UNIVERSITY OF OPOLE

Institute of Biology

SUMMARY OF DOCTORAL DISSERTATION

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HABITAT EVALUATION OF EUROPEAN TERRITORIES FOR INVASIVE TRUE BUG SPECIES (HEMIPTERA: HETEROPTERA), WITH PARTICULAR CONSIDERATION OF POLAND

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Opole 2023

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1. Introduction

The General Directorate for Environmental Protection in Poland defines invasive alien species (IAS) as species of plants, animals, pathogens and other organisms, occurring outside their native habitats, which may have a negative impact on the environment, economy or human health [1]. The protection of biodiversity from the undesirable impact of invasive species within the European Union is regulated by legislation, including *Regulation (EU) No 1143/2014 of The European Parliament and of The Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species*. The body that directly deals with the determination of the degree of invasiveness of alien species in Poland (on the basis of the Act of 11 August 2021 on alien species (Dz.U. 2021 poz. 1718)) s the General Directorate for Environmental Protection, which, within the framework of the project Development of principles for control and eradication of invasive alien species together with pilot activities and public education, analyses the pathways of IAS spread, develops a methodology for their eradication or control, and carries out activities of an informational and educational nature [2]. Invasive alien species not only have a negative impact on biodiversity, but also on the economy. It has been estimated that the economic losses caused by IAS activity in the USA, UK, Australia, South Africa, India and Brazil are in total $314 billion per year (Pimentel et al., 2001), in Germany between 1960 and 2020 it was almost $9 billion (Haubrock et al., 2021a), and in Italy between 1990 and 2020 it was over $800 million (Haubrock et al., 2021b). Nevertheless, it is often the economic sectors that are, more or less directly, responsible for the introduction of non-native species and, as a result, their invasion of new areas. An example of an unintentional introduction is the bug *Nysius huttoni* White, 1878 (Hemiptera: Lygaeidae), which first appeared in Europe probably with apples transported from New Zealand to the Belgian port of Antwerp (Aukema et al., 2005b; Tiwari & Wratten, 2019). Alien species introduced intentionally, on the other hand, are usually plants, especially ornamental ones. Along with them, the pests living on them also enter the new areas, as will be discussed later. Just as important as the environmental or economic impact of alien species is the identification of their pathways of spread. This makes it possible not only to trace the history of invasions, but above all to develop effective strategies to eradicate or control these species. Humans have the greatest impact on the spread of species – trade and transport are the most common direct cause of active and accidental introductions of IAS'. The ongoing era of globalisation is responsible not only for the reduction of trade barriers, but also for the increase in tourism on an unprecedented scale, which also contributes to the introduction of non-native species to foreign lands (Hulme, 2009; Katsanevakis et al., 2013; Padayachee et al., 2017). Invasive species monitoring is therefore essential to take appropriate steps to minimise the risk of an IAS spreading into a specific area.

Data on the occurrence of alien species can be used not only for monitoring them or analysing their dispersal history, but also in ecological niche modeling (ENM). The ENM process uses computer algorithms that, based on the realized niche of a species, predict its fundamental niche; in practice, areas with environmental conditions that allow individuals of a species not only to survive, but also to reproduce, are determined. This makes it possible to determine the potential range of a species, which is why in the literature we may also encounter another name for this type of analysis, described as species distribution modeling (SDM). However, this term can be misleading, as it actually predicts the range of areas with favourable habitat conditions for the species, rather than specifically the range of the species (Pearson, 2007). ENM algorithms are constantly being developed and the methodology for their use adapted to different types of research. They are used not only in modeling the ecological niche of a species, predicting its historical and future range, but also in estimating the impact of climate change on agriculture, species conservation planning within conservation biology, or in various types of forecasting, such as predicting areas with increased risk of snakebite or risk of forest fire (Sillero et al., 2021). However, ENM methods are not without their disadvantages - without proper data preparation, predictor selection, model calibration and output interpretation, the modeling result may not be reliable (Zhu and Qiao, 2016). It is also important to bear in mind that environmental variables do not determine every dimension of a species' niche. Besides, the observed individuals may have only just appeared in the area, which does not at all mean that the conditions there are suitable for its development (Pearson, 2007). The software used in this study was Maxent 3.4.1 (Phillips et al., 2020), which is one of the most widely used software in ecological niche modeling (Elith et al., 2011; Khan et al., 2022; Philips et al., 2017). The foundation of its algorithm is a machine-learning technique based on the principle of maximum entropy - based on a search for a distribution characterised by maximum entropy and given the limits of the environmental variables of the species' known sites, Maxent estimates which areas have climatic conditions in which the species will survive and reproduce (Pearson, 2007; Philips et al., 2006; Philips et al., 2017). Field studies testing the validity of the predictions obtained by Maxent have shown that it is a very good tool for determining a species' realized niche and produces statistically significant results on its potential distribution (Rebelo & Jones, 2010; Smith et al., 2021; West et al., 2016).

