

Climate change and topographic variations affect infestation by *Xyleutes ceramica* (Walker, 1865) (Lepidoptera: Cossidae) in teak plantations in Thailand

THANAPOL CHOOCHUEN^{1,2}, JIŘÍ FOIT¹ , PONTHEP MEUNPONG²,
WARONG SUKSAVATE^{3*}

¹Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

²Department of Silviculture, Faculty of Forestry, Kasetsart University, Bangkok, Thailand

³Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok, Thailand

*Corresponding author: jforwos@ku.ac.th

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Abstract: The teak bee-hole borer [*Xyleutes ceramica* (Walker, 1865)] is considered one of the most serious pests of teak (*Tectona grandis*) in Thailand. The present study investigates climatic and topographic variables affecting the infestation of teak trees by *X. ceramica* in 10 plantations and predicts the risk of infestation by the species under current and future climatic conditions in Thailand. At each plantation, 48 plots evenly distributed among twelve teak stands were sampled. The infested teak trees in the plots were assessed, and the coordinates of the tree positions were recorded. The maximum entropy (MaxEnt) model was used to assess the effects of environmental factors and predict the occurrence probability of the species using current and projected (2050) climate data based on the Shared Socioeconomic Pathways SSP1-2.6 and SSP5-8.5 scenarios from multiple global climate models. According to our results, high accuracy values [*AUC* (area under the curve) = 0.852, *TSS* (true skill statistics) = 0.775] of the model prediction were obtained, and the infestation was found to be driven much more by climate than by topographic characteristics. Above all, *X. ceramica* was found to prefer moderate temperatures in a highly distinct seasonal climate. Additionally, relatively low amounts of premonsoon rainfall are also found to be favoured by the species. The predicted risk map revealed that the northern region is the core area of *X. ceramica* infestation in Thailand under current and future climatic conditions, but the severity of infestation is predicted to gradually decrease under the predicted future climatic conditions. Recommendations for management to minimise tree damage caused by *X. ceramica* are also presented in this study.

Keywords: cossid moth; ecological requirement; environmental factor; global climate change; maximum entropy (MaxEnt); stem borer; *Tectona grandis*

Climate has a crucial effect on the growth, development and distribution of insects. Several studies have been conducted with the goal of identifying and understanding how climatic and environmental var-

iables influence the spatial distributions of specific pest species (Tang et al. 2019; Schneider et al. 2021; Fekrat, Farashi 2022; Horrocks et al. 2024). With respect to global climate change, researchers have

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highlighted that increased summer temperatures and shortened winter periods have resulted in rapid reproduction and faster growth of insect pests in temperate zones (Ma et al. 2021). In contrast, recent studies from the agricultural and forestry sectors have revealed that many tropical insects, even pest species, are projected to experience a decrease in growth rate because current temperature levels are already close to their optimal range (Halsch et al. 2021; Skendžić et al. 2021; Schneider et al. 2022). However, the positive or negative impacts of these factors on crop and forest yields generally depend on the adaptability of particular pest species as well as on the responses of their host plants and natural enemies to rising global temperatures (Halsch et al. 2021; Skendžić et al. 2021; Schneider et al. 2022). The outbreaks or spreading of insect pest attacks caused by climate change usually occur because of the insects' migration to new areas where favourable climatic conditions and suitable food sources are available. In temperate climates, prolonged drought and increasing temperature allow pests to shift their attack to new areas or host plant species because drought stress increases the susceptibility of their hosts. Tropical regions are also generally likely to face an increase in insect pest attacks, but the number of infestations in those regions is lower than that in temperate zones (Schneider et al. 2022).

Across large geographical areas, variability in topography, e.g. elevation, slope, and aspect, can potentially increase microclimate heterogeneity due to processes such as radiation, rain shading, and wind turbulence. The combination of climatic conditions and topographical characteristics is expected to influence the growing conditions of either trees or pests. This influence may potentially alter the short-term response of the host to drought and pests, as in cases of infestation of spruce and pine forests by bark beetles (Netherer et al. 2019; Nardi et al. 2022).

The teak bee-hole borer [*Xyleutes ceramica* (Walker, 1865)] is a large moth in the family *Cossidae* (Lepidoptera). Its larvae have been reported to develop under the bark and in the wood of several living woody plants in the family *Verbenaceae* and in some species in the families *Bignoniaceae*, *Fabaceae*, *Lythraceae* and *Theaceae* (Hutacharern and Choldumrongkul 1989). It is one of the most important insect pests of teak (*Tectona grandis*) plantations in Southeast Asia (Wylie, Spei-

ght 2012). The range of the pest includes Myanmar, Thailand, Malaysia, Indonesia, the Philippines and New Guinea. This species mainly causes technical damage by leaving permanent tunnels or holes in the wood, decreasing teak wood quality and timber value. It is widespread in northern Thailand and is considered the most serious pest of teak in Thailand (Hutacharern, Choldumrongkul 1989; Gotoh et al. 2007; Wylie, Speight 2012). Although *X. ceramica* is considered an endemic species, the risk of infestation by this pest may be strongly driven by climate change. Similarly, associations with climatic variables have been documented for some other cossid moths. For example, in *Zeuzera pyrina* (Linnaeus, 1761) and *Coryphodema tristis* (Drury, 1782), an association between the drought-stressed host and the drought-friendly nature of insects has been observed; this association is linked to warmer temperatures and low moisture content or precipitation (Adam et al. 2013; Kumbula et al. 2019; Fekrat, Farashi 2022). A global species distribution model incorporating future climate projections has been constructed for *Z. pyrina* and has shown a northwards expansion trend in the Northern Hemisphere and a southwards expansion trend in the Southern Hemisphere due to global warming (Fekrat, Farashi 2022).

