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Research article

The habitat-suitability models of the European mole cricket (*Gryllotalpa gryllotalpa*) as information tool for conservation and pest management

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ABSTRACT

The European mole cricket, *Gryllotalpa gryllotalpa*, feeds on a wide range of crops and can also damage plants with its burrowing activities. In suitable habitats (like those with damp, rich soils in flood plains), *G. gryllotalpa* numbers can increase to high levels. On the other hand, the abundance of *G. gryllotalpa* has dramatically decreased in north-western Europe partly due to direct eradication and excessive pest control. Using habitat suitability modelling, we identified areas suitable for *G. gryllotalpa* occurrence based on previous reports of its occurrence and based on environmental data. We limited our study area to regions where *G. gryllotalpa* is the only known *Gryllotalpa* species. The most important variables in our models were found to be relative air humidity and minimum soil temperature of the coldest month. We suggest that soil temperature is a limiting factor for European mole cricket occurrence in the Czech Republic because most areas in the country experience soil temperatures just below 0 °C, while most reports of *G. gryllotalpa* occurrence in Europe are from areas where the soil temperature does not drop below 0 °C. The models we have developed can provide information on possible occurrences of the mole cricket and thus improve the decision-making process both in the field of pest control and the conservation of this species.

1. Introduction

The European mole cricket, *Gryllotalpa gryllotalpa* (Linné 1758), feeds on a wide range of crops and damages plants with its burrowing activities locally [1]. In countries where *G. gryllotalpa* is abundant, it is considered a pest because it injures cereals, legumes, perennial grasses, potatoes, vegetable crops, beet, sunflower, tobacco, hemp, flax, and strawberry. It may also cause problem in nurseries where it may kill young plants and damage the roots of vines, fruit trees, and other trees [1]. The feeding injury to seedlings is cutworm-like and increases the probability of infection by plant pathogens [2]. Because *G. gryllotalpa* prefers to tunnel in moist habitats, it is regionally threatened by drainage; it is also threatened by pesticides and agricultural intensification (Heusiger, 1988; [3]. Although it is generally considered a weakly endangered species in Europe [3], the abundance of this species has dramatically decreased in north-western Europe partly due to direct eradication and pest control. *G. gryllotalpa* is now listed as Critically

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Endangered in Denmark [4], and is close to extinction in Lower Saxony and the United Kingdom [5,6].

Even though *G. gryllotalpa* numbers are declining in some regions [7,8], it is still a local pest in forest nurseries in Poland [9,10], Slovakia [11,12], and the Czech Republic, where it can kill young plants [13]. It also damages beet fields [14] and strawberry plantings in Latvia, where it feeds on the crowns and developing strawberry fruitlets or fruit [15]. Damage was even reported from tobacco fields in Austria [16] and in potato fields in Belarus [17]. Control of *G. gryllotalpa* has also been considered in Switzerland [18].

Gryllotalpa gryllotalpa can cause damage in vegetable gardens [19–23]. Although the frequency and extent of damage caused by the mole cricket has been poorly documented, many websites consider *G. gryllotalpa* to be harmful [24]. Recommended control measures include deep autumn ploughing, plowing of the soil between crop rows, trapping during the winter, pesticide application, the use of poison baits, and soil fumigation [1]. Although tillage and flooding have been successfully used to bring *G. gryllotalpa* to the soil surface and expose specimens to predators, chemical pesticides are widely used. The application of chemical pesticides is strongly promoted by the chemical pesticide industry, whereas the application of biopesticides has been weakly promoted and infrequently used.

Modeling species distributions with habitat suitability models (HSMs), ecological niche models (ENMs), or species distribution models (SDMs) [25,26] is a useful tool for preventing damages and risk analyses [27]. These methods allow researchers to analyze relationships between species occurrence and environmental data and to project the results in geographical space and in different time periods [25]. For insect pest management, HSMs and its variants (ENMs and SDMS) can be used to understand insect distribution and range limits [28], the potential for insect establishment in different areas [29], and the possibility of pest expansion or invasion under climate change [30,31]. Here, we used an HSMs to determine the current potential distribution of *G. gryllotalpa* in the Czech Republic.

In the current study, we attempted to identify geographical regions with habitats favor *G. gryllotalpa* abundance. *G. gryllotalpa* is thermophilic [32], and its occurrence is greatly affected by the temperatures that prevail when females mate and lay eggs, i.e., April to June [33]; 1960; [34]. *G. gryllotalpa* is sensitive to cold [33], therefore, the temperature in the winter months (November–February) could also limit the occurrence of *G. gryllotalpa*. *G. gryllotalpa* is hygrophilous [33,35]. The requirements for soil types are not known, but if we omit the cultivated habitats (gardens, fields, and nurseries), the habitats include those that have high soil water contents [22]; Schlumpfrecht and Waeber, 2002; [36]. The goals of the current research was to predict the geographical regions where *G. gryllotalpa* may occur, and confirm the importance of ecological factors suggested from literature.

