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MODELLING THE BIOCLIMATIC NICHE OF A COHORT OF SELECTED MITE SPECIES (ACARI, ACARIFORMES) ASSOCIATED WITH THE INFESTATION OF STORED PRODUCTS

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Modelling the Bioclimatic Niche of a Cohort of Selected Mite Species (Acari, Acariformes) Associated with the Infestation of Stored Products. Tytar, V. M., Oksentyuk, Ya. R. — In this study an attempt is made to highlight important variables shaping the current bioclimatic niche of a number of mite species associated with the infestation of stored products by employing a species distribution modeling (SDM) approach. Using the ENVIREM dataset of bioclimatic variables, performance of the most robust models was mostly influenced by: 1) indices based on potential evapotranspiration, which characterize ambient energy and are mostly correlated with temperature variables, moisture regimes, and 2) strong fluctuations in temperature reflecting the severity of climate and/or extreme weather events. Although the considered mite species occupy man-made ecosystems, they remain more or less affected by the surrounding bioclimatic environment and therefore could be subjected to contemporary climate change. In this respect investigations are needed to see how this will affect future management targets concerning the safety of food storages.

Key words: Acariformes, Astigmata, bioclimatic niche, Maxent, climate change, food storage.

Introduction

More than 50 species of mites have been found in association with stored products (Clemmons, Taylor, 2016). Mites are important pests in stored grain commodities not only due to the damage caused by their feeding, but their presence may lead to rejections resulting in a loss in revenue. In addition they are highly allergenic and have the potential to vector mycotoxin producing fungi within a storage environment which may result in associated health risks if stores are not properly managed (Collins, 2012). Stored-grain mites are, for the most part, cosmopolitan (Freeman, 1973). Most stored-grain arthropods are thought to have originated in India or the Middle East and have been transported throughout the world by human movement of foods (Cotton, 1956). The main limitations to the spread of stored-grain pests, besides the export and import of goods, and the regulatory efforts of importing countries, are temperature (T) and relative humidity (RH) (i. e. climate) (White et al., 2011). Mites are very common pests of stored grain and oilseeds, particularly in temperate areas with high RH, although they can also infest stored products in relatively dry and warm climates (Palyvos et al., 2008).

The most important factors that influence mite population development appear to be combinations of T, RH and moisture content (MC). A rise in T, RH and/or MC increases mite productivity, whereas a decrease in T, RH and/or MC content decreases productivity, with interactions occurring between the variables (Dunn, 2003).

Different mite species also have different requirements for development, although there is generally no upper limit for humidity (Cunnington, 1969). *Acarus siro* Linnaeus, 1758 has a greater rate of development in grain of higher MC and is less frequent in drier warmer climates (Cunnington, 1976). Under laboratory conditions, the lower and upper T limits for *A. siro* are around 2.5 and 31 °C respectively; with a lower RH limit of 62.5 % (dependent on T) (Cunnington, 1965), although Aspaly et al. (2007) found an upper T limit of 38 °C (at 85 % RH). *Lepidoglyphus destructor* (Schrank, 1781) is less tolerant of low humidities than *A. siro* and cannot complete development below much 65 % RH (dependent on T) (Cunnington, 1976). Its lower and upper T limits, are around 3 and 34 °C respectively (Cunnington 1976). *Tyrophagus putrescentiae* (Schrank, 1781) is more tolerant of high temperatures and can survive and breed readily above 30 °C; but is less tolerant of low temperatures and cannot develop much below 10 °C (Cunnington, 1969). As with the other storage mites, *T. putrescentiae* develops most rapidly at conditions of high RH, with a lower limit of 65 % (dependent on T) (Cunnington, 1969). The optimum conditions for rapid development in the laboratory are 25 °C and 90 % RH for *A. siro* and *L. destructor*, and 30 °C and 90 % RH for *T. putrescentiae* (Cunnington, 1976). Due to the wide range of preferred temperatures, *A. siro* and *L. destructor* can be classified as eurythermic, whereas *T. putrescentiae* is stenothermic and more thermophilous than the other species (Hubert et al., 2010). The species *T. putrescentiae* obviously gravitates in its life strategy to an r-strategy. It is thermophilic, is first to appear in stored products, rapidly increases in numbers, quickly spreads over the entire substrate, tends to consume substrates rich in nutrients, because of peculiarities of its digestive enzymes, and is first to disappear (Akimov, 1985). In addition, this species has no hypopial stage and is oriented towards establishing itself in new substrates. On the other hand, A.M. Cunnington considers limits of T and RH within which *A. siro* is able to complete its development are fairly restricted and this explains why, although often loosely described as a cosmopolitan species, its occurrence and distribution is largely confined to countries with a cool, moist climate (Cunnington, 1965).

Mite species can form a hypopial stage, which does not feed and can be resistant to unfavourable conditions such as desiccation (Griffiths, 1964) and low temperatures. For instance, there is a report of their survival at temperatures of -18 °C (Sinha, 1964). Interestingly, humidity is the main factor in bringing about termination of the hypopial stage which increases as levels rise above 70 % (Stratil, Knulle, 1985).

Mite growth is affected by a combination of physical and biological factors which have been established under current climatic conditions. These factors interact in a complex manner (Sinha, Wallace, 1973) and knowledge of the factors important in regulating mite development and infestations can allow for the most appropriate control measures to be undertaken (Collins, 2012). However, global climate patterns have shown to change notably (IPCC, 2018) and grain storage itself can be heavily affected by climate change. The conclusion that seasonal variations would have an effect on mite population (Sinha, 1968) indicates that climate change would also have similar effects (Moses et al., 2015).

Because of these concerns there is a need in developing approaches aiming to understand the relative importance of current factors as a baseline in shaping mite communities. One tool to do this is species distribution modeling (SDM) which employs suitability indices. Suitability indices describe the relationship between habitat suitability score and a given environmental variable of a target species. Habitat suitability is a way to predict the suitability of habitat at a certain location for a given species or group of species based on their observed affinity for particular environmental conditions (Yi et al., 2016; Ma, Sun, 2018).

SDMs are empirical tools in ecology, biogeography, natural resource management, and ecosystem management (Franklin, 2009). Among various SDMs, Maxent is highly regarded because it computes the probability distribution of a species by using maximum entropy rules (the greatest uniform distribution) and statistical mechanics (Elith et al., 2006). The model has the advantage that it needs only environmental information and species occurrences data (Elith et al., 2011). MaxEnt is most important for modelling the suitability distribution of limited occurrence data and predictions may be modelled using a very few sample occurrences (Hernandez et al., 2008); sample sizes as low as $n = 10$ with Maxent performed well (Wisz et al., 2008; Kumar, Stohlgren, 2009).

In this study we make an attempt through building reasonable and correct (according to evaluation results) SDMs to highlight the important variables shaping the current bioclimatic niche of selected mite species.