Because of the substantial economic importance of *X. ceramica*, several studies of this species have been conducted, providing information on its bionomy and behaviour, potential host plants, natural mortality and population dynamics, genetic structure and variation, and ecological requirements at the tree and stand levels (Hutacharern, Choldumrongkul 1989; Eungwijarnpanya et al. 1990; Pholvicha et al. 1992; Chairuangsirikul 1999; Gotoh et al. 2007; Rattanawanee et al. 2015; Panyamang et al. 2018; Tasen, Wiwatwitaya 2022; Choochuen et al. 2024). The literature suggests that the developmental stages of *X. ceramica* are closely synchronised with teak phenology, which itself is strongly affected by precipitation (Gotoh et al. 2007). However, no studies have focused on the association of *X. ceramica* infestation with climate, ongoing climate changes or other landscape-scale factors that may drive its distribution. Knowledge of the influences of landscape-scale environmental factors, especially climate, on the potential distribution of the species could allow forest managers to predict when and where spreads or outbreaks of the pest will oc-

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cur. Therefore, the main goal of this study was to assess the effects of environmental variables such as climate and topography on the infestation of teak plantations by *X. ceramica* and to create predicted risk maps for current and future climate scenarios on the basis of global climate projections. Management recommendations for the minimisation of tree damage caused by *X. ceramica* under climate change scenarios are also suggested based on the results of the present study and guidance for the management of pest species from previous studies.

MATERIAL AND METHODS

Study site. The study site covered areas in northern, northeastern, western and central Thailand. The boundary of the study site was delineated on the basis of the border of the provinces in which the Forest Industry Organization (FIO)'s teak plantations are located (teak production area covers more than 50% of the total area of each plantation). At all the teak plantations, the same control measures are implemented to mitigate damage caused by *X. ceramica*, including hand collecting, light trapping and utilising the pests' natural enemies, particularly predatory ants. All teak trees are planted at 4 m × 4 m spacing to increase management efficiency and profitability for medium- and poorer-quality sites (Noda, Himmapan 2014). To represent the different climatic regions in the area and define sampling sites, stratified sampling was implemented using 19 bioclimatic variables downloaded from the WorldClim dataset (Fick, Hijmans 2017). The value of each variable was rescaled, and the study area was then divided into 10 strata according to the scores of each variable using K-means clustering. The optimal number of 10 strata was estimated using the elbow method provided in K-means clustering algorithm via the factoextra package. The number and location of teak plantations used for sampling were selected on the basis of the following factors: the total area of a particular stratum; the availability of FIO teak plantations in a particular stratum; and the occurrence of *X. ceramica* reported by FIO. As described above, 7 strata met all the required characteristics. Ten plantations (hereafter referred to as localities) were selected from the 7 strata, as shown in Figure 1. The characteristics of the bioclimate and the number of localities in particular strata are shown

in Table S1 in the Electronic Supplementary Material (ESM).

Plot design. Within each locality, the sample plots were distributed among three age classes: the young-age class (1–10 years), the middle-age class (11–20 years) and the old-age class (exceeding 20 years). Twelve stands of different ages where the occurrence of *X. ceramica* has been reported were sampled across each locality: three stands in the young-age class, three stands in the middle-age class and six stands in the old-age class. The number of trees in old-age stands per plot was approximately 50% less than in the other classes due to the second thinning. Therefore, more stands in the old-age class were sampled to get an even number of sampled trees across age classes and to avoid bias from potential different infestation levels in younger and older-age classes. At each sampled stand, 4 circular plots with radii of 10 m were established. The centres of the plots were located at least 100 m apart and formed a square. Hence, all the plots were located at the apexes of a square with sides that were at least 100 m long (Figure 2). The total number of plots in each locality was 48; there were 12 plots with young stands, 12 plots with medium-aged stands and 24 plots with old stands.

Survey of infestation. In this study, the number of infested teak trees was used as a response variable to explore the effects of environmental factors on the probability of occurrence of *X. ceramica*. In Thailand, *X. ceramica* generally completes its life cycle within a period of one year, and the adults emerge between February and April. The early instar larvae of the new generation begin to penetrate the stems of the trees to feed on inner bark tissue, and the later instar larvae bore into the sapwood and heartwood. The larvae eject visible frass on their entrance holes during the development period (i.e. May to October). Therefore, the gallery of the species, consisting of a hole and ejected frass, was taken as a sign of infestation. Trees that displayed the gallery were subsequently identified as infested trees (Figure 3). A survey of infestation was implemented between May and June 2024. The infested trees were assessed, and the coordinates of the tree positions within each study plot were recorded.

Environmental variables. Bioclimate and topography were used to study the relationships between environmental factors and the probability

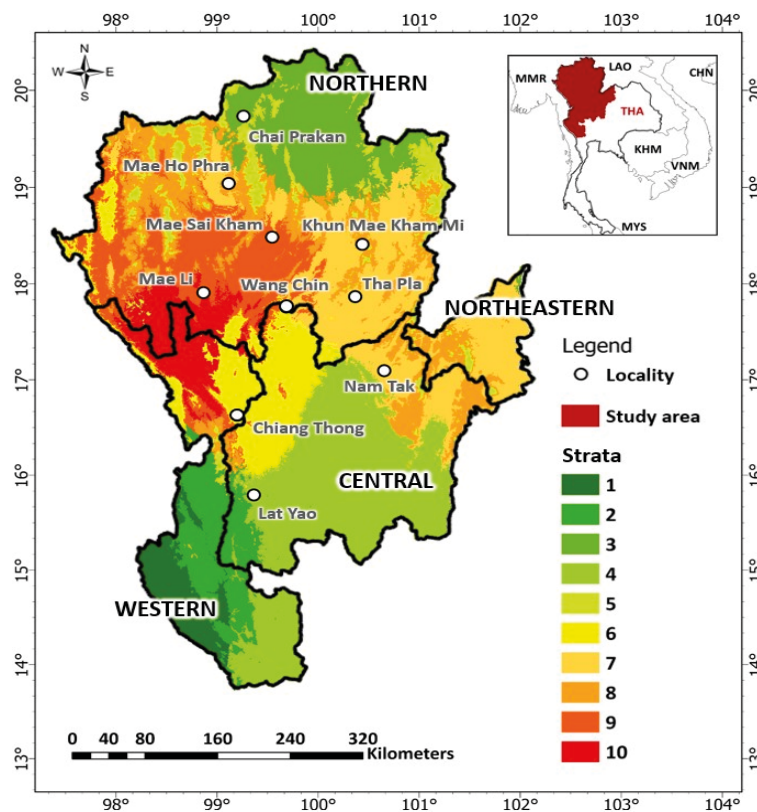


Figure 1. Bioclimatic strata of the study area according to the K-means method

Black line on the map – boundaries of different regions in Thailand within the study area; locality – name of teak plantations where the study was conducted