2. Materials and methods

2.1. Brief life history of Gryllotalpa gryllotalpa

European mole cricket is cylindrical-bodied, fossorial insect about 50 mm in males and 70 mm in females with small eyes and shovel-like fore limbs highly developed for burrowing. Mole crickets live almost entirely below ground, digging tunnels of different kinds for the major functions of life, including feeding, escape from predators, attracting a mate (by singing), mating, and raising of

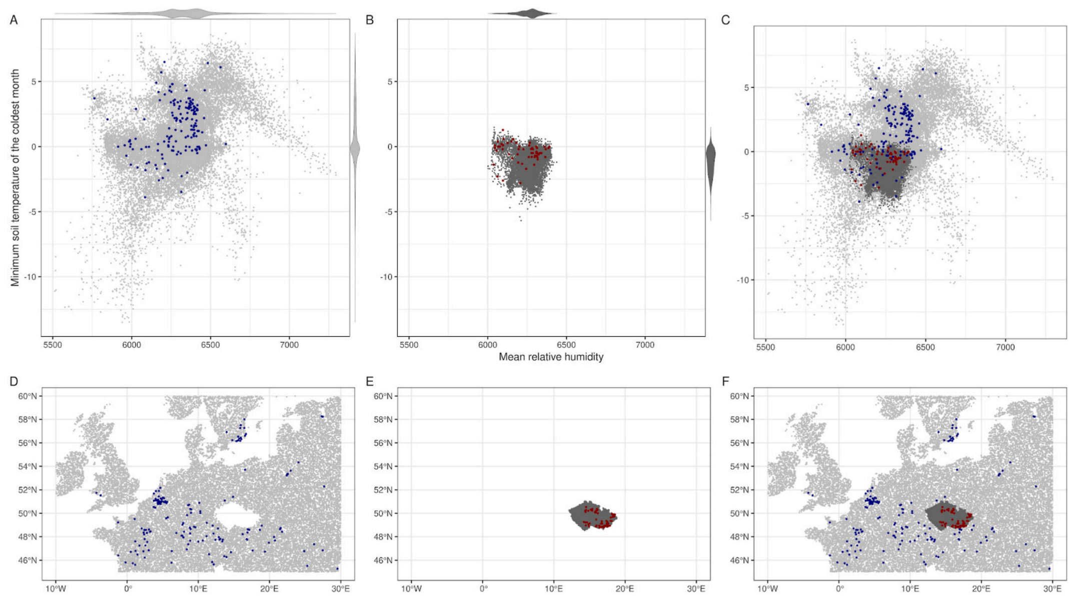

Fig. 1. Visualization of background and occurrence data in environmental (A–C) and geographical (D–F) space. Geographical space (A–C) is defined by longitude and latitude. Environmental space (A–C)) is defined by two variables with the highest relative importance in the models (relative air humidity on the X-axis and the minimum soil temperature of the coldest month on the Y-axis). The violin plots at the margins show the distribution of background data. Plots A and D show only training data: light-grey indicates background training points, and blue indicates training occurrences. Plots B and E show only testing data: dark-grey indicates background testing points, and red indicates testing occurrences. Plot C shows all of the data used in the environmental space, and plot F shows all of the data used in the geographical space.

young. Male mole crickets have an exceptionally loud song; they sing from a burrow that opens out into the air in the shape of an exponential horn. The song is an almost pure tone, modulated into chirps. It is used to attract females, either for mating, or for indicating favorable habitats for them to lay their eggs. After mating, a period of 1–2 weeks may occur before the female starts laying 100 to 350 eggs in an underground chamber in the spring eggs. They hatch ten to twenty days later, and female guards them for another two to three weeks. The eggs hatch in a few weeks, and as they grow, the nymphs consume a great deal of plant material either underground or on the surface. Mole crickets are active most of the year, *G. gryllotalpa* overwinters as nymphs first winter and young adults next winter before adults are ready to mates. It takes two years to reach maturity.

Adults of mole cricket can fly powerfully, if not with agility, but males do so infrequently. The females typically take wing soon after sunset, and are attracted to areas where males are calling, which they do for about an hour after sunset [20,22,33,36,37,76].