It is common that SDMs employ climatic variables, however climatic variables derived from climate datasets at coarse scale may not appropriately account for anthropogenic influences on microclimate (Fедerman et al., 2013; Varner, Dearing, 2014), particularly in human-made structures, which may be buffered in terms of temperature and moisture from the outdoor environment. For instance, this may apply to an array of mites associated with grain storage facilities, barns, houses, even apiaries. Nevertheless, grain mites are more common in temperate regions with cool moist climates (Palyvos et al., 2008), showing the significance of the macroclimate. In terms of the macroclimate, climates which experience mild winters and high RH offer a particular challenge in protecting commodities from mite infestation. Even within the storage facility surface temperatures generally mimic the ambient conditions with moisture changes at the surface lagging about 4 h behind the ambient RH (Sinha, 1973; Burrell, 1979 as cited in Armitage, Cook, 1999). There are considerations that differences in the composition of house dust mite species and their abundances may be attributed to the geo-climatic conditions that prevail in a given area (Lang, Mulla, 1977; Mumcuoglu et al., 1999). Studies have shown that honeybee pests (for example, *Varroa destructor* Anderson et Trueman, 2000) can survive only in certain optimal bioclimatic conditions. For instance, the optimal temperature, humidity, precipitation, altitude

and biomass/net primary productivity ranges for different honeybee pests can vary significantly (Makori et al., 2017); the quoted authors concluded that honeybee pests could be modelled using coarse scale bioclimatic data which were most relevant in all model results. Nonetheless, we have to accept the notion that microclimates are supposed to modulate the responses to the macroclimate, but currently the extent of such modulation in a coarse scale modelling exercise is difficult to verify.

Material and methods

Study area

The area is geographically located between 49°26' to 52°1' N latitudes and 25°57' to 29°43' E longitudes, with an altitude ranging up to 319 m.

Using the Koppen-Geiger climate classification (McMahon, 2007), the type of climate in the study area is classified as “humid continental” and represents its “cool summer” version. It has little warming or precipitation effects from the northern Atlantic. The cool summer subtype is marked by mild summers, long cold winters and less precipitation than the hot summer subtype, however, short periods of extreme heat are not uncommon.

The historic average annual temperature in the study area is 7.17 °C and the average annual precipitation — 636 mm. Average monthly temperature and precipitation, as well as average monthly relative humidity, substantially vary across the year (fig. 1–3). July on average is the warmest month (18.7 °C), January — the coldest (−5.8 °C); July on average is the wettest month (92.2 mm), February and March are the driest (31.3 mm); on average in November relative humidity is the highest (75.7 %), in May it dips to 51.6 %. The average monthly temperature and precipitation are highly correlated ($r = 0.86$, p -value < 0.05), whereas the average monthly relative humidity is inversely correlated with both the average monthly temperature and precipitation ($r = -0.79$ and -0.61 , respectively, p -value < 0.05).

In terms of the Holdridge life zones system used to understand biome characteristics (Holdridge, 1947), the target area is recognized as “cool temperate wet forest”, containing pure or mixed stands of broad-leaved deciduous or needle-leaved evergreen tree (predominantly Scots pine, *Pinus silvestris* Linnaeus) growth forms, with a seasonal green understory of herbs.

According to the GLC2000 landcover classification (Bartholomé, Belward, 2005), most of the study area is considered to consist of “Cultivated and managed areas” (36 %) and in summary around 35 % of the area is under various types of tree cover and/or other natural vegetation.

The anthropogenic impact on the study area can be assessed by the Global Human Footprint Index (Wildlife Conservation Society, 2005), where a value of zero represents the least impacted part of the biome (“wildest”) and a value of 100 represents the most influenced (least “wild”) part of the biome. In our case this index consists of an average score of around 34, meaning the overall human pressure on the environment is fairly low.

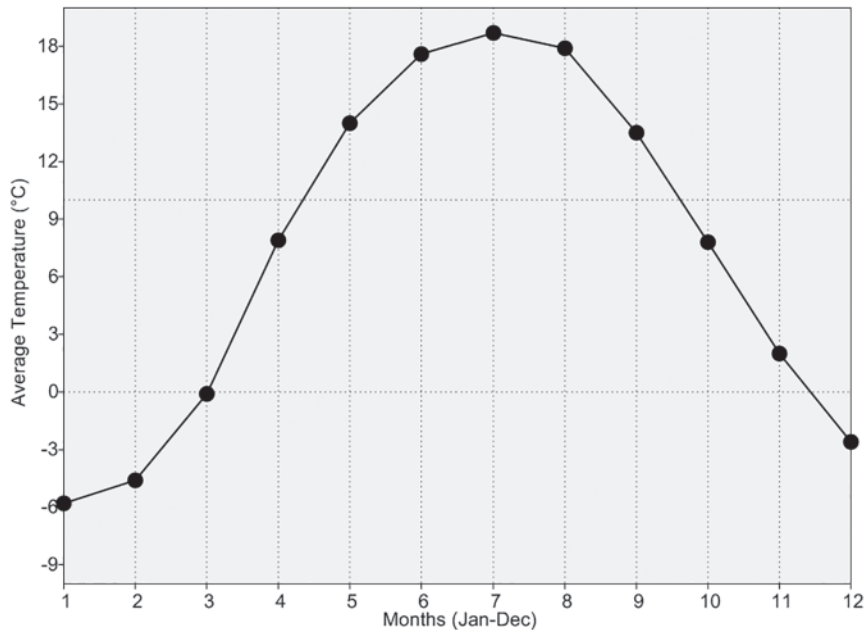


Fig.1. Average monthly temperature.

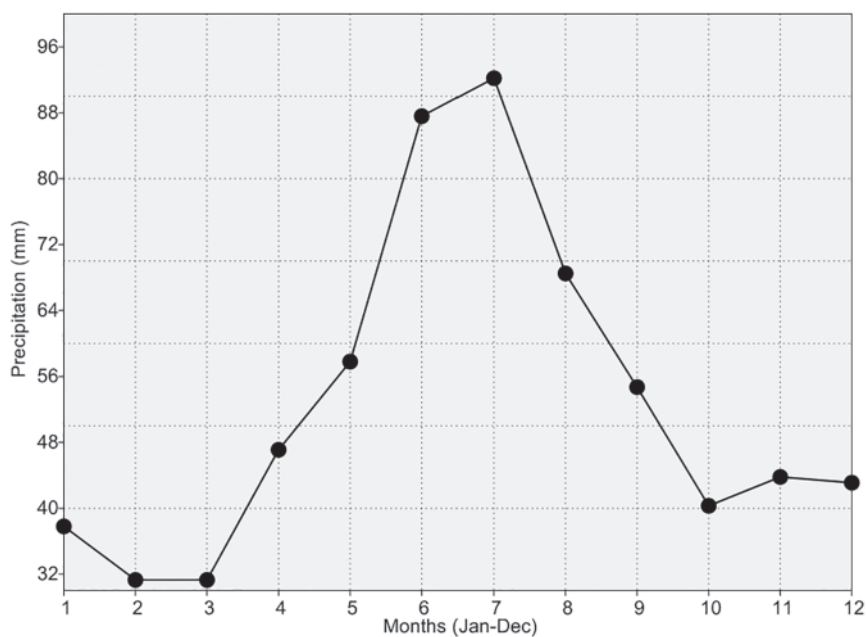


Fig. 2. Average monthly precipitation.

