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Modelling Climate Change Impacts on the Geographic Distribution of a Major Termite Pest, *Odontotermes obesus* (Rambur, 1842) (Blattodea: Termitidae) in India

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ABSTRACT

The mound-building termite, *Odontotermes obesus* (Rambur) (Blattodea: Termitidae), is recognized as a major agricultural pest, attacking a wide range of cash crops and capable of causing yield losses from 10% to complete crop failure. This study represents the first attempt to model the potential distribution of *O. obesus* in India using the MaxEnt algorithm with bioclimatic predictors, while also assessing future distributional shifts under climate change. Projections were derived from the Beijing Climate Center Climate System Model (BCC-CSM) under two Shared Socioeconomic Pathways (SSP1-2.6 and SSP5-8.5) for 2050 and 2070. Precipitation-related variables, particularly of the wettest month, warmest quarter, coldest quarter, and driest month, were identified as the most influential drivers of habitat suitability. All models yielded area under curve (AUC) values greater than 0.9, confirming their high discriminatory power and predictive reliability. At present, 48.0% of India's geographic area is predicted to provide climatically suitable habitat for *O. obesus*. Future scenarios indicate significant range expansion under high-emission pathways, with intensification in present hotspots and colonization of new regions. Conversely, a substantial contraction in habitat suitability under the low-emission scenario indicates that mitigation of global warming may limit the future expansion of this pest. These findings provide a critical foundation for anticipating climate-driven shifts in *O. obesus* distribution and underscore the broader implications for pest management, ecosystem functioning, biodiversity, and environmental change.

Keywords: habitat suitability, mound-building termite, species distribution modelling.

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INTRODUCTION

Termites (Insecta: Blattodea) are among the most ancient and ecologically significant soil macrofauna in tropical and subtropical ecosystems (Bignell, 2019). Although termites play vital roles as decomposers and ecosystem engineers, some of them are economically damaging as pests. They are among the most destructive and economically significant insect pests of structural wood (Rajmohana et al., 2019). Globally, only about 12.4% of termite species are known pests (Krishna, Grimaldi, Krishna, & Engel, 2013), yet their destructive potential can amount to billions of dollars in structural and agricultural losses annually (Evans, Forschler, & Grace, 2013; Duquesne & Fournier, 2024). India incurs an estimated annual loss of about USD 35 million due to termite infestations (Verma, Sharma, & Prasad, 2009).

To date, 327 termite species are reported from India (Baraik et al. in press; Amina & Rajmohana, 2025; Roy et al., 2025), of which 92 species are listed as pests, including both minor and major pests (Krishna et al., 2013; Shanbhag & Sundararaj, 2013; Rajmohana et al., 2019). Among these, 23 termite species are categorized as major pests (Rajmohana et al., 2019). *Odontotermes obesus* (Rambur, 1842) (Fig. 1) is one of the most important, widely distributed major pest species in India, including its adjacent countries like Bangladesh, Bhutan, China, Myanmar and Pakistan (Mukherjee, Maiti, & Saha, 2008; Krishna et al., 2013). This mound-building species is recognized for its pestiferous behaviour in agroforestry and timber systems (Chakraborty & Singh, 2020). Mounds constructed by *O. obesus* exhibit considerable variation in size, shape, and construction, with mature forms typically appearing as tall, tower-like structures that taper apically, often reinforced with buttresses (Roonwall, 1977). Apart from forests, the species commonly infests several agriculturally important cash crops (Chandel, Verma, Baloda, Suman, & Abhishek, 2019). Mound-building termites display strong habitat adaptation, which enhances their survival potential (Mukherjee et al., 2008). With a preference for well-drained, loamy soils, the species exhibits tolerance to a wide range of microhabitats, including disturbed landscapes. Their colonies often have multiple interconnected mounds, and foraging activity occurs both above and below ground. This subterranean species plays a crucial role in wood decomposition, especially in symbiosis with *Termitomyces* fungi, which grow in the fungus combs within the mound (Schalk et al., 2021).