2.2. Study design and data analysis

Using available information on *G. gryllotalpa* occurrence as related to environmental variables, we used HSM to identify habitats in forests, farms, and gardens that favor *G. gryllotalpa* occurrence We analyzed the data with Maxent 3.4.3 [38] in the *sdm* package [39] in R [40]. Maxent is a machine learning method widely used for modeling species distributions with presence-only data [41,42]. It takes presence locations (occurrences), environmental data from these locations and sample of background locations in the study area as input, and uses maximum entropy principle to estimate the distribution in geographic and environmental space [41,43]. The exact mathematical definition is described by Ref. [41] (approach of maximizing the entropy in geographical space), and further statistical explanation by Ref. [43] (approach of minimizing the relative entropy of environmental data from the occurrence points relative to environmental data sampled from background points).

We limited the study to an arbitrarily defined area (10°W 45°N,30°E 60°N, see Fig. 1C) to increase the probability that the information on occurrence concerned only *G. gryllotalpa* and not co-occurring species [44–46] that had been misidentified as *G. gryllotalpa* [47]. Because *G. gryllotalpa* is widespread in Europe, we sampled background data in the whole study area, i.e., we considered the accessible area, the M component from the BAM diagram (B - suitable biotic niche space, A - suitable abiotic niche space, M − accessible area for species; see Ref. [26] to be the whole study area.

2.3. Environmental data

As predictors, we preselected nine environmental variables based on the known ecological and habitat preferences of *G. gryllotalpa* (see above). The following environmental variables were selected: minimum soil temperature of the coldest month and mean soil temperature of the warmest quarter from SoilTemp [48]; mean relative air humidity from CHELSA [49], the Thornthwaite aridity index and Climatic moisture index (relative wetness and aridity) calculated with the *envirem* package [50] from the CHELSA dataset [49]; predicted probabilities of gleysols and fluvisols from SoilGrids2 [51]; the compound topographic index from Geomorpho90 [52]; and the annual mean of the water table depth [53]. All variables are summarised in Table 1. All variables were available as raster data; to obtain the same spatial resolution for all variables, we resampled to match the resolution of the CHELSA dataset, which was the dataset with the lowest resolution (30 arc-second resolution).

2.4. Occurrence data

Presence data were aggregated from GBIF [54], iNaturalist (iNaturalist, 2021), the Czech national species occurrence database of NCA CR [55], the Slovakia national occurrence database [47,56]; and data from personal databases collected by professionals and citizens in Czech Republic. Data in the Czech Republic were mostly collected by experienced orthopterologists, who have been comprehensively sampling Orthoptera species throughout the area for decades (team and its activities see Ref. [57]. Other data from the Czech Republic are from professional nature conservation and NGO workers and from the public. All presence data were subsampled to fit the temporal period (1979–2013) and the spatial resolution (accuracy up to 1 km) of the used CHELSA climate variables. To reduce sampling bias, we used spatial filtering with the 1201388194 *spThin* package [58] and only retained the occurrences that

Table 1
Preselected environmental variables.

Variable	Source dataset	Reference
Minimum soil temperature of the coldest month[a]	SoilTemp	[48]
Mean soil temperature of the warmest quarter[a]	SoilTemp	[48]
Mean relative air humidity	CHELSA	[49]
Thornthwaite aridity index	ENVIREM (CHELSA)[b]	[49,50]
Climatic moisture index	ENVIREM (CHELSA)[b]	[49,50]
Predicted probability of fluvisols	SoilGrids2	[51]
Predicted probability of gleysols	SoilGrids2	[51]
CTI - compound topographic index (also known as topographic wetness index - TWI)	Geomorpho90	[52]
WTD – water table depth (annual mean)	Global patterns of groundwater table depth (WTD)	[53]

[a] Depth interval 5–15 cm.
[b] ENVIREM variables were calculated from CHELSA climatic data.

were at least 10 km from each other.

2.5. Habitat suitability model

Before the analysis, we divided the entire study area into two subareas: a calibration area (the whole study area excluding the Czech Republic) and a testing or projection area (only the Czech Republic). Czech Republic boundaries were defined by a polygon from the GADM dataset [59]. We masked environmental data by projection area (Fig. 1A and B), and the rest of the environmental data (the calibration area) were analyzed for multicollinearity with the variance inflation factor (VIF) from the *usdm* package [60] with a correlation threshold of 0.7. Data with high collinearity were automatically removed from further analysis. To ensure the possibility of extrapolating model results to the projection area, we checked the dissimilarity of environmental conditions in the calibration vs. projection areas with ExDet [61] implemented in the *ecospat* package [62]. We split the occurrence data into training and testing datasets in the same manner as the environmental data (i.e., the training dataset only included occurrences within the calibration area; the testing dataset only included occurrences within the testing area). We consider the occurrence data in the Czech Republic to be independent from the data in the rest of the whole study area because they are independent spatially and are still within the geographical and environmental space defined with occurrences in the training dataset (Fig. 1). To obtain background data from the calibration area and projection area, we sampled 30,000 random points in the calibration area and 10,000 random points in the projection area.