of occurrence of *X. ceramica*. Bioclimatic variables were downloaded from the WorldClim dataset as mentioned above. The topographic variables in-

cluded elevation, slope, diurnal anisotropic heat, the topographic wetness index and the topographic position index; all of these were derived from

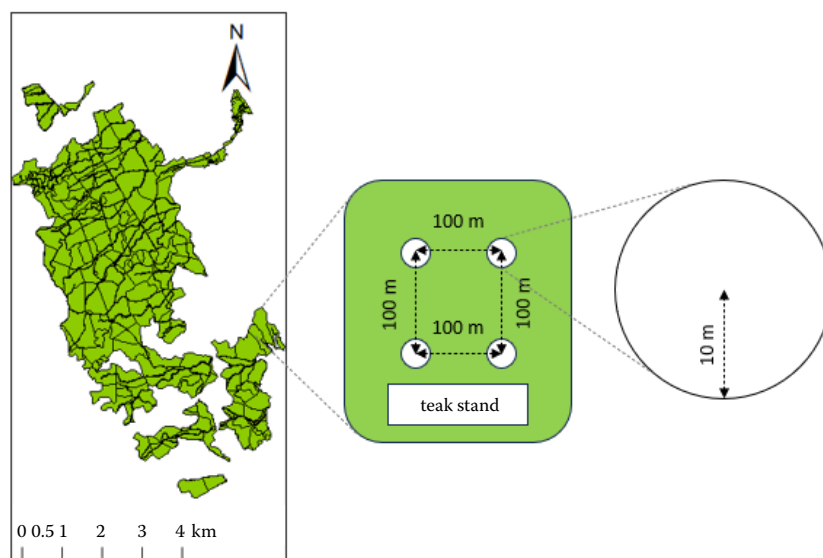


Figure 2. An example of the locality covered and the design of the sampling plot; each polygon represents a different teak stand within the locality

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Figure 3. Red circles highlight a gallery of *Xyleutes ceramica* on the trunk of a teak tree; the gallery is composed of an entrance hole and ejected frass

a digital elevation model obtained from a 30-m Shuttle Radar Topography Mission (SRTM) elevation data (NASA JPL 2020). All the environmental variables were standardised, and layers of those variables were then clipped according to the extent of the sampled stands in each locality to be used as the study area for modelling the probability of occurrence of the species.

Statistical analysis. According to a previous study by Choochuen et al. (2024), the possible error caused by non-detected infested trees was mentioned due to the challenge of identifying the presence of the gallery of *X. ceramica* on the trunk of some taller trees, due to limitations in sight distance and obscuration from the teak crown. Therefore, in this study, modelling using presence-only data (infested trees) was used to prevent this potential error. The maximum entropy (MaxEnt) algorithm is renowned for generating a species distribution model based only on the occurrence points of a particular species and for its ability to address complex interactions between responses and explanatory variables. MaxEnt is also capable of evaluating the importance of environmental variables and explaining the relationships between the probabilities of species occurrence and environmental variables. Therefore, MaxEnt was used to investigate the influences of landscape-scale environmental factors on the probability of occurrence of *X. ceramica*. The MaxEnt modelling and evaluation procedures were implemented via the dismo package (Hijmans et al. 2023) in R (R Core Team 2021).

Before modelling, a variable selection step was implemented to eliminate multicollinearity and overfitting of the model. In this step, the environmental variables were retained in the model on the basis of Pearson's correlation evaluation ($r = \pm 0.8$) (Khan et al. 2022). Consequently, 15 of the 24 environmental variables were included in the preliminary modelling (Table 1). The correlation values for all the environmental variables are shown in Table S2 in the ESM.

During the modelling process, a spatial resolution of 30 m (lower than the distance between sample plots) was employed to minimise spatial sampling bias. A bias file was created using the MASS package to be included in all MaxEnt models. The inclusion of this bias file in the MaxEnt model effectively adjusts the background point by using environmental data and introducing the same spatial bias as that which exists in the occurrence data (Gao et al. 2021; Khan et al. 2022). The preliminary MaxEnt model was generated from 15 explanatory variables after splitting the data into a training set and a testing set; 70% of the data was used in the training set, and the remaining 30% was used to test the predictive ability of the trained model. The model was generated using 30 bootstrapping replicates with 5 000 maximum iterations, a 0.00001 convergence threshold, and 5 000 background points (the maximum number allowed by the extent of the sampled stands) (see Elith et al. 2011 for details on optimising MaxEnt models). Environmental variables with an average relative contribution higher than 4% were identified as significant explanatory variables (Khan

Table 1. Environmental variables used in the preliminary MaxEnt model predicting the probability of occurrence of *Xyleutes ceramica* in Thailand

Type	Variable	Description
Bioclimate	BIO1	annual mean temperature (°C)
	BIO3	isothermality (°C)
	BIO4	temperature seasonality (°C)
	BIO5	maximum temperature in warmest month (°C)
	BIO6	minimum temperature in coldest month (°C)
	BIO7	annual temperature range (°C)
	BIO12	annual precipitation (mm)
	BIO15	precipitation seasonality (%)
	BIO17	precipitation during driest quarter (mm)
	BIO18	precipitation during warmest quarter (mm)
	BIO19	precipitation during coldest quarter (mm)
Topography	SLP	slope (%)
	DAH	diurnal anisotropic heat
	TPI	topographic position index
	TWI	topographic wetness index

et al. 2022) and subsequently included in the final model. The area under the curve (*AUC*) and the true skill statistics (*TSS*) were used to evaluate the performance of the final model and assess the reliability of model predictions. *AUC* and *TSS* values greater than 0.5 indicate performance better than random chance across all thresholds, and values greater than 0.9 indicate high robustness of the model (Moreno-Ibarra et al. 2021). Lastly, a partial dependence plot was used to visualise the marginal effect of the selected significant explanatory variables on the probability of occurrence of *X. ceramica*.