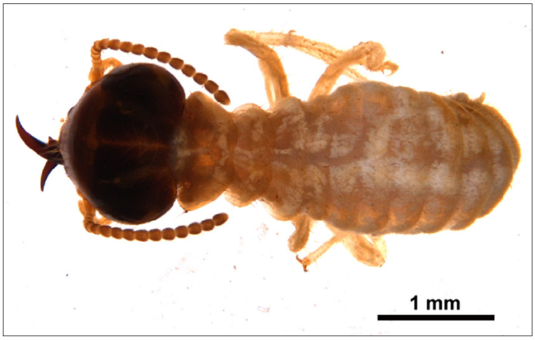

Figure 1. *Odototermes obesus (*Rambur), soldier

Recent studies reveal that termite-mediated wood decay and foraging activities are highly temperature-sensitive, with decay rates increasing significantly under warming scenarios (Zanne et al., 2022). Climate change-induced shifts in rainfall and temperature regimes could drastically alter termite distributions (Chakraborty, Singh, Singh, & Jeeva, 2021; Istifanus, Abdelmutalab, Pirk &Yusuf 2023). However, no studies have been conducted from India to date to assess the current and future potential distribution of any pest termites under climate change scenarios.

Species distribution modelling (SDM) is a widely adopted analytical framework in biogeography and ecological studies for predicting the potential geographic range of species (Liu et al., 2021). The spatial distribution of a species is governed by its dispersal capacity and the interactions between biotic components and abiotic environmental variables that collectively define its ecological niche (Owens, Bentley, & Peterson, 2012). Despite advancements in modelling techniques, the distributional patterns of numerous taxa with economic importance, particularly in tropical regions, remain inadequately documented (Anderson & Martínez-Meyer, 2004). Earlier studies by Crist (1998); Li, Fujisaki, & Su (2013); Tonini, Divino, Lasinio, Hochmair, & Scheffrahn (2014); Cramer, von Holdt, Uys, & Midgley (2017); Istifanus et al. (2023); da Cunha, Ferreira, Tessarolo, & Nabout (2018); Duquesne & Fournier (2024, 2025) used species distribution modelling to predict the potential distribution and habitat suitability of termite species. To date, no species distribution modelling studies on termite pest species have been conducted in India. Hence, this pioneering study aims to model the current and future habitat suitability of *O. obesus* in India, under two Shared Socioeconomic Pathways (SSP1-2.6 and SSP5-8.5). The widespread incidence of *O. obesus* as a pest in both natural and agricultural systems, combined with the diversity of climatic zones in India, makes it an ideal species for assessing potential range shifts under future climate scenarios.

MATERIAL AND METHODS

Species occurrence data

A total of 148 occurrence records of *O. obesus* (Fig. 2) were compiled from published literature (Kushwaha, 1956; Lahiri & Ghosh, 1980; Gold, Wightman, & Pimbert, 1991; Venkateswara et al. 2005; Kumar, Naveed, & BB, 2006; Manzoor & Akhtar, 2006; Mukherjee et al. 2008; Thakur & Kumar, 2012; Raut, 2013; Parween, Bhandari, & Raza, 2016; Saha et al., 2016; Shanbagh, Kabbaj, Sundararaj, & Jouquet, 2017; Mishra, Bhattacharyya, Gogoi, Bhagawati, & Bhattacharjee, 2018; Biswas & Deba, 2019; Intodia, 2019; Harit et al., 2021; Velayuthan, Kalleshwaraswamy, Thangavelu, Kulandaivel, & Palanisamy, 2022; Bhanupriya, Mukherjee, Kakkar, & Gupta, 2023; Ranjith, Nisha, & Ramya, 2023; Agarwal et al., 2024; Ali, Sharma, & Singha, 2024; Ingle & Pardeshi, 2024; Saikia, Kalita, & Das, 2024), the Global Biodiversity Information Facility (GBIF 2025: https://www.gbif.org/) and curated specimen data from the National Zoological Collection (NZC), Zoological Survey of India (ZSI), Kolkata. The curated data also includes specimens collected through recent faunistic field surveys conducted across various locations in India from 2017 to 2025. As an initial measure to minimize spatial autocorrelation among occurrence points, duplicate records from identical geographic locations were removed, retaining only unique occurrence points for further analysis. Specimens were identified using standard taxonomic keys (Chhotani, 1997) and deposited in NZC, ZSI, Kolkata.