Maxent has two parameters' settings for controlling model complexity: feature classes and regularization [63]. Feature classes allows the fitting of various complex dependencies (linear (L), quadratic (Q), product (P), threshold (T), and hinge (H)), and the regularization parameter controls the closeness of the fit of the animal distribution (see Refs. [42,63]. We used the *ENMeval* package [64] to optimize Maxent performance by electing the best potential combination of these parameters. Our optimization consisted of 160 model runs with 5-fold cross-validations in combinations of 8 feature class settings (LQ, LQP, LQT, LQH, LQHT, LQTP, LQHP, and LQHPT) and 20 beta regularization multipliers (0.5–10.0 in 0.5 steps). From these models, we chose one combination of feature class and regularization multiplier that produced a model with the lowest AICc value (delta AICc = 0) [65]. We ran 10 replicates of the model with 5-fold cross-validation (resulting in 50 model replicates). Beside the cross-validation (dependent test), each model replicate was tested with the independent dataset. Two ensembles raster outputs were constructed from all replicates: raster weighted by area under the ROC curve (AUC) and raster with mean of thresholded (binary) presence-absence predictions [39]. To define the threshold, we used the maximum of sensitivity and specificity sum method (max($se + sp$)). We also calculated uncertainty map represented by the standard deviation of all model replicates results. Such a map indicates the areas with the highest variability across model replicates, i.e., the areas where predictions are more uncertain in geographical space (Figs. 2C and 3).

To evaluate the resulting model, we used the continuous Boyce Index (CBI) [66,67], the symmetric extremal dependence index (SEDI) [68], sensitivity, and the binomial test. Threshold-dependent metrics were calculated with the max($se + sp$) threshold method.

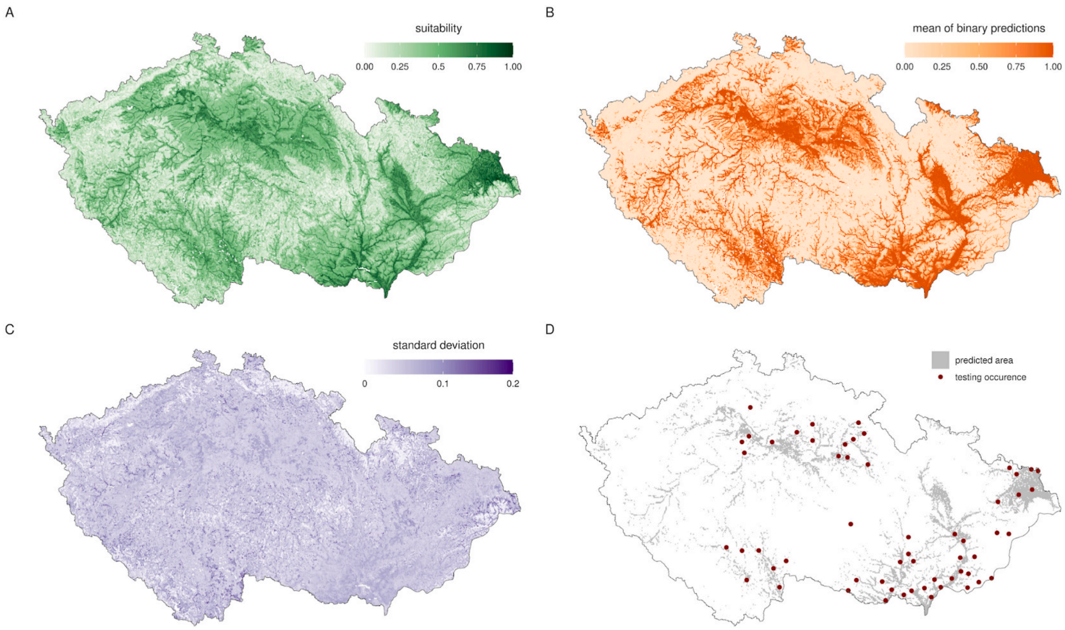

Fig. 2. A) Ensemble model weighted by AUC: 0 = least suitable, and 1 = most suitable. B) Ensemble model mean of thresholded presence-absence outputs: 0 = least suitable, 1 = most suitable. C) Uncertainty represented by standard deviation: 0 = least uncertainy, i.e., no variability across model replicates. D) Ensemble model represented by agreement of all thresholded presence-absence outputs: grey predicted area with mean value 1 are represented by gery colour, and red points represent testing occurrences.