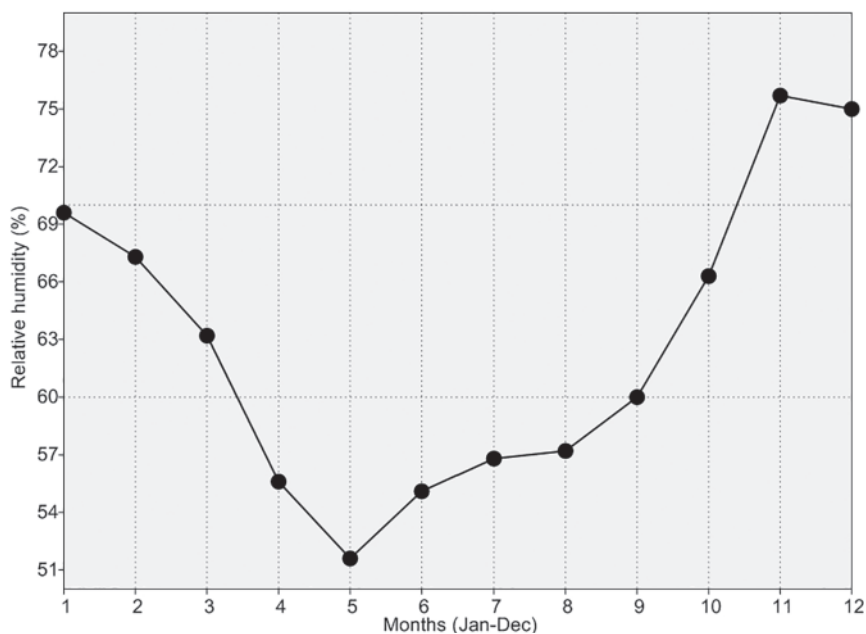


Fig. 3. Average monthly relative humidity.

Species occurrence data and climatic predictors

The study used presence-only species collection techniques for data collection. The presence-only data collection technique is favoured over the presence-absence data collection technique as the latter leads to pseudo-absence data of species occurrence (Gormley et al., 2011). The species occurrence data used in this study were obtained from the various field surveys 200 a total of 63 occurrence points of 30 acaridid species were identified and included in this study (table 1). For modelling purposes species with occurrences ≥ 10 were considered.

The species distribution points were plotted in a GIS environment using the SAGA GIS software (Conrad et al., 2015).

There are many variables (including hydrological-thermal) that are thought to be relevant to species' ecology and geographic distribution. In this study we used two sets of such variables. In the first place we used

Table 1. Occurrence of acaridid mites

Family	Species	Occurrence points	Feeding substrate							
			1	2	3	4	5	6		
Suidasidae	<i>Suidasia nesbitti</i> Hughes, 1948	1	+							
	<i>Acarus siro</i> Linnaeus, 1758	35	+	+	+	+	+	+		
	<i>A. farris</i> (Oudemans, 1905)	10	+	+		+				
	<i>A. tyrophagoides</i> (Zachvatkin, 1941)	5	+	+		+				
	<i>Mycetoglyphus fungivorus</i> Oudemans, 1932	1				+			+	
	<i>Tyrolichus casei</i> Oudemans, 1910	5	+	+						
	<i>Tyrophagus putrescentiae</i> (Schrank, 1781)	16	+	+		+	+			
	<i>T. molitor</i> Zachvatkin, 1941	12	+	+		+	+	+		
	<i>T. perniciosus</i> Zachvatkin, 1941	8	+	+				+	+	
	<i>T. humerosus</i> (Oudemans, 1923)	3	+			+				
Acaridae	<i>T. longior</i> (Gervais, 1844)	2	+					+		
	<i>T. formicetorum</i> Volgin, 1948	1	+							
	<i>T. mixtus</i> Volgin, 1948	1		+						
	<i>Schwiebea nova</i> (Oudemans, 1906)	1		+						
	<i>Neoacotyledon sokolovi</i> (Zachvatkin, 1940)	7	+						+	
	<i>Sancassania berlesei</i> (Michael, 1903)	6							+	
	<i>S. sphaerogaster</i> (Zachvatkin, 1937)	7							+	
	<i>S. rodionovi</i> (Zachvatkin, 1935)	3							+	
	<i>S. mycophagus</i> (Megnin, 1874)	1							+	
	<i>S. oudemansi</i> (Zachvatkin, 1937)	1							+	
	<i>Rhizoglyphus echinopus</i> (Fumouze et Robin, 1868)	3							+	
	Glycyphagidae	<i>Glycyphagus domesticus</i> (De Geer, 1778)	57	+	+	+	+	+	+	+
		<i>Lepidoglyphus destructor</i> (Schrank, 1781)	55	+	+	+	+	+	+	+
		<i>L. fustifer</i> (Oudemans, 1903)	8	+	+				+	
		<i>L. burchanensis</i> Oudemans, 1903	3		+		+			
<i>L. michaeli</i> Oudemans, 1903		3		+		+				
<i>L. pilosus</i> (Oudemans, 1906)		2		+						
Chortoglyphidae	<i>Gohieria fusca</i> (Oudemans, 1902)	3		+		+				
	<i>Chortoglyphus arcuatus</i> (Troupeau, 1879)	1		+						
Aeroglyphidae	<i>Aeroglyphus peregrinans</i> (Berlese, 1892)	5						+		

Note. 1 — oilseed crops; 2 — grain; 3 — fodder; 4 — hay and straw; 5 — litter, dead bees and ambrosia from beehive bottoms; 6 — spoiled vegetable crops (root and tuberous crops).

the widely accepted bioclimatic potential predictor variables for species distribution and suitability analysis (Hijmans et al., 2005). These bioclimatic predictors are ecologically more sensitive to differentiate the physiological tolerances of a habitat (Thompson et al., 2009) than simple temperature and precipitation predictors (Graham, Hijmans, 2006; Kumar et al., 2009). Information on the bioclimatic parameters was collected as raster layers from the WorldClim website (<http://www.worldclim.org/current>) with a spatial resolution of 30 arc seconds (this is about 1 km at the equator). The dataset was prepared by the interpolation of the historical records (1950–2000) of monthly precipitation and monthly temperature (Hijmans et al., 2005). These 19 bioclimatic variables indicate a general trend of precipitation and temperature, extremity and seasonality of temperature. Bioclimatic predictors were used to characterize the species' bioclimatic profile.

Secondly, we have used a recently reconsidered (in terms of biological significance) set of 16 climatic and two topographic variables (the ENVIREM dataset, downloaded from <http://envirem.github.io>), many of which are likely to have direct relevance to ecological or physiological processes determining species distributions (Title, Bemmels, 2018). Considering the relative evenness of the terrain in the study area, topographic variables were excluded from the analysis.