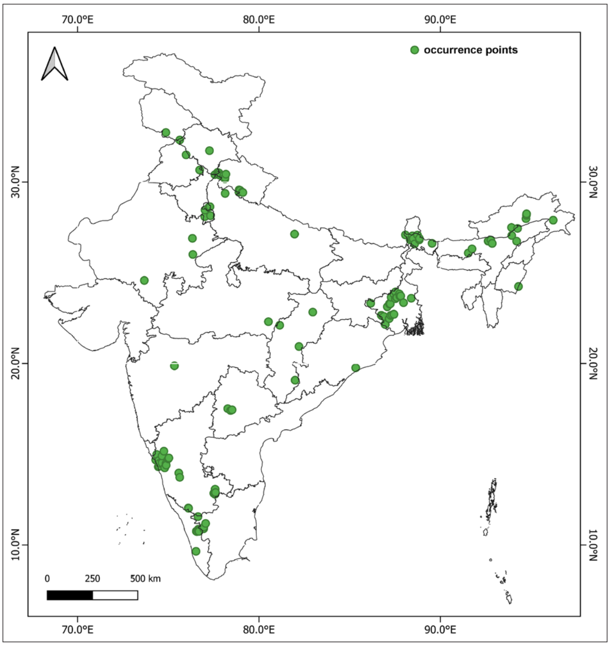

Figure 2. Occurrence points of *O. obesus* across India.

Environmental parameters

Climate parameters (BIO01-BIO19) were downloaded from the WorldClim dataset v.2.1 (http://www.worldclim.org/) as the current climate data, with a spatial resolution of 30 arc seconds. To reduce multicollinearity among variables and prevent model overfitting, it was necessary to filter these 19 environmental variables (Morales, Fernández, & Baca-González, 2017). Initially, we imported the distribution data of the target species and the 19 environmental factors into MaxEnt version 3.4.4 (American Museum of Natural History, New York, USA), utilizing default parameters for pre-training, and a jackknife method to determine the contribution rate of each environmental factor. Subsequently, Pearson's correlation coefficient (r) was computed between all pairs of variables using the 'terra' package in R version 4.4.2 (R Core Team, Vienna, Austria). Highly correlated variable pairs ($|r| > 0.8$) were identified to assess redundancy (Fig. 3). To further refine variable selection and account for multicollinearity, a Variance Inflation Factor (VIF) analysis was performed using the 'usdm' package in R. The VIF measures the inflation of variance in a regression model due to multicollinearity. A threshold of VIF ≥ 10 was applied to iteratively exclude collinear variables, retaining only those with acceptable levels of multicollinearity. The final set of non-collinear variables was used for subsequent species distribution modelling.

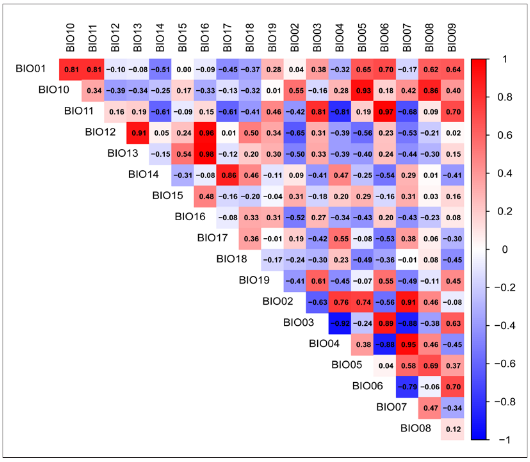

Figure 3. Correlation analysis results of the environmental variables (BIO01-BIO19). Red indicates a positive correlation and blue indicates a negative correlation.

Future climate projections were based on the Beijing Climate Center Climate System Model (BCC-CSM2-MR), using two Shared Socioeconomic Pathways (SSPs): SSP1-2.6 (sustainable development) and SSP5-8.5 (business-as-usual) (Riahi et al., 2017; Liu et al., 2021). Climate data were extracted for two future periods, 2041-2060 (2050s) and 2061-2080 (2070s), to evaluate potential shifts in the distribution of *O. obesus* under different future development scenarios.