Predicting the risk map for infestation by *X. ceramica* in current and future scenarios. The final model developed using covariates within the extent of the sampled stands in each locality in the previous step was used to create a risk map of current infestations for the entire study area by extrapolation onto new layers of covariates on the basis of selected significant variables within the entire study area (Figure 1). In developing the future predicted risk map, the final model was projected onto future climate scenarios using the same procedure that was used to develop the current risk map. Shared Socioeconomic Pathways (SSPs) 1-2.6 and 5-8.5 were used as the future scenarios to represent the lowest and highest greenhouse gas emission pathways, respectively. The future climate projections were derived from three General Circulation Mod-

els (GCMs), including EC-Earth3, EC-Earth3-Veg, and CNRM-CM6, provided in the Coupled Model Intercomparison Project phase 6 (CMIP6), selected for the year 2050 (averaging over the period 2041–2060). These GCMs were chosen based on their demonstrated performance in simulating temperature and precipitation for Southeast Asia with minimal bias, as evaluated by recent studies (Iqbal et al. 2021; Desmet, Ngo-Duc 2022). EC-Earth3 and EC-Earth3-Veg are among the top models for accurately simulating rainfall and wind patterns for mainland Southeast Asia, while CNRM-CM6 was identified as the best performer for temperature projections. To improve the robustness of the future climate projections, an ensemble mean of the selected GCMs was employed by averaging the outputs of EC-Earth3, EC-Earth3-Veg, and CNRM-CM6. The ensemble approach mitigates individual model biases and uncertainties, providing reliability for assessing infestation risks across climate scenarios. The predicted risk maps for infestation by *X. ceramica* were obtained in the logistic format, and the occurrence probabilities ranging from 0 to 1 were reclassified using the reclassification function of QGIS 3.34.7. For ease of the determination of pest management strategies, three categories of infestation risk were defined: high infestation risk (> 0.6), medium infestation risk ($> 0.2 \leq 0.6$) and low infestation risk (≤ 0.2).

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RESULTS

A total of 6 434 teak trees in the studied localities in northern, western and central Thailand, in which the occurrence of *X. ceramica* has been reported, were sampled. On average, 18.9% of the sampled trees (i.e. 1 215 trees) were infested by *X. ceramica*. Detailed information on the number of trees sampled and infestations by *X. ceramica* in each locality is provided in Table 2.

The MaxEnt models were generated using 850 training points, representing trees infested by *X. ceramica*. The final model yielded average *AUC* and *TSS* values of 0.873 and 0.798, respectively, for the training set. For the testing set, the *AUC* and *TSS* values were 0.852 and 0.775, respectively, indicating the model's good ability to capture variations in environmental variables and its high predictive performance. The contributions of the individual environmental variables to the probability of occurrence were evaluated via the relative

average contribution and the average permutation importance. Overall, the associations between bioclimatic conditions and probability of occurrence were comparatively stronger than the associations between topographic characteristics and probability of occurrence (see Table S3 in the ESM). The significant environmental variables that were included in the final model (those whose relative average contribution exceeded the threshold of 4%) are shown in Table 3.

The occurrence of *X. ceramica* was mostly explained by temperature seasonality, as indicated by the fact that this variable had the greatest relative contribution value. Less significant effects were produced by precipitation seasonality, followed by the mean annual temperature. Annual temperature range and precipitation during the warmest quarter were also confirmed as influential environmental variables, but their explanatory power was rather negligible. When the effects of each variable are isolated, temperature sea-

Table 2. Summary of the infestation of teak trees by *Xyleutes ceramica* in 10 localities in Thailand (the severity of infestation is represented by the percentage of sampled trees that were found to be infested)

Locality	Number of trees		Severity of infestation (%)
	infested trees	total	
Chai Prakan	166	616	26.9
Chiang Thong	131	664	19.8
Khun Mae Kham Mi	99	623	15.9
Lat Yao	34	649	5.2
Mae Ho Phra	112	668	16.8
Mae Li	196	650	30.2
Mae Sai Kham	113	641	17.6
Nam Tak	125	652	19.1
Tha Pla	104	637	16.4
Wang Chin	135	634	21.3
Total	1 215	6 434	18.9 (average)

Table 3. Significant environmental variables identified in the final MaxEnt model (the average relative contribution and relative permutation importance were derived from 30 replicates)

Variable	Average contribution (%)	Average permutation (%)
Temperature seasonality (<i>BIO4</i>)	42.2	32.9
Precipitation seasonality (<i>BIO15</i>)	21.8	14.8
Annual mean temperature (<i>BIO1</i>)	19.4	23.5
Annual temperature range (<i>BIO7</i>)	8.7	17.2
Precipitation of warmest quarter (<i>BIO18</i>)	7.9	11.6

sonality remains highly explanatory, as indicated by the fact that it has the greatest permutation importance value; the second most significant variable is the mean annual temperature, followed by the annual temperature range (Table 3). The probability of occurrence of the species peaked when the temperature seasonality was 27 °C and the precipitation seasonality was 70%. It also peaked when the mean annual temperature

was 23 °C to 26 °C. The probability of occurrence of the species was positively associated with the annual temperature range. However, the increase appeared to plateau at temperature values greater than 24.5 °C. Conversely, the probability of occurrence of the species was negatively associated with precipitation during the warmest quarter, and the optimal amount of precipitation was less than 400 mm (Figure 4).