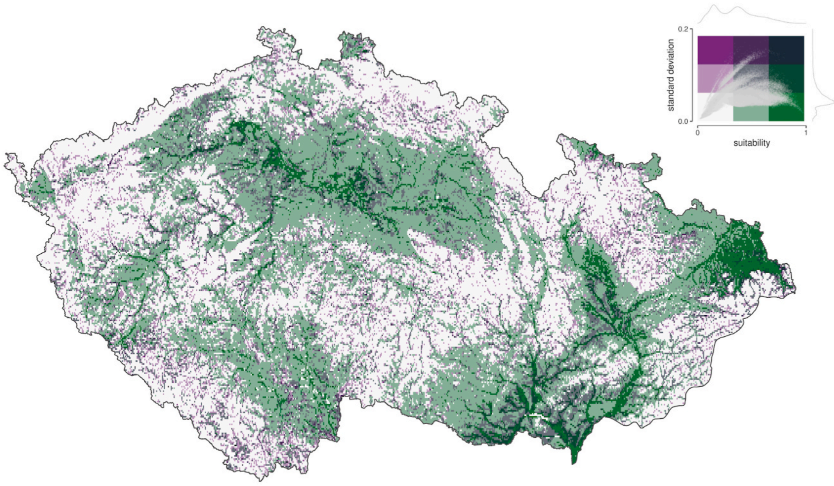

Fig. 3. Bivariate map of ensemble continuous prediction and uncertainty represented by its standard deviation. Suitability is shown on the X axis of the legend, depicted in the green scale: 0 = least suitable, and 1 = most suitable. Uncertainty is shown on the Y axis of the legend, depicted in the purple scale: 0 = the least uncertainty, and 0.2 = the most uncertainty. The light grey color represents areas predicted to be the least suitable and with the lowest uncertainty, and the dark blue grey color represents areas predicted to be the most suitable and with the highest uncertainty. Point cloud and density plots in the legend represent the distribution of values in the area.

The CBI is a threshold-independent metric suitable for presence-only models, which measures how model predictions differ from random distribution of presences [67]. Values of CBI varies between −1 and 1, while 0 mean that model prediction is similar to random prediction, positive values mean that prediction is better than random i.e. evaluation data set is consistent with prediction, and negative values mean that prediction is worse than random i.e. counter predictions - evaluation data set falls to unsuitable areas [67]. CBI was calculated with the function *ecospat.boyce* in the *ecospat* package. The SEDI is a threshold-dependent metric which was recently introduced as an alternative to true skill statistics in niche modeling; it provides threshold-dependent metrics suitable for presence-background models, due to lowered sensitivity to prevalence (Wunderlich, 2019). Similarly to the CBI, values of SEDI varies between −1 and 1, while positive values indicates prediction better than random and vice versa [68]. SEDI was calculated by the R script provided as a supplement of [69]. Sensitivity (Se, the true positive rate or TTP) is a threshold-dependent metric that indicates the proportion of predicted presences from all presences. For the mean of the thresholded presence-absence ensemble, a one-tailed binomial test was used to determine whether the number of successfully predicted presences was greater than expected by chance, in this case defined by the proportion of the predicted area [70]. For the latter test, we used the *binom.test* function from base R. The SEDI and binomial tests were performed on the ensemble of thresholded outputs, in which a pixel was counted as suitable only when it was suitable in all model replicates. Relative variable importance was reported using permutation based on the Pearson correlation metric with *sdm* R package [39].

Simplified modelling workflow is depicted in Fig. 4. The R code (data download, pre-processing, models, and visualizations) is available as supplementary material (Appendix A) and on the GitHub (link will be provided after acceptance). Occurrence data that were not publicly available for direct download are also provided in the same manner, according to the owners' sharing permissions.

3. Results

After occurrence filtering, we retained 162 training and 57 testing occurrence points as input for the model. Based on the VIF analysis, we removed 1 of the 9 environmental variables (Climatic moisture index). The ExDet test confirmed that there is no novelty in environment in the testing area (mean = 0.01 ± 0.01). Based on ENMeval optimization results, we choose LQT feature class setting and the regularization parameter 1.5. The most important variables in the model based on cross-validation testing were the mean relative humidity (relative importance = 30%), the minimum soil temperature of the coldest month (relative importance = 23%), and the Thornthwaite aridity index (relative importance = 13%). For the independent testing dataset, mean soil temperature of the warmest quarter had the highest relative importance (26%), followed by the Thornthwaite aridity index (14%), and the compound topographic index (12%) (see Table 2).

The results (means ± SD) of the dependent validation tests were as follows: CBI = 0.79 ± 0.09, SEDI = 0.57 ± 0.06, and sensitivity = 0.72 ± 0.12, with a threshold = 0.57 ± 0.11. The means ± SD of the independent validation tests were CBI = 0.72 ± 0.1, SEDI = 0.55 ± 0.03, and sensitivity = 0.73 ± 0.11, with a threshold = 0.44 ± 0.08. The results of the test of the mean of thresholded presence-absence ensemble with independent data were as follows: SEDI 0.57 and a significant binomial test ($p < 0.001$) with 47% successfully predicted presences (i.e., sensitivity = 0.47) in predicted suitability in the 9% of the entire testing area (Fig. 2D). The CBI of the test of continuous ensemble prediction weighted by AUC with independent data was 0.93. The range of the standard deviation of all model replicates predictions in the testing area was 0.01–0.20 (mean = 0.05 ± 0.02).