Model optimization

Using default parameters in MaxEnt modelling can lead to excessive model complexity and reduced predictive performance (Morales et al., 2017). This issue is primarily linked to two critical parameters in MaxEnt: the feature classes (FC) and the regularization multiplier (RM) (Akaike, 1974; Zhu & Qiao, 2016). Therefore, in this study, the MaxEnt model was first optimized using the 'ENMeval' package in R. The RM was varied from 0.5 to 4.0 at intervals of 0.5, resulting in eight RM values. For FC, five feature class combinations were tested: L, LQ, LQH, LQHP, and LQHPT, where L = linear, Q = quadratic, H = hinge, P = product, and T = threshold. The ENMeval package was used to evaluate all 40 possible FC-RM combinations, and model performance and complexity were assessed using the corrected Akaike information criterion (AICc).

MaxEnt modelling

MaxEnt was used to model the potential geographic distribution of the species across different time periods. For model construction, 75% of the occurrence data was used for training and the remaining 25% for validation. The model was run with 10 replicates using bootstrapping as the sampling method. The logistic output format was applied, and the final results represent the average across all replicates. The Jackknife test was employed to assess the contribution of individual environmental variables to the model. Model performance was evaluated using the area under curve (AUC) of the receiver operating characteristic (ROC) curve, which provides a threshold-independent measure of predictive accuracy (Hanley & McNeil, 1982). The AUC values range from 0 to 1, with higher values indicating better model performance (Zhao et al., 2021). Swets (1988) classified the AUC values into three categories: 0.5-0.7, 0.7-0.9, and > 0.9, which indicate poor, moderate, and high model performance, respectively.

Habitat suitability division and visualization

MaxEnt generated habitat suitability predictions as ASCII grid files, assigning a probability value (p) between 0 and 1 to each cell, indicating the likelihood of species presence. These outputs were processed and visualized in QGIS version 3.26.1 (QGIS Development Team, Open-Source Geospatial Foundation Project, USA), where the raster calculator tool was used to classify habitat suitability. Suitability was categorized into four distinct classes: unsuitable ($p < 0.1$), low suitability ($0.1 \leq p < 0.3$), moderate suitability ($0.3 \leq p < 0.5$), and high suitability ($p \geq 0.5$), following Yan et al. (2021).

RESULTS

Environmental parameters and model optimization

A total of 10 out of 19 climatic variables were selected for modelling the potential distribution of the *O. obesus*, namely, mean diurnal range (BIO02), isothermality (BIO03), mean temperature of wettest quarter (BIO08), mean temperature of driest quarter (BIO09), precipitation of wettest month (BIO13), precipitation of driest month (BIO14), precipitation seasonality (BIO15), precipitation of driest quarter (BIO17), precipitation of warmest quarter (BIO18), and precipitation of coldest quarter (BIO19). The model with the lowest AICc (ΔAICc = 0) was considered optimal, which corresponded to the LQHP feature class with RM = 0.5 (Fig. 4).

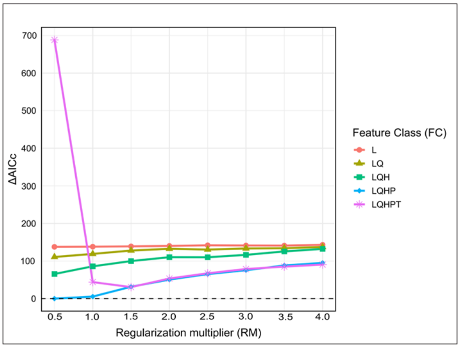

Figure 4. ΔAICc for *O. obesus* from models under different parameter combinations.

Model validation and influencing bioclimatic variables

The MaxEnt model demonstrated high predictive performance for both current and future suitability distributions of *O. obesus*. For the current distribution, the mean AUC value across 10 replicate runs was 0.927, indicating strong predictive ability and model reliability (Fig. 5). Across all future scenarios, mean AUC values ranged from 0.916 to 0.926 (SSP1-2.6 in 2050 = 0.926, SSP1-2.6 in 2070 = 0.925, SSP5-8.5 in 2050 = 0.92, SSP5-8.5 in 2070 = 0.916), further confirming the robustness of the models.