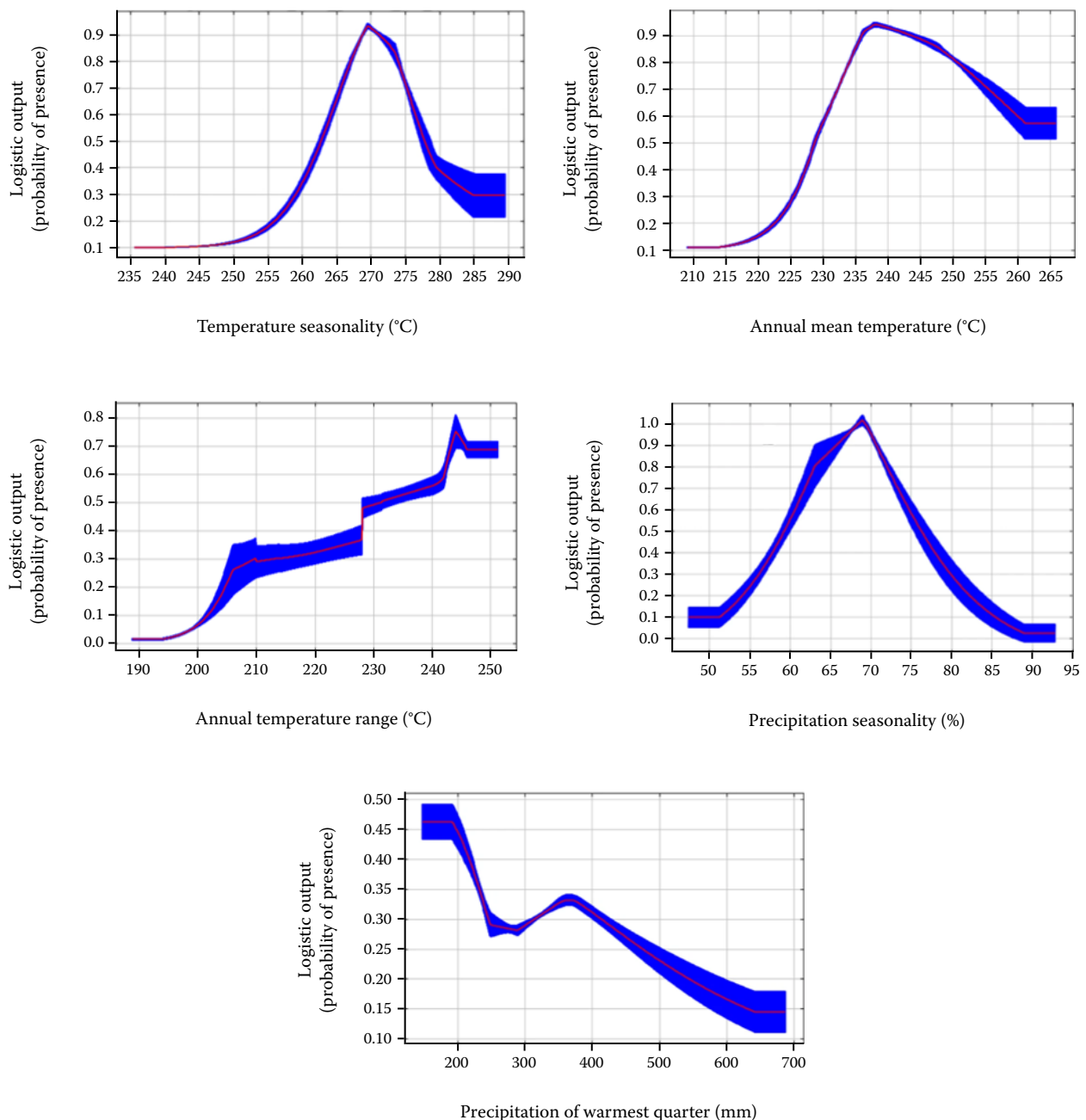


Figure 4. Partial dependence plots showing the marginal effect of selected significant explanatory variables on the probability of occurrence of *Xyleutes ceramica*

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The predicted risk of infestation by *X. ceramica* under the current conditions revealed that high- and medium-risk areas are distributed mainly in northern Thailand, with larger magnitudes of risk recorded in the central and western parts of the region. In addition, risks of small magnitude were found in some parts of central and western Thailand. Low-risk areas were concentrated in the western and central regions of the country, and risks of small magnitude were found in some parts of the northern and northeastern regions. According to future predictions, the high-risk area in the northern region showed the most obvious future decline in risk, with small areas remaining around the central and western parts of the region, whereas the risk level in low-risk areas apparently increased, with a large magnitude found in the central and northeastern regions under climatic conditions for the year 2050 in both scenarios SSP1-2.6 and SSP5-8.5 compared with current conditions. In scenario SSP1-2.6, the medium-risk areas increased and replaced the high-risk areas in the northern re-

gion. In addition, the risk areas in the northeastern region mostly shifted to the northern region. However, in scenario SSP5-8.5, the risk obviously decreased and was concentrated in the central and western parts of the northern region. Thus, under two future climate scenarios, the northern region generally remains the leading zone with high- and medium-risk areas especially around the central and western parts of the region (Figure 5).

Overall, compared with the current conditions, there was a net decrease in high-risk areas for infestation by *X. ceramica* throughout the entire study area in future projections for the year 2050 in both climate scenarios. The magnitudes of the decreases in high-risk areas were 17% and 23% in scenarios SSP1-2.6 and SSP5-8.5, respectively. The net area predicted to have medium infestation risk increased by 6% in 2050 in scenario SSP1-2.6 but decreased by 6% in scenario SSP5-8.5. Finally, low-risk areas showed a net increase in 2050 under both climate scenarios. The increases in low-risk areas were 12% and 23% in scenarios SSP1-2.6 and SSP5-8.5, respectively (Table 4).