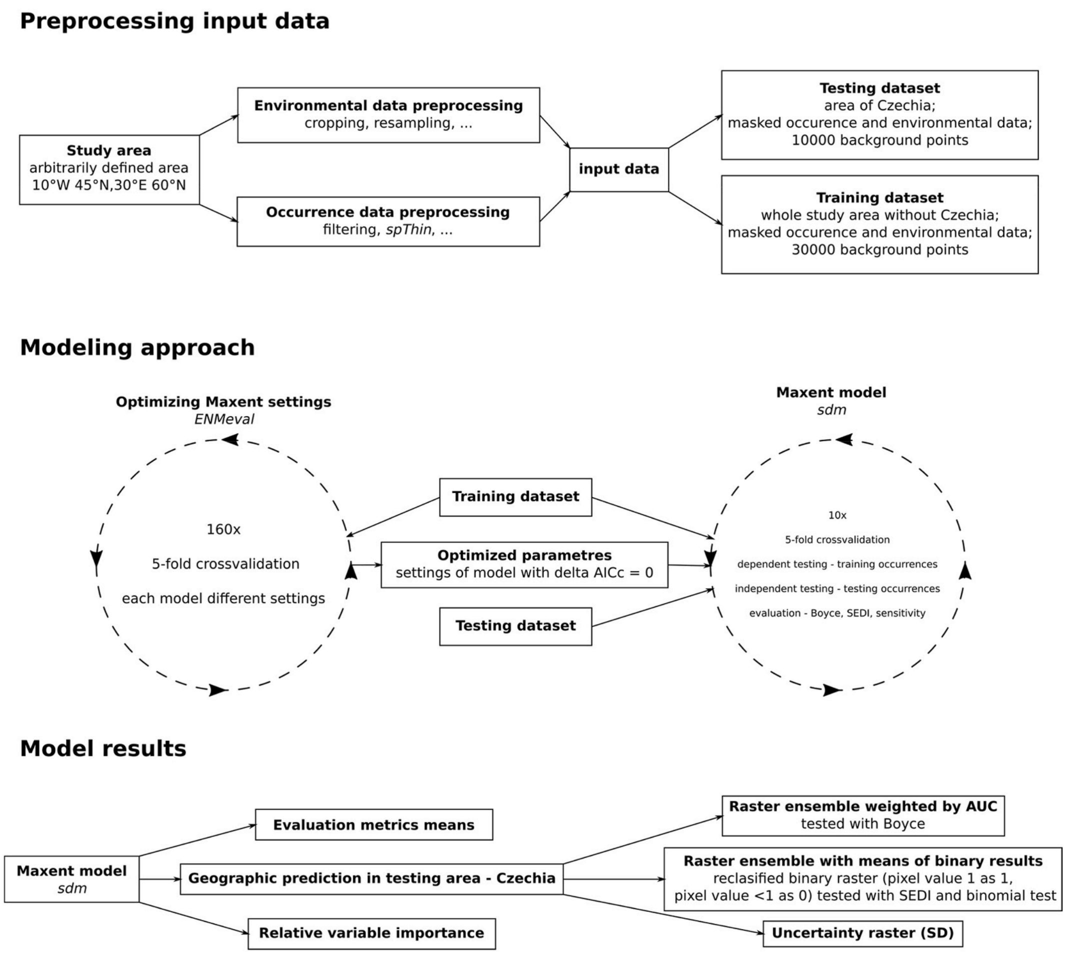

Fig. 4. Flow diagram of simplified modeling approach including preprocessing data, optimization and running Maxent models, and model results.

Table 2
Relative variable importance (%) according to dependent test.

Environmental variable	Dependent test (cross-validation)
Mean relative humidity	30
Minimum soil temperature of the coldest month	23
Thornthwaite aridity index	13
Mean soil temperature of the warmest quarter	12
Fluvisols	11
Compound topographic index	9
Water table depth	5
Gleysols	4

4. Discussion

In this study, we used HSM to estimate areas with suitable conditions for the occurrence of the European mole cricket, *G. gryllotalpa.* Our model was based on climate, soil properties, and topography. In the Czech Republic, the potentially suitable areas are mostly in the lowlands, with the largest area in Moravia and Silesia, especially in the southern and central parts, and in the lower parts of northern Moravia and Silesia. In Bohemia, the most suitable conditions occur mainly in the floodplain of the river Elbe and in southern Bohemia, which is a humid basin with thousands of ponds (Fig. 2A and B). The uncertainty in the ensemble prediction represented by the standard deviation was lowest in mountainous areas with low predicted suitability and was highest in areas with the most consistent predictions of high suitability across the models.