Results from the Jackknife test revealed that amongst the bioclimatic variables, precipitation of wettest month (BIO13) contributed the most to model training gain for current distribution, followed by precipitation of the warmest quarter (BIO18) and other bioclimatic variables (Fig. 5b, Table 1). Precipitation of driest month (BIO14) provided the highest gain when used alone, indicating it is the most informative single predictor in the current climate (Fig. 5b). Whereas, precipitation of driest quarter (BIO18) caused the greatest reduction in gain when omitted, suggesting it provides unique information not captured by other variables (Fig. 5b). Under SSP1-2.6 scenarios, precipitation of coldest quarter (BIO19) and precipitation of the warmest quarter (BIO18) contributed the most in the 2050s and 2070s, respectively (Table 1). Whereas, under SSP5-8.5 scenarios, precipitation of wettest month (BIO13) contributed the most in both 2050s and 2070s (Table 1). The Fig. 6 indicates response curves of these bioclimatic variables in the current climatic scenario. The results also signify that there was an overall positive nonlinear response detected for all precipitation-related climatic predictors except precipitation of driest month (BIO14) for the species. The response curve describes the relationship between bioclimatic predictors and the probability of species suitability.

Table 1. Percentage of contributions of the bioclimatic variables (bold values indicate the highest contribution within each scenario).

Codes	Bioclimatic variable	Current climate	SSP1-2.6		SSP5-8.5	
			2050	2070	2050	2070
BIO02	Mean diurnal range	5.8	7.3	4.1	4.0	4.1
BIO03	Isothermality	3.9	2.9	2.9	4.6	2.5
BIO08	Mean temperature of wettest quarter	2.8	1.6	6.8	3.4	2.9
BIO09	Mean temperature of driest quarter	2.5	6.3	4.6	6.5	9.3
BIO13	Precipitation of wettest month	**25.3**	20.8	21.2	**27.6**	**27.4**
BIO14	Precipitation of driest month	8.1	4.6	6.4	5.5	6.5
BIO15	Precipitation seasonality	4.5	2.6	4.4	4.2	4.0
BIO17	Precipitation of driest quarter	6.1	5.9	4.1	5.0	7.4
BIO18	Precipitation of warmest quarter	22.2	20.6	**25.9**	22.3	14.7
BIO19	Precipitation of coldest quarter	18.8	**27.5**	19.6	16.8	21.2

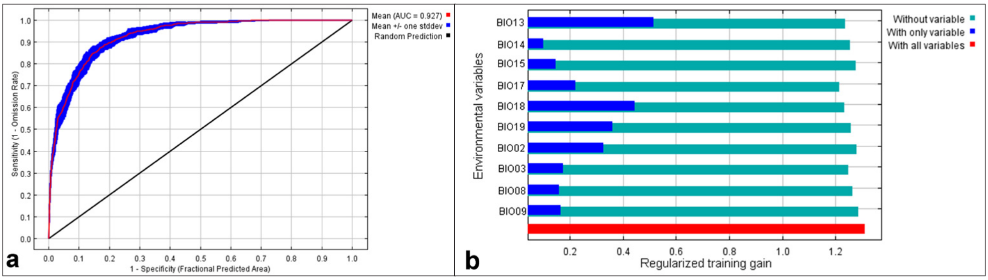

Figure 5. ROC curve and Jackknife test plots. a) The ROC curve for *O. obesus* under the current climate; b) the Jackknife test results of regularized training gain for the current distribution of *O. obesus*.