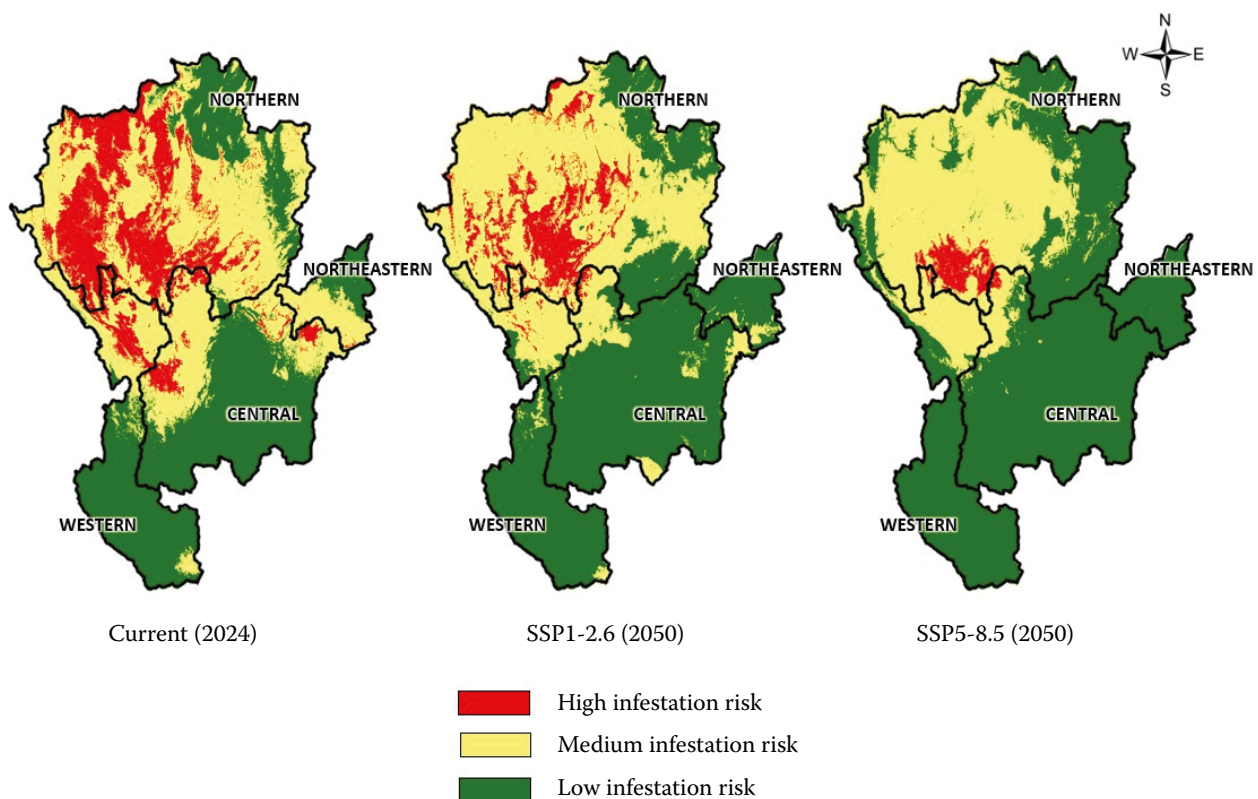


Figure 5. Predicted risk maps for infestation by *Xyleutes ceramica* based on current and future climate scenarios

Black line on the maps – boundaries of different regions in Thailand within the study area; SSP – Shared Socioeconomic Pathways

Table 4. Estimated risk area categorised by severity of infestation for the current and future climate scenarios (the number in the parenthesis is the percentage of the entire study area represented by each risk category)

Severity of infestation	current (2024)	Risk area (km ²)	
		future (2050)	
		SSP1-2.6	SSP5-8.5
Low	80 076 (40%)	103 465 (52%)	126 531 (63%)
Medium	70 146 (35%)	81 211 (41%)	69 150 (35%)
High	50 194 (25%)	15 740 (8%)	4 735 (2%)
Total		200 416	

SSP – Shared Socioeconomic Pathways

DISCUSSION

The present study investigated various environmental factors affecting infestations of teak plantations by *X. ceramica* in Thailand. According to our results, infestation by *X. ceramica* is mainly driven by climate, whereas topographic characteristics do not have significant effects. Above all, temperature seasonality and mean annual temperature were found to be the most important factors affecting the occurrence of the species when those factors were tested in isolation. *X. ceramica* is likely to prefer moderate temperatures in highly distinct seasonal environments. Additionally, the condition under which there is a relatively low amount of rainfall during the warmest quarter was also favoured by the species. The above predictions show that, under current and future climatic conditions, the habitats that are highly favourable to the species are mainly distributed in northern Thailand. However, the risk of infestation by this species gradually decreases under the predicted future climatic conditions, indicating low adaptability of *X. ceramica* to the changing climate.

As mentioned above, infestation of teak plantations by *X. ceramica* was found to be much more driven by large-scale climate than by microclimate, the latter of which is influenced by topographic variations. Diurnal anisotropic heat was the most important topographic variable, but it was considered to have no significant effect and was omitted from the final model because its relative average contribution fell below the 4% threshold (see Table S2 in the ESM). Additionally, regarding habitat selection by insects, temperature and elevation are often suggested to be the most important factors that determine the potential distributions of several species. However, it is important to note that

temperature usually correlates with elevation, i.e. temperature decreases with increasing altitude. Moreover, a Pearson's correlation test of our results confirmed the existence of a correlation between elevation and mean annual temperature. Thus, elevation was excluded from this study, and variables related to temperature were selected because their effects on insects are generally easier to interpret.