The most important sets of variables assessed in performance of models were identified using the Maxent Variable Selection package in R (developed by Jueterbock et al., 2016). The program first tests for Pearson correlation (set for $r < 0.8$), then through an iterative process tests different regularization values, correlation and contribution of variables (set for $> 5\%$) to determine the best possible set of variables by sample size corrected Akaike information criteria (Akaike, 1975) and AUC (see 2.3). In Maxent, the regularization parameter (β) prevents overfitting, that is,

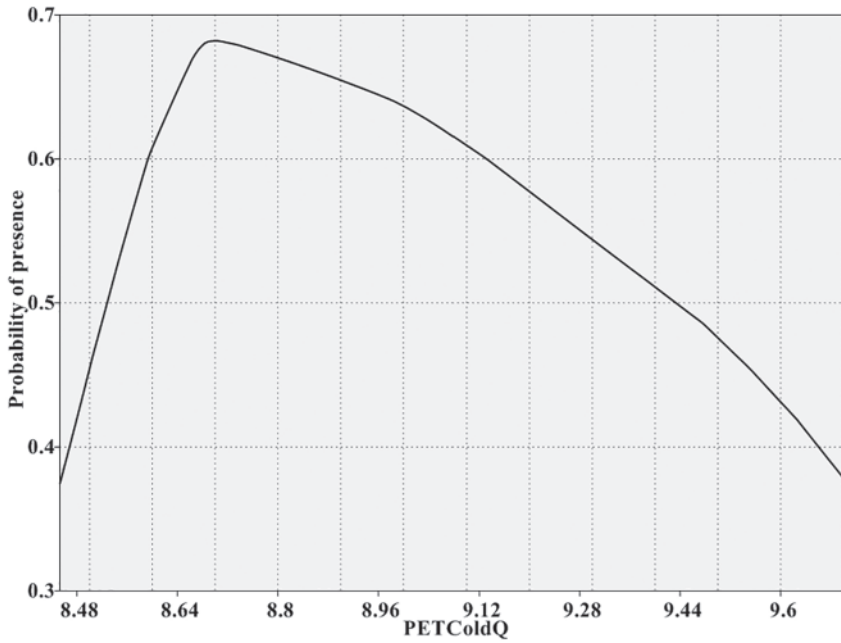


Fig. 4. Response of *A. siro* to PETcoldQ.

the model loses the ability of generalizing beyond the fitting data. The best possible sets of variables were selected for models which produced the highest AUC for the test dataset (Warren, Seifert, 2011).

Predictive niche modelling

The study used Maxent (Maximum Entropy, version 3.3.3k downloaded from <http://www.cs.princeton.edu>). Pseudo-absence points (used instead of true absences) were randomly generated within a convex hull encompassing 63 presence points. Within the settings window, a bootstrap replicate run (i. e., sampling with replacement) type was selected for 50 replicates with a random test percentage of 30 percent used. The option

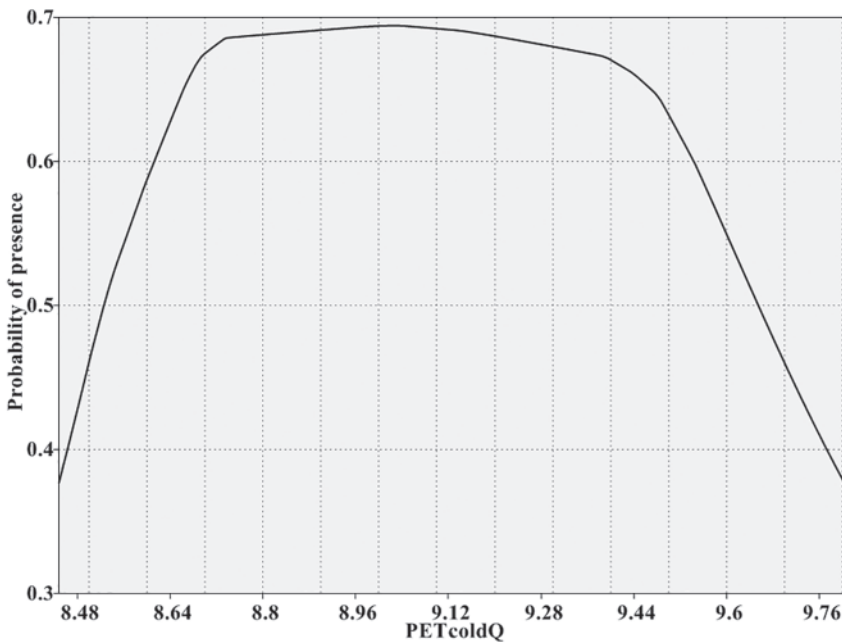


Fig. 5. Response of *L. destructor* to PETcoldQ.

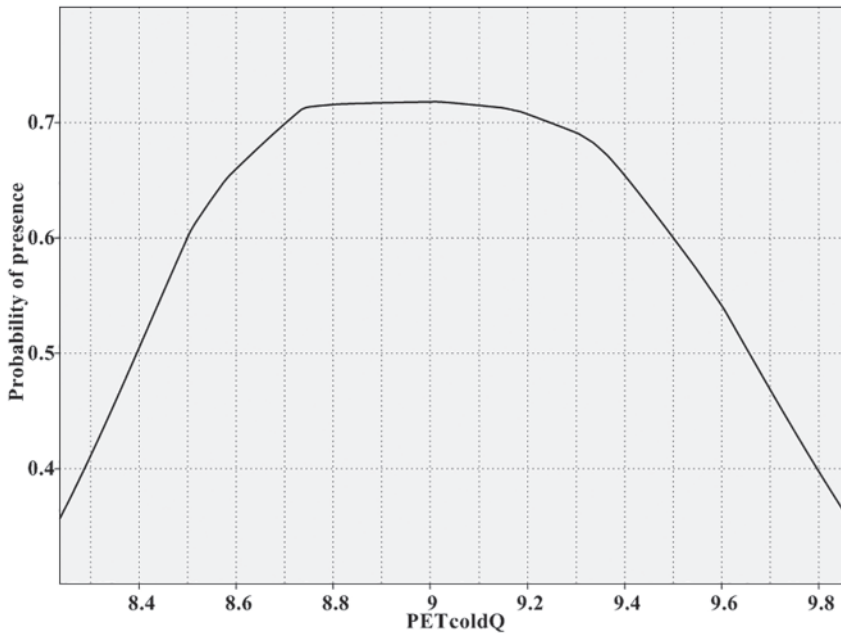


Fig. 6. Response of *Gl. domesticus* to PETcoldQ.

to use a random seed was chosen so that each replicate run would start with a random seed to ensure that a separate test/train dataset was used for each of the replicate models. An independent dataset was not available for model assessment and we did not want to partition the dataset into test and training data, and lose valuable training data. As an alternative, bootstrap replication splits the dataset multiple times, and in each case, predictive performance is assessed against the test dataset. This allows for all occurrence data to be used with a random partition performed with each Maxent replicate run.

Maxent provides output data in various formats. The logistic format (values range from 0 to 1) is recommended, because it allows for an easier and potentially more accurate interpretation of habitat suitability compared to the other approaches (Baldwin, 2009).