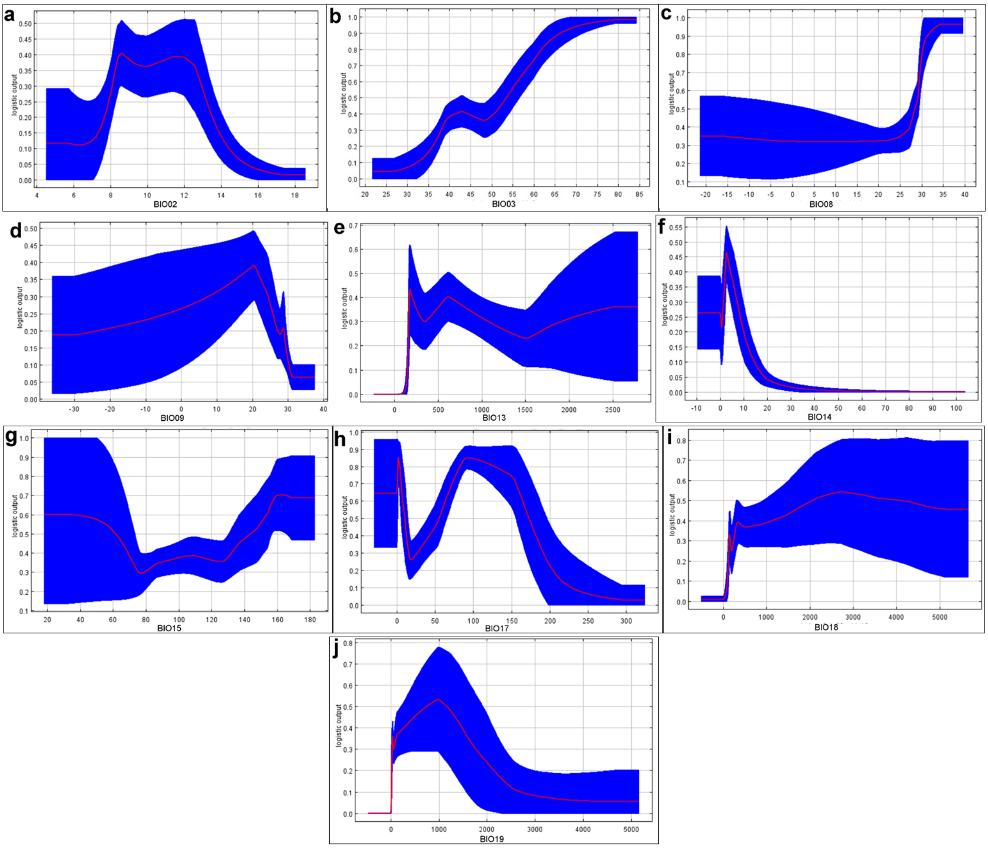

Figure 6. Relationships between selected bioclimatic predictors and probability of species suitability of *O. obesus*. a) Temperature seasonality (BIO02), b) isothermality (BIO03), c) mean temperature of wettest quarter (BIO08), d) mean temperature of driest quarter (BIO09), e) precipitation of wettest month (BIO13), f) precipitation of driest month (BIO14), g) precipitation seasonality (BIO15), h) precipitation of driest quarter (BIO17), i) precipitation of warmest quarter (BIO18), j) precipitation of coldest quarter (BIO19). The y-axis represents the probability of presence (logistic output). Red curves show the average response, and blue margins are ± SD calculated by 10 replicate runs.

Habitat suitability for *O. obesus* under current and future climate

The suitability distributions of *O. obesus* under current and future bio-climatic conditions are shown in Fig. 7. The relative changes in the distribution of suitable climate space were estimated by the difference between the current and future distribution at multiple climatic scenarios. Under current climatic conditions, the model identified 48.0% (1572121.81 sq. km) of the study area as low to high suitability class, while 52.0% (2797396.37 sq. km) of the area was identified as unsuitable (Table 2). The high suitability index is detected in the states of Arunachal Pradesh, Assam, Delhi, Goa, Karnataka, Uttarakhand, Kerala, Meghalaya, West Bengal, and the northern borders between Uttar Pradesh and Bihar (Fig. 7a).

The habitat suitability results under future climatic conditions, as predicted by BCC-CSM SSP1-2.6 and SSP5-8.5 scenarios, suggest that climate change will differentially affect the predicted distribution of *O. obesus*. The total climatically suitable area for *O. obesus* in India (low, moderate, and high classes combined) is currently estimated at 1.57 million sq. km (Table 2). Under the SSP1-2.6 scenario for 2050 and 2070, this area is projected to decline by 3.47% by 2050 and 4.28% by 2070 (Table 2, Fig. 7b-c), whereas under SSP5-8.5 it is projected to expand by 2.73% by 2050 and 10.28% by (Table 2, Fig. 7d-e).