The predicted risk map revealed that the northern region, especially the central and western parts of that region, forms the core area of *X. ceramica* infestation in Thailand. This finding is consistent with a previous study of the genetic structure and variation of *X. ceramica* in northern Thailand. That study found that the species is very low in diversity and that most of its populations have likely originated from the central part of the region, with a geographic barrier to gene flow being a significant factor that affects the demography of the species (Rattanawanee et al. 2015; Panyamang et al. 2018). According to the distribution of the raster values of each significant bioclimatic variable in our study (data not shown), greater temperature seasonality and precipitation seasonality usually occur within the northern region, and these variables thus better represent the effects of environmental conditions on the occurrence of the species at the landscape scale. However, the impact of precipitation seasonality decreased substantially when that variable was used in isolation or if temperature seasonality was excluded from the model (Table 3), indicating that there are some correlations between these two variables. Moreover, the mean annual temperature better represents important effects on the occurrence of the species at the regional scale, as greater values are generally concentrated in lowland areas. *X. ceramica* clearly appeared to be more sensitive

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to temperature than to precipitation; the temperature variables presented higher permutation importance values than did precipitation seasonality and precipitation in the warmest quarter.

Effects of seasonality. Seasonality was the most important factor affecting the occurrence of *X. ceramica*. In terms of insect–host interactions, seasonal weather plays an important role in the growth, development and phenology of insects and host plants, determining insect behaviour (Hill et al. 2021). Some studies conducted in tropical forests have reported high abundance and diversity of adult lepidopterans in the dry season when the temperature is sufficiently high and appears to be favourable for the emergence of adults. In that case, the flight period of adults usually occurs during the late dry season, allowing concentration of the main abundance of caterpillars at the beginning of the growing seasons of their host plants in the early wet period (Maicher et al. 2018). In Thailand, teak is naturally distributed in the northern region, where there is a monsoon climate in which the wet and dry seasons are clearly distinct (Kaosa-ard 1981). Generally, the weather in northern Thailand comprises three seasons, i.e. a rainy season, a dry and cool season (winter), and a dry and hot season (summer) (Sanguansub et al. 2020). *X. ceramica* has a one-year life cycle in which the larvae develop during the rainy season, during which teak actively grows (Gotoh et al. 2007). During the winter, teak begins to lose its leaves and stops actively growing. At that time, mature larvae of *X. ceramica* begin to pupate inside the tree. In summer, the temperature increases due to the sunny climate, allowing adults of the species to emerge and reproduce. The next generation of larvae subsequently thrive when they are allowed to grow during the rainy season. However, the optimal temperature for the emergence of adults has never been reported. In addition, *X. ceramica* is a weak-flying species, and the presence of a closed understorey in forest stands was found to be a potential obstacle limiting the ability of the species to find and reach another appropriate host tree, resulting in a low dispersal ability of the species (Gotoh et al. 2007; Choochuen et al. 2024). Thus, apart from the suitable temperature in summer, it is possible that forest stands that have sparse foliage due to seasonal leaf shedding and/or low amounts of precipitation during the dry period can support flight activity and mating succession of the species. The possibility of being dis-

turbed by rain has also been documented for other wood-boring insects that usually emerge during summer in seasonal tropical forests in northern Thailand (Sanguansub et al. 2020).

With respect to the effects of climate change on the life cycles of insects, a change in seasonal weather patterns, especially temperature, can disrupt insects' growth, survival and reproduction by shifting their seasonal activities to periods with unprecedented conditions such as extremely dry or wet conditions, a lack of food sources, and abundant natural enemies (Hill et al. 2021). Under favourable conditions, *X. ceramica* has a short period in the year to reproduce only one generation (voltinism). Moreover, as most of its life cycle is spent inside the tree, the period of time that begins when the pupae become moths to the first instar is the most susceptible to disturbances (Tasen, Wiwatwitaya 2022). Thus, changes in temperature in winter and/or summer might impact the timing of pupation and/or the emergence of adults, resulting in flight activity occurring too early or too late and consequently decreasing the reproductive success of the adults as well as the survival of the next generation of larvae due to unfavourable conditions.

Effects of temperature. In a previous study, Choochuen et al. (2024) reported that *X. ceramica* appears to prefer a warmer microclimate influenced by a more open canopy of teak stands. In this study, diurnal anisotropic heat, which embodies the combined characteristics of temperature and topographic solar radiation, both of which are influenced by slope and aspect, was used as an indicator of the microclimate (Böhner, AntoniĆ 2009). However, our results indicate that the effects of large-scale climate are much more important to the species than are the effects of the microclimate and show that this species is likely to prefer moderate temperatures between 23 °C and 26 °C. According to the results of our future infestation risk prediction, the increased temperature due to global warming is suggested to be higher than the optimal threshold for *X. ceramica*, resulting in the loss of climatically suitable habitats for this species. This finding contrasts with the likely effect of increased temperature on other cossid pest species that live in temperate zones and have been reported to prefer relatively high temperatures, such as *Prionoxystus robiniae* (Peck, 1818) and *Cossus insularis* (Staudinger, 1892) (Nakanishi et al. 2016; Hannon et al. 2017). More-

over, the potential distributions of some species, such as *Z. pyrina* and *C. tristis*, have been found to be positively affected by global warming (Kumbula et al. 2019; Fekrat, Farashi 2022). Concerning the effects of rising global temperature on insects, recent work from the agricultural and forestry sectors has revealed that tropical insects are likely affected by warming conditions differently than are insects in temperate zones because the current temperature level in the tropics is already close to the tropical insects' tolerance range. Many tropical insects, even pest species, are subsequently predicted to experience decreased growth rates, whereas insects that live in temperate zones are anticipated to experience increased growth rates (Halsch et al. 2021; Skendžić et al. 2021). With respect to tropical lepidopterans, several studies have reported that a warming temperature results in uphill shifts in the numbers of butterflies and moths in tropical lowland ecosystems (García-Robledo et al. 2016; Cheng et al. 2019). Accordingly, global warming is expected to limit the growth rate and extend the life cycle of *X. ceramica*, and the risk of infestation of teak plantations by this pest is predicted to decrease, especially in lowland areas where the temperature exceeds the tolerance range of the pest species.