Because *G. gryllotalpa* is hydrophilic and is sensitive to low temperatures [33], it is most abundant in regions with a Mediterranean climate (Italy and southern France) (Alonso and Herrera, 1982). The climate in some regions of the Czech Republic is also suitable for *G. gryllotalpa* because the climate is transitional between oceanic and continental with a predominance of westerly winds, frequent alternation of individual frontal systems, and relatively abundant precipitation [71].

Our predicted suitability corresponds to historical records of *G. gryllotalpa* outbreaks in 1941–1944 in part of the former Protectorate of Bohemia and Moravia (the reduced Czech Republic during the occupation of the Third Reich) [72]. The authors of the latter report, which was written in Czech and has been rarely if ever cited, explain the patterns of presence and absence, and explain that the low abundance in some lowland areas that have shallow soils, such as the Boskovice furrow in central Moravia (for position see Ref. [73], is due to the *G. gryllotalpa* requirement for deep soils for development. In addition, many soils in this area are inadequate because they are dominated by coarse sands that are not suitable for the building of *G. gryllotalpa* nests [74]. *G. gryllotalpa* requires a heavy and viscous soil for burrowing and nest building. Even where the soils are deep or otherwise suitable in this area, they tend to be either too dry or too moist [72]. Although our model shows a narrow strip of high suitability in the Boskovice furrow, *G. gryllotalpa* is currently documented only from the most southern part of the furrow. The area of occurrence has generally not changed since 1940s, but our unpublished surveys indicate that *G. gryllotalpa* abundance has significantly decreased. We assume that this is due to radical changes in the landscape during the communist period (field consolidation, land reclamation, and land drying) (Kubačák 1995). Soil properties are key factors in *G. gryllotalpa* habitat preferences. Among the two preselected soil types, only fluvisols substantially contributed (12%) to our final model. The soil environment is clearly important to *G. gryllotalpa* because the insect is adapted to living underground, where it creates tunnels that serve for feeding, protection, and mating [75]. As a hygrophilous species, *G. gryllotalpa* mostly inhabits moist areas [19]. Although [76] state that *G. gryllotalpa* prefers drier habitats with loose soils, these authors also note that *G. gryllotalpa* can live near watercourses, because it is very well protected from moisture by its body structure. In general, *G. gryllotalpa* requires loose and moist sandy or clay soils. The species does not tolerate permanently wet soils or dry sandy soils [23]. Another reason why *G. gryllotalpa* lives in moist habitats is that moisture may be necessary for egg development. The embryonic development requires high soil moisture and a nest temperature $>15\ ^\circ C$ [33]. This corresponds with the contributions of variables in our model, in which habitat moisture was represented by relative air humidity, by the compound topographic index (indicating wetness), and by a fluvisol soil type, which typically forms in river basins. Temperature in our model was represented by the mean soil temperature of the warmest quarter of the year and by the minimum soil temperature in the coldest month. We assume that the mean soil temperature of the warmest quarter is important for the development of nymphs, and that the minimum soil temperature in the coldest month is important for the survival of overwintering adults [22]. states that *G. gryllotalpa* in Baden-Württemberg inhabits warm lowlands because it prefers the slightly higher temperatures in those areas [77]. From the visualization of environmental space (Fig. 1E and F), we suggest that the minimum soil temperature in the coldest month could be a limiting factor for *G. gryllotalpa* distribution in the Czech Republic, because there are very few places in the Czech Republic with minimum soil temperatures $>0\ ^\circ C$, unlike warmer places occupied by this species in the rest of the studied area (Fig. 1D, F). We hypothesize that an increase in this minimum soil temperature could lead to the spread of *G. gryllotalpa* in the Czech Republic.

Our results show that areas recently occupied by *G. gryllotalpa* are in climatically favorable lowlands at mid altitudes and with soils well supplied with water. The occurrence of *G. gryllotalpa* is determined by suitable soils and by the depth of groundwater because *G. gryllotalpa* must have access to groundwater throughout the year, especially in dry periods. On the other hand, groundwater levels must not rise too high because this could wash the crickets away, especially from autumn to spring when the adults overwinter in the soil at a depth of 1.5–2.0 m and sometimes deeper [72]. We suggest that some areas predicted by our models as suitable may not correspond with the actual occurrence of the species, because a suitable habitat may not be present at a certain place. Those parts of the landscape that are used for intensive agriculture and technical-urban development have been so greatly altered that they are unsuitable for the occurrence of most animals [78], including *G. gryllotalpa* [23]. Suitable habitats outside of gardens are also reduced by land reclamation because of soil compaction [22]. As a result, there is a decrease in the occurrence of *G. gryllotalpa* in intensively managed localities. Because *G. gryllotalpa* prefers locations without chemical application or deep plowing, *G. gryllotalpa* mainly occurs in gardens and yards [22]. *G. gryllotalpa* also finds alternative habitats in excavated sand pits if the bottom of the sand pit is below the level of groundwater and has increased concentrations of clay. Such localities may be outside the area defined by our prediction.