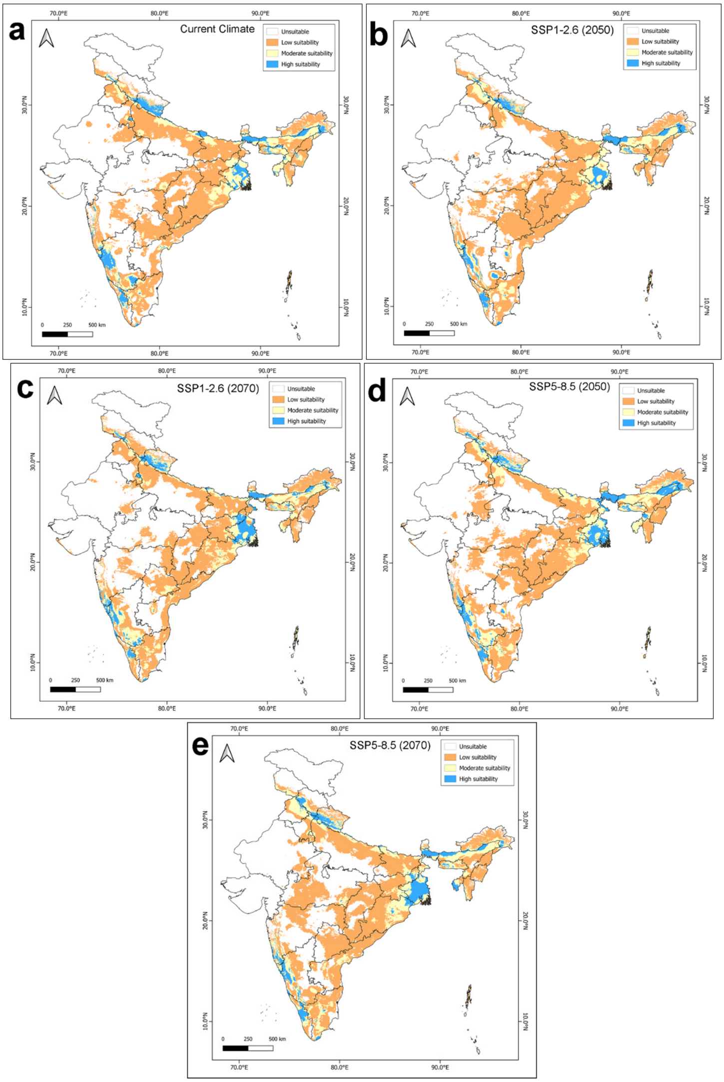

Figure 7. Suitable habitat maps for *O. obesus*. a) Under the current climate, b) under the SSP1-2.6 scenario in 2050, c) under the SSP1-2.6 scenario in 2070, d) under the SSP5-8.5 scenario in 2050, e) under the SSP5-8.5 scenario in 2070.

Table 2. Current and future habitat suitability areas (in square kilometers) for *O. obesus* in India.

Habitat suitability class	Current climate	SSP1-2.6		SSP5-8.5	
		2050	2070	2050	2070
Unsuitable	1696955.73	1760258.13	1773021.42	1662789.21	1544140.03
Low suitability	1100440.64	1090942.84	1050664.16	1086614.69	1211424.70
Moderate suitability	341762.92	318745.27	332150.16	376335.39	381079.78
High suitability	129918.25	107855.08	121965.54	152060.77	141156.36

DISCUSSION

Although only 12.4% of known termite species are considered pests globally, they are highly polyphagous and among the most destructive, causing severe damage to a wide range of agricultural and horticultural crops, forest trees, and stored products. Pest termites can potentially cause up to 100% yield loss when infestation occurs during the early growth stages of crops (Rana, Chandel, Verma, & Joshi, 2021; Ranjith et al., 2023) reported that *O. obesus* and *Microtermes obesi* Holmgren account for almost 80% loss of agriculturally important crops in South Asia. Temperature and precipitation are critical environmental variables that directly influence termite survival, colony development, and wood decomposition dynamics (Zanne et al., 2022). Given that climatic variables exert a stronger influence on species distributions than other abiotic factors (Tang, Yuan, Li, & Zhang, 2021), the present study focused exclusively on climatic predictors for ecological niche modelling. This study represents the first species distribution modelling of *O. obesus*. The current MaxEnt model predicts high habitat suitability for *O. obesus* in the states of Arunachal Pradesh, Assam, Delhi, Goa, Karnataka, Uttarakhand, Kerala, Meghalaya, West Bengal, and along the northern borders of Uttar Pradesh and Bihar (Fig. 6). This is consistent with its reported altitudinal distribution ranging from the plains to elevations of up to 3,400 m in the Indian Himalayas (Mukherjee et al., 2008).