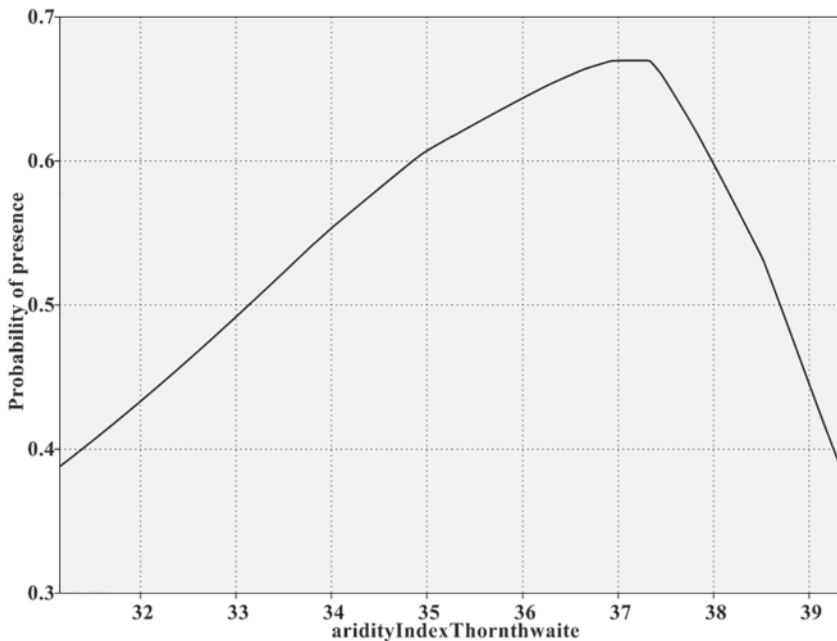


Fig. 7. Response of *A. siro* to aridityIndexThornthwaite.

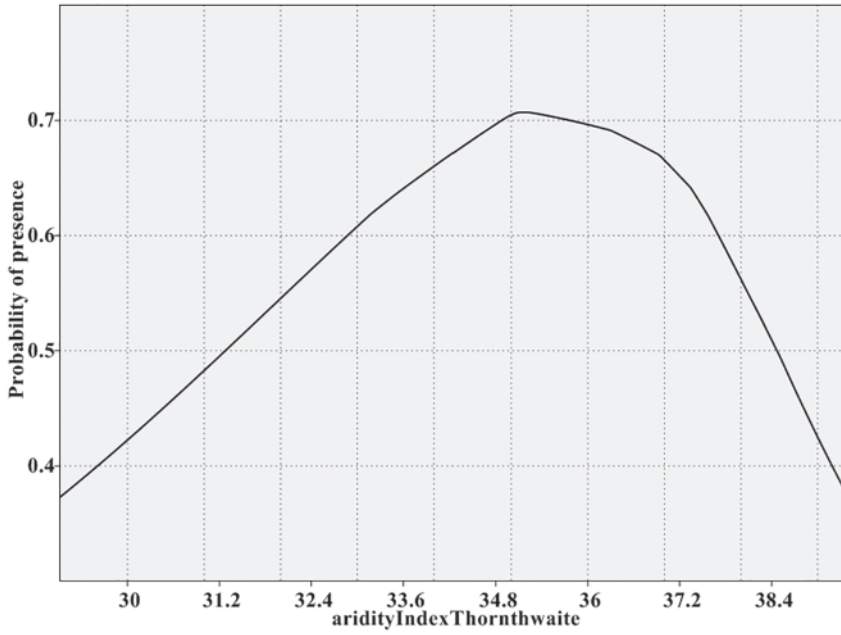


Fig. 8. Response of *L. destructor* to aridityIndexThornthwaite.

Maxent modeling can determine the importance of environmental variables. In one option the contribution for each variable can be determined by randomly permuting the values of that variable and measuring the resulting model performance. Better performance means that the model depends heavily on that variable (for explicitness values are normalized to give percentages). The second option uses a jackknife test and the regularized gain change during each iteration of the training algorithm. The environmental variable with the highest gain is considered to have the most useful information by itself, whereas the variable causing the largest decrease in the model's gain contains the most information not found in the other environmental variables. These options are used to determine the importance of the environmental variables and to observe whether or not the predictive distribution responded to each variable as expected.

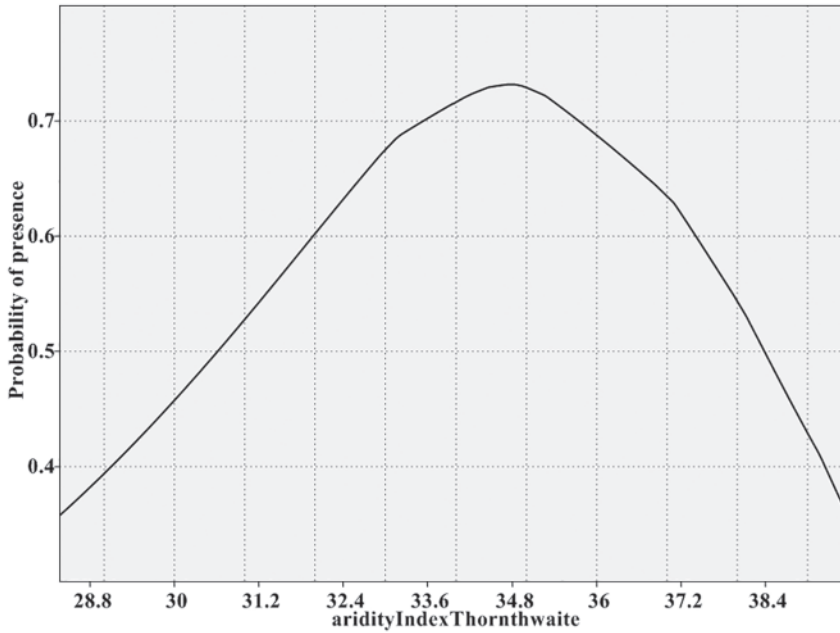


Fig. 9. Response of *Gl. domesticus* to aridityIndexThornthwaite.

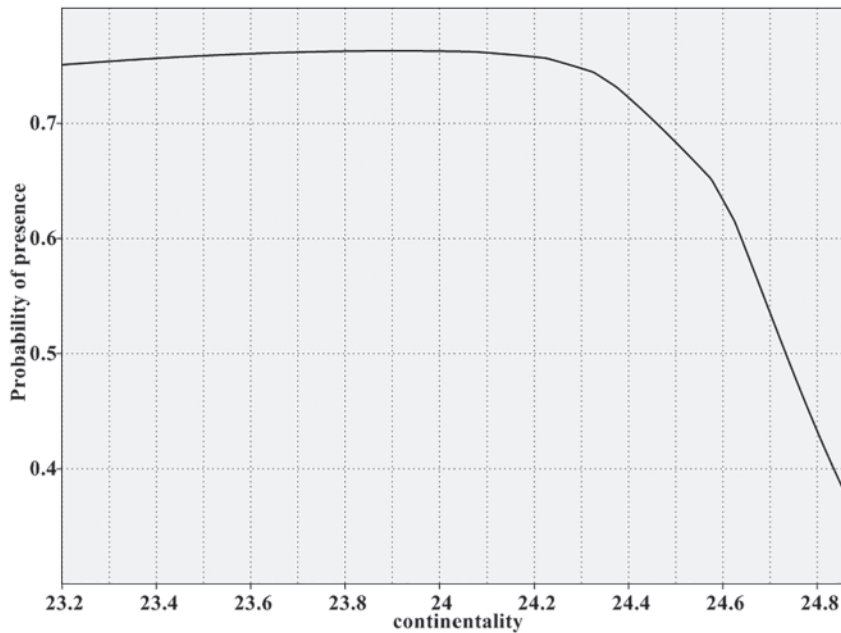


Fig. 10. Response of *L. destructor* to continentality.