We do not know exactly the maximum spread rate of *G. gryllotalpa* [37] but [79] estimated the maximum spread rate of the mole crickets *Neoscapteriscus vicinus* (Scudder, 1869) and *N. borellii* (Giglio-Tos, 1894) at 20 km.year^{-1}. If we assume a similar spread ratio for *G.gryllotalpa* to spread, it will spread very quickly as the climate warms as it already happened in the warm years of the 1990s in Bavaria [22]. Of course, the soil temperature of the coldest month must be increasing, but also moist habitats must be available. It is obvious that wetlands are drying up recently [80]. Although *G. gryllotalpa* does not inhabit continuous forest stands [72], it can be harmful in forest nurseries [23]. For this reason, textbooks have traditionally mentioned *G. gryllotalpa* as a pest, although we have recently found only two forest nurseries in the territory of the Czech Republic where damage has been reported [13,81]. Both forest nurseries are in southern Moravia in an area ideal for the occurrence of *G. gryllotalpa*. We therefore suspect that *G. gryllotalpa* occurrence is permanent and that the damage is chronic in that area. In the reports on the occurrence of pests in forests, however, *G. gryllotalpa* has not been mentioned even once in the last 20 years in the Czech Republic [82] and has been mentioned only once in Slovakia [12]. This does not mean that all cases have been reported. It is very likely that the owners of forest nurseries are not interested in publicizing damage. However, even if *G. gryllotalpa* does cause damage in nurseries, we suspect that only a small proportion of the 300 forest nurseries in the Czech Republic [83] would be affected. The problem is greater in private gardens or small vegetable fields, because it is unlikely that gardens will be replaced or not established because of mole cricket occurrence. The owners of private gardens or small vegetable fields should be made aware that if their property is in suitable places for the occurrence of the mole cricket, the abundance of the cricket can substantially increase under suitable climatic conditions. The owners should also be informed that the control of *G. gryllotalpa* is difficult, and that permitted methods may not be effective [84].

Habitat conservation is a priority to maintain the numbers of *G. gryllotalpa* in areas where its abundance is decreasing. The model we created could be used to protect species in other European countries. In areas suitable for the potential occurrence of *G. gryllotalpa,* it is advisable to carry out an extensive survey of the occurrence and determine its abundance. It is advisable to listen to the singing of the males in May. The study could be used to highlight areas suitable for conservation translocation and areas where the species can spread on its own. *G. gryllotalpa* may be relocated to a suitable habitat even from gardens, as [85] suggested, where they multiply.

5. Conclusions

Using habitat suitability modeling, we identified areas suitable for the occurrence of *G. gryllotalpa* in the Czech Republic. The main explanatory variables were air temperature, humidity, and soil type. Our results indicate that suitable areas are generally close to rivers, but that the most suitable areas are larger wetlands, especially the south Bohemian Pond system and the floodplains of the largest rivers. Information on the occurrence of *G. gryllotalpa* in the area used for model training is very limited because occurrence in suitable areas is very polydisjunctive. *G. gryllotalpa* prefers small gardens under simple management and without deep plowing. In such ideal habitats, *G. gryllotalpa* can reproduce very rapidly. While we independently validated our prediction only for the Czech Republic, cross-validation tests of training data also showed satisfactory results for the rest of the study area, i.e., the presented model can be used throughout Central Europe. However, we recommend the development of custom models for specific countries; such models should consider recent and historical occurrences and should be tested with independent datasets. *G. gryllotalpa* is a marginal problem in forest nurseries but can cause ongoing damage in forest nurseries located in areas with ideal habitat. The study could be used to select suitable habitats for occurrence and highlight areas suitable for conservation translocation.

Author contribution statement

Jaroslav Holuša and Oto Kaláb: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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Data availability statement

Data will be made available on request.

Credit author statement

JH: Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Validation; Writing - original draft; Writing - review & editing; OK: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Validation; Writing - original draft; Writing – review & editing; Both authors significantly contributed to this manuscript and have read and approved the manuscript in its current form.

Declaration of interest's statement

The authors declare no competing interests.

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Appendix A. Supplementary data

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