Under future climate change projections (SSP5-8.5), the suitable habitat of *O. obesus* is expected to expand substantially, indicating a potential increase in its ecological and economic impact. By 2070, moderate to high-suitability zones are projected to spread across the Gangetic Plains, Western Ghats, Deccan Peninsula, Himalayan and North Eastern region of India. These zones are to become highly suitable under this high-emission scenario, highlighting the possible range shifts and heightened risks associated with climate change. These projections are consistent with global patterns indicating that elevated temperatures accelerate wood decomposition and enhance termite activity (Chakraborty et al., 2021; Zanne et al., 2022). Interestingly, habitat suitability for *O. obesus* decreased under the low-emission, controlled climate scenario (SSP1-2.6), suggesting that mitigation of greenhouse gas emissions and stabilization of climate conditions may restrict its potential range expansion. This highlights the importance of sustainable climate policies, as reduced warming not only limits broader ecological disruptions but may also help contain the spread of pest species such as *O. obesus*. As a mound-building wood-feeding species, *O. obesus* appears well-adapted to warming conditions, potentially enabling colonization of novel habitats without adhering to conventional latitudinal range shifts. This observation aligns with previous studies from Nigeria (Istifanus et al., 2023) and broader global models, which suggest that termite range expansions are often heterogeneous and shaped by microclimatic refugia (Istifanus et al., 2023; Duquesne & Fournier, 2024). This range expansion under warmer climatic conditions may reflect either an ecological niche modification or phenotypic plasticity in response to changing climatic conditions. Newly emerging zones of climatic suitability coincide with key cropland and horticultural belts, including West Bengal, Kerala, and Karnataka, thereby increasing the likelihood of infestation in economically critical areas. The predicted range expansion into semi-urban and agriculturally altered landscapes indicates a high degree of tolerance to anthropogenic disturbance and underscores the influence of land-use change as an additional driver of distributional dynamics.

Modelling the potential distribution of major pest species across diverse insect groups is well established and supported by earlier studies (Barredo et al., 2015; Choudhary, Kumari, & Fand, 2019; de la Vega & Corley, 2019; Hosni, Al-Khalaf, Nasser, Abou-Shaara, & Radwan, 2022; Duquesne & Fournier, 2025), and has been widely used to monitor pest distributions and inform management strategies. Agriculture dominates both the landscape and the economy of India. *Odontotermes obesus* is a serious pest of several economically important crops in India, including wheat, maize, rice, pulses, groundnut, soybean, castor, chilli/capsicum, cotton, sugarcane, and guar, with reported yield losses ranging from 10% to complete crop failure (Rana et al., 2021; Ranjith et al., 2023). The current distribution model estimates that 48.0% of the country's territory is suitable for this species, underscoring the urgent need for enhanced monitoring. Although chemical control remains the primary management strategy adopted by farmers, it is often unsustainable and imposes significant economic burdens. Moreover, complete elimination or prevention of termites in cropped areas is neither feasible nor ecologically desirable. Several indigenous traditional practices exist, but these are largely localized and show limited consistency across regions. Incorporating such practices within a well-planned Integrated Pest Management (IPM) framework could help reduce pesticide dependence and environmental risks (Rana et al., 2021). The use of entomopathogenic agents, as a component of IPM, holds particular promise, although further research is needed to fully explore their potential against termites infesting agriculturally important crops. The findings of this study provide spatially explicit data critical for guiding targeted surveillance, IPM strategies, and early-warning systems, particularly in newly suitable and agriculturally vulnerable regions.

This study reveals critical insights into the distributional dynamics of *O. obesus* under climate change, demonstrating its ecological plasticity and the emergence of new risk zones. The projected range shifts have profound implications for ecosystem processes and pest management in vulnerable agroclimatic regions of India. Integrating species-specific models into climate adaptation strategies, alongside sustainable climate policies, will be essential to mitigate both ecological disruption and the spread of destructive pest species.

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Author contributions

BK: Data curation, Investigation, Methodology, Visualization, Writing-original draft, Writing - review & editing. **RD:** Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Visualization, Writing-original draft, Writing - review & editing. **SD, JB and BB:** Data curation, Investigation. **KR:** Investigation, Methodology, Project administration, Supervision, Validation, Writing - original draft, Writing - review & editing.

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