Maxent also allows the construction of response curves to illustrate the effect of selected variables on habitat suitability (consequently, on the probability of occurrence and giving an idea of where for each variable, under the constraints and conditions of the modelling situation, the focal species has its optimum). These response curves consist of the specific environmental variable as the x-axis and, on the y-axis, the predicted probability of suitable conditions as defined by the logistic output. Upward trends for variables indicate a positive relationship; downward movements represent a negative relationship; and the magnitude of these movements indicates the strength of the relationship (Baldwin, 2009).

An important part of determining the ability of niche models to predict the distribution of a species is having a measure of fit. The performance of the Maxent model is usually evaluated by the threshold-independent receiver operating characteristic (ROC) approach (calculating the area under the ROC curve (AUC) as a measure of prediction success). The ROC curve is a graphical method that represents the relationship between the false-positive fraction (one minus the specificity) and the sensitivity for a range of thresholds. It has a range of 0–1, with a value greater than 0.5 indicating a better-than-random performance event (Fielding, Bell, 1997). A rough classification guide is the traditional academic point system (Swets, 1988): poor (0.5–0.6), fair (0.6–0.7), good (0.7–0.8), very good (0.8–0.9) and excellent (0.9–1.0). Secondly, the threshold-dependent binomial test of omission (Phillips et al., 2006) was employed. The omission test was calculated at a “minimum training presence” threshold. At this threshold, the fractional predicted area shows the fraction of all the pixels that were predicted suitable for the species. P-values of omission rates in optimal models are considered to be less than 0.05 (Anderson et al., 2003).

In addition, for comparative purposes, niche overlap was measured using the Schoener’s index of niche breadth (D) (Warren et al., 2008). Indices may range from 0 (indicating that niche models are completely different) to 1 (indicating that niche models are identical).

Results

Model validation and influencing bioclimatic variables

The most important sets of variables assessed in performance of models were identified separately for the bioclimatic parameters from the WorldClim database and the ENVIREM dataset (table 2).

Maxent produces two ROC curves based on either the initial (training) data and on the validation (test) data with associated AUC values. The indicators were obtained using 30 % of the training data as test localities for evaluating the performance statistics. The omission test was calculated at a Minimum training presence threshold value. At this threshold, the

Table 2. Results of Maxent variable selection

Bioclimatic parameters from the WorldClim database		
BIO 3: Isothermality		
BIO 6: Min Temperature of Coldest Month		
BIO 7: Temperature Annual Range		
BIO 14: Precipitation of Driest Month		
BIO 15: Precipitation Seasonality		
BIO 19: Precipitation of Coldest Quarter		
Species	β	Variables
<i>A. farris</i>	1	BIO 3, BIO 7, BIO 15, BIO 19
<i>A. siro</i>	1	BIO 3, BIO 7, BIO 15, BIO 19
<i>L. destructor</i>	1	BIO 3, BIO 6, BIO 15, BIO 19
<i>Gl. domesticus</i>	2	BIO 3, BIO 15, BIO 19
<i>T. molitor</i>	1	BIO 3, BIO 14, BIO 15
<i>T. putrescentiae</i>	1	BIO 3, BIO 14
Climatic variables from the ENVIREM dataset (abbreviations in parentheses) :		
Thornthwaite aridity index (aridityIndexThornthwaite),		
Climatic moisture index (climaticMoistureIndex),		
Continentality (continentality),		
Emberger's pluviothermic quotient (embergerQ),		
Minimum temperature of the warmest month (minTempWarmestMonth),		
Maximum temperature of the coldest month (maxTempColdestMonth),		
Monthly variability in potential evapotranspiration (PET)(PETseasonality),		
Mean monthly PET of coldest quarter (PETColdestQuarter)		
Species	β	Variables
<i>A. farris</i>	1	aridityIndexThornthwaite, climaticMoistureIndex, continentality, embergerQ, minTempWarmestMonth
<i>A. siro</i>	1	aridityIndexThornthwaite, continentality, PETColdestQuarter
<i>L. destructor</i>	1	aridityIndexThornthwaite, continentality, PETColdestQuarter, PETseasonality
<i>Gl. domesticus</i>	1	aridityIndexThornthwaite, continentality, PETColdestQuarter, PETseasonality, maxTempColdestMonth
<i>T. molitor</i>	2	aridityIndexThornthwaite, climaticMoistureIndex, continentality
<i>T. putrescentiae</i>	1	aridityIndexThornthwaite, embergerQ, PETColdestQuarter, PETseasonality

fractional predicted area shows the fraction of all the pixels that were predicted suitable for the species. Results of threshold-dependent omission test and threshold-independent ROC test are presented in table 3 and 3a (statistically significant p-values < 0.05 are marked with an asterisk*).

In terms of the threshold-dependent tests, models incorporating bioclimatic parameters from the WorldClim database performed poorly (in all cases p-values above 0.05), whereas models using climatic variables from the ENVIREM dataset showed better performance (p-values less than 0.05) regarding such species as *A. siro*, *L. destructor* and *Gl. domesticus*. The calculated ROC showed that the AUC values of training datasets and test data sets were on average higher in models using climatic variables from the ENVIREM dataset, particularly for the models considering the mentioned species. These AUC values appear to be centred around 0.8, meaning good (0.7–0.8) and/or very good (0.8–0.9) performance and indicating the ability of the models to recognize and order a certain point in the considered area as suitable or unsuitable. This result was obtained for both the training and the test data, with relatively small differences in AUC values (AUC_{diff}) suggesting a robust performance of the Maxent algorithm to capture the changes in certain environmental variables over point localities.

Table 4 gives estimates of the relative contributions of environmental variables from the ENVIREM dataset to the Maxent models for *A. siro*, *L. destructor* and *Gl. domesticus* based on permutation importance.

Based on the jackknifing analysis results, the highest gain in the *A. siro* model when used in isolation is PETcoldQ, which therefore appears to have the most useful information

Table 3. Results of threshold-dependent omission test and threshold-independent ROC test

Models using bioclimatic parameters from the WorldClim database						
Species	Threshold-dependent test		p-value	Threshold-independent test		
	Fractional predicted area	Test omission rate		Test AUC	Training AUC	AUC _{diff}
<i>A. farris</i>	0.5449	0.0900	0.361	0.6449	0.7249	0.0800
<i>A. siro</i>	0.8484	0.0820	0.350	0.5850	0.7009	0.1159
<i>L. destructor</i>	0.8859	0.0320	0.416	0.6369	0.6919	0.0550
<i>Gl. domesticus</i>	0.8933	0.0267	0.431	0.6499	0.6756	0.0257
<i>T. molitor</i>	0.6776	0.1000	0.387	0.6982	0.7570	0.0588
<i>T. putrescentiae</i>	0.7612	0.0300	0.397	0.6526	0.6869	0.0343

Table 3a. Results of threshold-dependent omission test and threshold-independent ROC test