Effects of precipitation. A recent study revealed that herbivorous tropical insects are sensitive to changes in the amount, intensity, and frequency of precipitation at the same level of increasing temperature (Newell et al. 2023). However, our results revealed that the impact of precipitation on *X. ceramica* was less important than that of temperature. *X. ceramica* is not significantly affected by changes in the amount of annual rainfall, indicating that it tolerates a wide range of rainfall and humidity; however, it was found to be affected by the amount of rainfall during the warmest quarter, which is generally between March and May. The warmest quarter of the year in Thailand, which typically includes April and May, is also a premonsoon period in which heavy rains often come with summer storms (Chantraket et al. 2013). As mentioned above regarding the possibility of adults being disturbed by rain, heavy rain and strong winds that overlap with the emergence period of *X. ceramica*, which generally occurs between February and April, probably disrupt the flight and mating activities of the adults that emerge at the end of the period, consequently decreasing reproductive success. In addition, Shrestha (2019) reports

that eggs and larvae of several insect species can be washed away by heavy rain and flooding. Thus, this condition could also occur for the eggs and/or larvae of *X. ceramica* that have just hatched from eggs during this period. Accordingly, the mortality of *X. ceramica* is expected to increase at locations where adults emerge late and where the intensity of premonsoon rainfall is relatively high.

Limitations of the study, recommendations for management and future research. In this study, *X. ceramica* infestations at various large teak plantations in Thailand, located in different climatic regions, were investigated. The sample size used in this study is expected to be sufficient to represent the effects of climate and topography on the probability of occurrence of the species in teak plantations in Thailand. However, temporal effects of the environmental variables were not incorporated into the model due to non-continuous pest monitoring at the localities and the limited study time of the project. Several years of repeat monitoring would enable the utilisation of time series data in the MaxEnt model, enabling changes in infestation patterns due to temporal effects from climate and topography to be elucidated. Additionally, climatic conditions vary greatly within South-east Asia; thus, the combined effects of climate and topography found in this study might slightly differ from those in other countries in the region. Therefore, the present study's results should be validated by further investigations in teak plantations across the region where infestations of *X. ceramica* have been reported.

With respect to results application for teak plantations management, the current and future infestation risk maps predicted by the MaxEnt model used in this study can be considered together with knowledge of the bionomy and ecological requirements of the species described in previous studies to support decision-making in the management of teak plantations by forest managers and policy-makers. For example, planting pure teak stands and implementing low-intensity management of pest species are acceptable alternatives for sites classified as having low infestation risk under current and future climate scenarios. On the other hand, at sites classified as having high or moderate infestation risk, teak plantations should be established and managed as stands that are mixed with other non-host commercial tree species that also thrive under those climatic conditions, and under-

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stories with more than 30% coverage should be promoted and maintained in the stand to prevent the expansion of infestations and reduce the susceptibility of the stand to pest species (Choochuen et al. 2024). However, further investigation of the optimal planting patterns and the proportions of teak trees and other forest tree species is needed. Furthermore, pheromone traps are suggested to allow mass trapping and intensive pest monitoring at those sites, especially on large plantations. More importantly, owing to the low dispersal ability of the pest species, the transportation of infested teak seedlings is expected to be a potential factor causing the spread of infestations out of the pest's natural range or suitable habitats. Early detection and control of infested plants is an efficient way of preventing the introduction of pest species to new habitats caused by plant transportation.

Further investigations are necessary to confirm the findings of this study and to gain deeper insight into the effects of temperature on this species at various stages of its life cycle. The inclusion of degree-day accumulation in insect pest distribution models has been widely suggested, as it is considered a potential factor that can be used to accurately predict the development and emergence of insects (Herms 2004; Kumar et al. 2014; Crimmins et al. 2020). However, degree-day accumulation was not included as a variable in this study because of the lack of regional weather data. In a previous study, we also suggested investigating the development of larvae and the seasonal emergence patterns of adults under different environmental conditions for the precise monitoring and control of the pest in particular sites. Further studies on the optimum temperature and degree-day accumulation for the development of larvae and pupae, as well as for the emergence of adults, are strongly recommended to make it possible to achieve an understanding of the developmental behavioural plasticity of the species and to accurately predict its activity. Such knowledge would contribute to the precise monitoring and effective control of the pest at specific sites.

CONCLUSION

The results of this study and information from the literature show that the distribution of *X. ceramica* is strongly influenced by the environmental conditions in which teak naturally grows. However, pre-

diction of the potential natural distribution of teak in Southeast Asia under climate change shows that it is likely to remain stable in areas that are suitable for the natural growth of teak in Thailand (Trisurat et al. 2022). In contrast, the probability of infestation by *X. ceramica* is predicted to decrease in the future. Therefore, *X. ceramica* is expected to be directly affected by the changing climate and increasing temperature rather than by changes in the growth or phenology of its host tree.

The ecological niches occupied by *X. ceramica* depend primarily on highly distinct seasonal climates and moderate temperatures ranging from 23 °C to 26 °C. Additionally, a relatively low amount of premonsoon rainfall was found to support the occurrence of the species. The infestations caused by this species are expected to remain concentrated in northern Thailand under current and future climatic conditions, but the severity of infestation is predicted to gradually decrease under future climatic conditions, indicating low adaptability of the species to the changing climate. Changes in the seasonal patterns of climate and increasing temperature are the main driving factors that are expected to decrease the growth, development and survival of this species and to extend its life cycle. However, further investigations are needed to clarify the effects of temperature on *X. ceramica* at different stages of its life cycle. With respect to teak plantation management, mixed-species planting and intensive monitoring of pest species should be implemented in high- and medium-risk areas. In contrast, management in low-risk areas can be more flexible.

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