the genera *Stolotermites*, *Zootermopsis*, and *Porotermites* are damp or deadwood burrowers,

while species in the genera *Microhodotermites* and *Hodotermites* construct above ground dumps and conical mounds. We chose to include soil variables for all species as soil can express both direct effects on mound construction, or indirect effects on decay of rotten logs (Holt and Lepage 2000).

Termite Species Distribution Modeling

Before modeling, we processed our occurrences to account for sampling bias, delineated a study extent to sample background records, and omitted highly correlated environmental variables. We spatially thinned occurrence records by 5 km to prevent spatial autocorrelation and pseudoreplication of the same termite mound (Krishna et al. 2013a, b; Aiello-Lammens et al. 2015) (Table 1). We investigated collinearity among our environmental variables within each species using the ‘vifcor’ and ‘vifstep’ functions in the *usdm* package (Naimi 2017). The ‘vifcor’ function finds the pair of variables which possesses the highest linear correlation, then excludes the variable having the highest variance inflation factor (VIF). This process is repeated until no variables remain with correlations higher than the correlation threshold. The ‘vifstep’ function calculates the VIF for all variables, then excludes any with a VIF higher than the threshold. We set our correlation threshold at 0.9, and VIF threshold at 10 (Dohoo et al. 1997, Lin 2008). We sampled 25,000 random background points over a study extent defined as the minimum convex polygon around all localities for each species buffered by 555 km (approx. 5 °C). We chose this study extent to include areas within the species’ dispersal limitations (Krishna et al. 2013a, b), as well as hypothesized regions currently under sampled.

Results

A total of 300 candidate models were built for our termite’s species (25 per species). Settings varied considerably among statistically significant optimal species models, spanning from simple models with few feature classes, low regularization, and low parameters to relatively complex with multiple feature classes, high regularization, and

high parameters; however, no pattern of model complexity was identified among species or families (Table 2). All optimal models possessed partial ROC p-values and delta AICc values of 0. AUC values of the testing data (AUC_{test}) ranged from 0.62 to 0.95, 10% omission rate ranged from 0.00 to 0.33, and AICc values ranged from 274 to 4117, and the number of parameters retained in optimal models ranged from 1 to 24. Response curves for variables of high permutation importance revealed predominantly simple positive and negative linear or hinge-loss relationships of suitability (suitability remains constant after a variable threshold), with *Microhodotermes viator*, *Mastotermes darwiniensis*, *Stolotermes victoriensis*, and *Porotermes adamsoni* expressing positive quadratic relationships (Table 3). All occurrence records, environmental data, candidate models, calibration results, final models, and R code to generate models can be accessed via dryad digital repository (<https://datadryad.org/stash/share/X475eeVQ8cVb1WzC2U1Pkc9GAN1y1f-dmspozGfphcs>).

Discussion

In recent years, community science databases (i.e., iNaturalist) have provided an alternate option for filling gaps in occurrence data for data-poor species with great potential for habitat suitability modeling for endangered or lesser-known arthropods (Coxen et al. 2017, Bradter et al. 2018, Hochmair et al. 2020). However, such modeling has for the most part been only applied to vertebrate species with research into lesser-known arthropod species lagging (Silva et al. 2013, 2016; Wang et al. 2018). The sparse models using insect occurrence data have been used to estimate migration routes (Menchetti et al. 2019, Kass et al. 2020), range shift responses (Urbani et al. 2017), and expansion of invasive species ranges including native and invasive termites (Maynard et al. 2015, Hill et al. 2017, Hyseni and Garrick 2019). Here, we presented the first suite of modeled potential distributions for a diversity of basal termite genera of economic importance, utilizing randomly sampled occurrence data.

Conclusion

This study marks the first attempt to create habitat suitability maps of basal termite genera. Although models of species were less robust than others, more occurrence data is constantly being acquired through a litany of scientific and public sources, community science databases, and digitization of museum collections. Species sampled in this analysis hold importance for their evolutionary history as well as their importance as pests such as *M. darwiniensis* which used to have a pandemic distribution and is considered one of the most destructive in their region (Watson and Gay 1970, Watson and Abbey 1993, Thistleton et al. 2007). These maps will be useful for termite biologists working in field settings to collect and observe these species. Future studies could utilize our models as a baseline for predictions of future habitat suitability of species in the face of habitat destruction such as forest fires or used in conjunction with paleoclimates to understand past changes in distribution patterns of these basal termite species.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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Data Availability Statement

Data from this study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k6dj9w7v> (Goodman, 2022).

Author Contributions

Conceptualization, J.W., and A.G.M.; methodology, A.M.G.; software, A.M.G.; validation, A.M.G., J.W.; formal analysis, J.A., J.B., A.C., B.H., H.J., Z.B.M., A.O., S.B.M., and M.W.; investigation, A.M.G., J.A., J.B., A.C., B.H., H.J., Z.M.M., A.O., S.B.M., and M.W.; resources, J.W.; data curation, A.M.G.; writing—original draft preparation, A.M.G., and J.W.; writing—review and editing, A.M.G., J.A., J.B., A.C., B.H., H.J., Z.B.M., A.O., S.B.M., M.W., and J.W.; visualization, A.M.G., J.A., J.B., A.C., B.H., H.J., Z.B.M., A.O., S.B.M., and M.W.; supervision, J.W.; project administration, J.W.; funding acquisition, J.W. All authors have read and agreed to the published version of the manuscript.

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