Models using climatic variables from the ENVIREM dataset						
Species	Threshold-dependent test		p-value	Threshold-independent test		
	Fractional predicted area	Test omission rate		Test AUC	Training AUC	AUC _{diff}
<i>A. farris</i>	0.5627	0.1133	0.364	0.6206	0.6960	0.0754
<i>A. siro</i>	0.5852	0.0760	0.048*	0.7545	0.8256	0.0711
<i>L. destructor</i>	0.5788	0.0413	0.003*	0.7855	0.8304	0.0449
<i>Gl. domesticus</i>	0.5623	0.0450	0.004*	0.7950	0.8374	0.0424
<i>T. molitor</i>	0.8700	0.0600	0.423	0.5454	0.5831	0.0377
<i>T. putrescentiae</i>	0.6504	0.0700	0.330	0.6783	0.7292	0.0509

by itself. The environmental variable that decreases the gain the most when it is omitted is PETcoldQ, which therefore appears to have the most information that is not present in the other variables. For the *L. destructor* model the environmental variable with the highest gain when used in isolation is aridityIndexThornthwaite, which therefore appears to have the most useful information by itself, whereas the environmental variable that decreases the gain the most when it is omitted is PETcoldQ, which therefore appears to have the most information that is not present in the other variables. Finally, the environmental variable with the highest gain in the *Gl. domesticus* model when used in isolation is aridityIndexThornthwaite, which therefore appears to have the most useful information by itself, and the environmental variable that decreases the gain the most when it is omitted is PETcoldQ, which therefore appears to have the most information that is not present in the other variables.

In summary, based on the jackknifing analysis and permutation importance, the environmental variables that most strongly influenced the habitat suitability for the considered mite species are PETcoldQ and the aridityIndexThornthwaite. Their joint contribution amounted 88.4 %, 49.4 %, and 42.4 % in the models for *A. siro*, *L. destructor* and *Gl. domesticus*, respectively. In addition, continentality was an important variable affecting the bioclimatic niche of each of the analyzed species, particularly *L. destructor*.

Table 4. Contributions of environmental variables (expressed as %) to Maxent model performance

Variables	<i>A. siro</i>	<i>L. destructor</i>	<i>Gl. domesticus</i>
aridityIndexThornthwaite	41.1	21.1	16.0
continentality	11.6	24.6	14.0
maxTempColdestMonth	–	–	21.7
PETseasonality	–	26.1	21.9
PETColdestQuarter	47.3	28.3	26.4

This strong association is evident in the Maxent response curves. These curves allow to see how each environmental variable affects the Maxent prediction by showing how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value (figs 4–9). The 10 percentile training presence logistic threshold value, which provides a better ecologically significant result when compared with more restricted thresholds values (Phillips, Dudík, 2008), was used for the cut-off.

Discussion

According to the measures of fit applied to determine the ability of niche models to predict the distribution of the considered mite species, ENVIREM-based models, at least for *A. siro*, *L. destructor* and *Gl. domesticus*, outperformed models using bioclimatic variables from WorldClim (Hijmans et al., 2005). WorldClim variables are the most commonly employed set of environmental data layers used for this purpose, on account of their high resolution, global coverage, and availability, however the biological suitability of these bioclimatic variables and other such environmental datasets for niche modeling has been questioned. In the recently proposed ENVIREM dataset variables have been selected on the grounds that they are likely to have direct relevance to ecological or physiological processes determining distributions of many species (Title, Bemmels, 2018). They should therefore facilitate ecologically-informed variable selection, and may also result in improved model performance using statistical variable-thinning approaches. These variables have been largely derived from the same underlying dataset as the bioclimatic variables from WorldClim (e. g., both “continentality” and “Temperature annual range” are reflections of the range of temperatures between warm and cold season), but are intended to complement the existing WorldClim dataset (Hijmans et al. 2005) by introducing novel information not captured by this database. Through several case studies, P. O. Title and J. B. Bemmels (2018) had shown that the ENVIREM variables improved model performance and were valuable additions to the set of variables that are currently widely used in species distribution modeling. In our modeling exercise the ENVIREM variables too had substantially improved model performance by using novel information captured in the PETcoldQ and aridityIndexThornthwaite variables.

A variety of abiotic factors, such as temperature and precipitation, are consistently found to be primary determinants of species distributions at broad scales (Wiens, 2011), but prominent amongst the former is evapotranspiration (ET), often found to be one of the best climatic correlates shaping the ecological niche together with species distributions and richness (Currie, 1991; Fisher et al., 2011). This was supported in our research where PETcoldQ appeared to play a profound role. ET estimates provide an indication of ecologically important aspects of climate linked to energy and water supply and can be used as measures of ecological energy regimes. The rate of ET depends on the intensity of solar radiation, air temperature, humidity and wind speed, and is estimated indirectly from meteorological temperature (Clarke, 2017). Potential evapotranspiration (PET) is considered a measure of ambient energy and is often correlated with temperature variables (Hawkins et al., 2003). Despite this importance, a quantitative synthesis analyzing the contribution of over 400 distinct environmental variables to 2040 Maxent species’ distribution models PET is poorly represented: summer PET is accounted for in 34 articles, whereas winter PET only in three (Bradie, Leung, 2017). Strong hump-shaped relationships between the probability of presence and PETcoldQ were observed for all the three species of mites for which there were reliable SDMs. Probability of presence first increased, and then decreased with increasing PETcoldQ, suggesting that moisture could be a limiting factor since it is frozen when energy input is at the lowest during the coldest months of the year. On the other hand, increasing energy input at this time

of the year may cause the release of excessive moisture. This moisture in combination with winter coldness is likely to act synergistically and could create critical conditions. Therefore there is an apparent optimum of energy input for the cold season under which the considered species are able to survive.

The more complex climatic indices included in the ENVIREM variables (e. g., thermicity, aridity, moisture, Emberger's pluviothermic quotient, monthly variability in potential evapotranspiration) are considered to characterize environmental conditions that are more directly physiologically relevant to a given species than simple descriptors of climate such as temperature or precipitation alone (Title, Bemmels, 2018). One of these, the Thornthwaite aridity index, found to be influential in shaping the abiotic niche of the considered species, is an indication of moisture deficit and employs evapotranspiration and precipitation factors. In the same way, as for the PETcoldQ, strong hump-shaped relationships between the probability of presence and aridityIndexThornthwaite were observed for the mites species for which there were reliable SDMs, assuming an optimum between "too dry" and "too wet" conditions. Another variable from this cohort, the monthly variability in potential evapotranspiration (PETseasonality), has been found to be important in shaping the abiotic niche in two of the considered mite species: *L. destructor* and *Gl. domesticus*.

Other influential variables, namely, continentality (calculated as the average temperature of warmest month minus the average temperature of coldest month) and the maximum temperature of the coldest month (maxTempColdestMonth), are more straightforward in their interpretation: increasing continentality reduces the probability of presence (i. e., habitat suitability) (fig. 10, exemplified by *L. destructor*), whereas raising maxTempColdestMonth enhances the probability of presence in the model for *Gl. domesticus* (fig. 11).

In terms of the bioclimatic niche the considered mite species display substantial niche overlap. Niches of *L. destructor* and *Gl. domesticus* are almost identical (Schoener's $D = 0.929$), what could be assumed by the similarity of the response curves and the predictor variables they share in common. The niche of *A. siro* also considerably overlaps with the

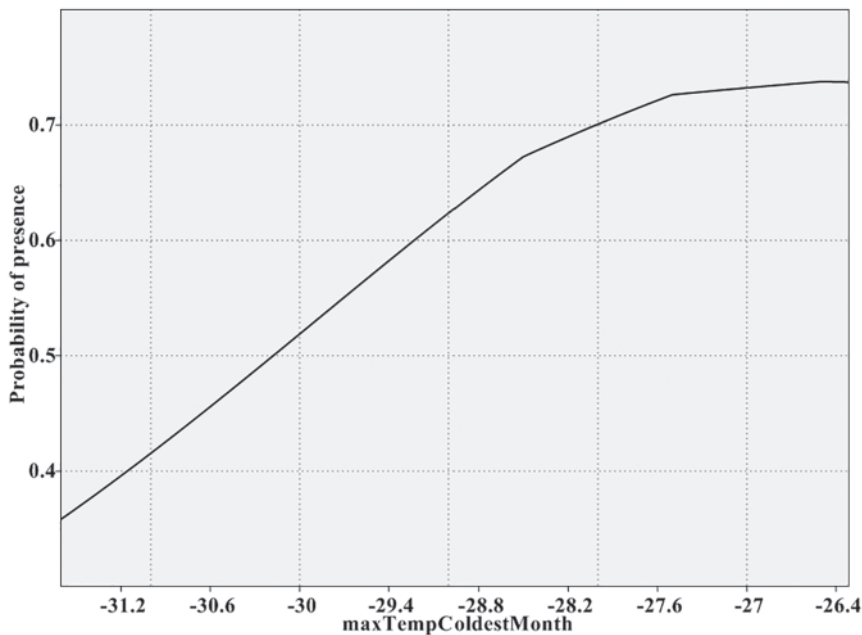


Fig. 11. Response of *Gl. domesticus* to maxTempColdestMonth.

niches of the two former species, but to a somewhat lesser extent (a 90 % overlap with the niche of *L. destructor* and an 87.5f % overlap with the niche of *Gl. domesticus*).

Based on our analysis, the bioclimatic variables that influence suitable areas for the mite species analyzed seem mostly to be represented by PET-based indices characterizing ambient energy, which are often correlated with temperature variables, moisture regimes, and strong fluctuations in temperature reflecting the severity of climate and/or extreme weather events. In terms of statistical significance, these relationships have been confirmed in models created for the species *A. siro*, *L. destructor* and *Gl. domesticus*, for which there has been sufficient point data. Matching relationships seem to exist for *A. farris*, *T. molitor* and *T. putrescentiae*, however the available data on these species are perhaps too scarce to make any robust conclusions.

In this study we focused on an attempt to highlight important variables shaping the current bioclimatic niche of a selected cohort of mite species infesting grain storages, realizing that mite persistence is affected by a combination of physical and biological factors which interact in a complex manner (Sinha, Wallace, 1973), including interactions regarding indoor and outdoor environments. Though microclimates are supposed to modulate the responses to the macroclimate, our coarse scale modeling exercise has shown the importance and significance of bioclimatic variables in shaping the niche of the considered mite species.

Traditionally, determining such driving factors would require laborious field measurements of the key environmental variables in natural populations. However, the recent development of remote sensing technologies and rapidly accumulating environmental data derived from geographic information systems (GIS) now provide information on the patterns of environmental variation at a variety of scales. In combination with species occurrence data, these tools permit detailed description of the environmental conditions at georeferenced natural population localities for one or more species (Nakazato et al., 2010).

Importantly, the use of SDMs has allowed to identify the environmental and climatic features that characterize the species' niche (their "bioclimate envelope"). On the other hand, the SDMs showed that the predictive performance of the models (calculated using AUC) never reached values, which could be attributed to the category "excellent" (AUC > 0.9). This occurs when ecological parameters are omitted from the modelling framework and lead to an inaccurate or insufficient description of the species' distribution and niche (Hanspach et al., 2010). In our case this could be expected as far as only bioclimatic parameters were used and it is reasonable to suggest that factors other than climate limit distributions and shape the niches of the considered mite species. Including other biologically relevant parameters and non-climate variables can contribute important information to SDMs, especially when modelers have specific knowledge about how these variables relate to the species (Bucklin et al., 2016).

In addition, broadly characterized as "cosmopolitan", the considered mite species can be hypothesized to be more generalist than ones with smaller home ranges. Because of this they are inherently difficult to model as their ecological requirements are less clear. This is in line with results from previous studies, which show that species with wider ranges are less well predicted (Segurado, Araújo, 2004).

Stored grain is a man-made ecosystem undergoing persistent interactions between several abiotic and biotic factors, and which more or less is affected by the surrounding bioclimatic environment. As noticed before, grain storage itself can be heavily affected by climate change (Moses et al., 2015), therefore safe food grain storages by themselves are considered as a measure to adapt to the changing global climates (UNEP, 2010). Global climate patterns have been shown to change notably and are predicted to continue to change in the future. Most of the several dozens of predictive models indicate that average temperature can increase by 1.7–5.3 °C, as a result of doubling CO₂ concentration within

next 60–100 years. 2.3 °C is a value most often mentioned what means an increase by 0.3 °C a decade (IPCC, 2007).

Predictions based on the emission scenario A1B (Kriticos et al., 2012) and targeting the year 2030 show that specific climate changes will affect our study area that are likely to have a profound effect on mite development with increases in numbers and growth rates. Winter months are expected to be wetter and warmer. Heightening temperatures during the coldest weeks will definitely favour the considered species. On the other hand, summers are predicted to be hotter and drier, and could lower the average monthly relative humidity (RH), which even today (fig. 3) seems to be critical for the warmest months. For practical reasons investigations are needed to see how future management targets will be met, based on the latest climate scenarios and projected climate changes.

Conclusions

The use of SDMs (specifically Maxent, based on the maximum entropy approach) has allowed to identify climatic features that characterize the species' niche (their "bioclimate envelope") of a cohort of mite species known to be associated with stored grains and other foods.

Using the ENVIREM dataset of bioclimatic variables, performance of the most robust models was mostly influenced by: 1) indices based on potential evapotranspiration, which characterize ambient energy and are mostly correlated with temperature variables, moisture regimes, and 2) strong fluctuations in temperature reflecting the severity of climate and/or extreme weather events.

Most likely because only bioclimatic parameters were employed the performance of the SDMs (evaluated by the AUC) was < 0.9, reasonably suggesting that factors other than climate limit distributions and shape the niches of the considered mite species. Including other biologically relevant parameters and non-climate variables could contribute to the better performance of the corresponding SDMs and give new insights into the bioecology of the species.

Although the considered mite species occupy man-made ecosystems, they remain more or less affected by the surrounding bioclimatic environment and therefore could be subjected to contemporary climate change. In this respect investigations are needed to see how this will affect future management targets.

Conflicts of Interest

The authors declare no conflict of interest.

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