True bugs (Hemiptera: Heteroptera) are the largest and most diverse group of hemimetabolous insects, inhabiting a variety of habitats, including aquatic ones (Schuh & Slater, 1995; Schuh & Weirauch, 2020). They are economically important insects. Species feeding on plants, including crops, can lead to, among other things, tissue damage at the feeding site, drooping or deformation of immature fruit, necrosis, production of germless seeds, or disruption of vegetative growth, resulting in losses of billions of dollars (Schaefer & Panizzi, 2000). Cimicidae, which are hematophages, cause multimillion-dollar damage to the poultry industry, the hospitality industry, and private and communal households (Reinhardt & Siva-Jothy, 2007). Some species of Triatominae (Heteroptera: Reduviidae) are vectors of the parasite *Trypanosoma cruzi* Chagas, 1909 (Trypanosomatida: Trypanosomatidae), causing Chagas disease in humans. An estimated 20 million people struggle with it and 90 million are exposed to the disease every year (Schaefer & Panizzi, 2000). Predatory Heteroptera, on the other hand, are used to control pests of crop plants, thus reducing the amount of pesticides used

(Perdikis et al., 2011; Schaefer & Panizzi, 2000). In 2008, the first paper comprehensively describing invasive species of Heteroptera in Europe was published (Rabitsch, 2008), subsequently supplemented by new data (Rabitsch, 2010). The author distinguishes between the following categories among non-native Heteroptera species: species alien to Europe, species alien within Europe (native to some European countries and invasive to others), cryptogenic species (uncertainty as to whether a species is alien or native) and species introduced from continental Europe to its islands. A total of 48 invasive species were considered, representing approximately 1.7% of all species of true bugs found in Europe (Rabitsch, 2010). The main reason for their appearance in Europe is accidental introduction with ornamental plants imported from their native range, as well as entrapment by means of transport (Putchkov, 2013; Rabitsch, 2010). There are not many studies in the literature on true bugs using ecological niche modeling (e.g. Bugaj-Nawrocka et al., 2020; Chłond et al., 2019; Lis B. et al, 2022; Murienne et al., 2009; Sandoval-Ruiz et al., 2012; Sundar et al., 2021), especially as regards European sites (Bugaj-Nawrocka et al., 2021; Chłond & Bugaj-Nawrocka, 2015; Minghetti et al., 2020). These papers mainly concern *Halyomorpha halys* (Stål, 1855) (Pentatomomorpha: Pentatomidae) and Leptoglossus occidentalis Heidemann, 1910 (Pentatomomorpha: Coreidae), less frequently other species (Dellape et al., 2017; Kistner, 2017; Malek et al., 2018; Montemayor et al., 2015; Olivera et al., 2021; Pinto et al., 2014; Streito et al., 2021; Tytar & Kozynenko, 2020; Zhu et al., 2014; Zielinska & Lis B., 2020; Zielinska & Lis J.A., 2020).

The aim of the present study was to model the ecological niche of invasive Heteroptera species and, on the basis of the results obtained, to determine the degree of habitat suitability of each of them in Europe (including countries with only part of their territory on the European continent), with particular consideration of Poland. This will allow to estimate which areas are most at risk if IAS' were to appear in them, which may ultimately assist the relevant institutions and specialists in monitoring and eradicating invasive Heteroptera species.

2. Material and methods

2.1. Occurrence data

In the present study, the location data for 40 species of true bugs (Table 1) were used, which were obtained from scientific publications, own observations and those of the thesis supervisor (data not yet published), as well as from internet databases (i.a.: GBIF Global Biodiversity Information Facility [5], NBN Atlas [6], Observation.org [7], Waarneming.nl [8], Mapa Bioróżnorodności BioMap [9], EPPO Global Database [10], Gatunki obce w Polsce (IOP PAN) [3], Pluskwiaki różnoskrzydłe (Hemiptera: Heteroptera) Polski [11], Insektarium [12], British Bugs [13]). Geographical coordinates were converted to decimal format in the WGS84 reference system. If no geographical coordinates were given in the source material, the location information (e.g. town, street) was georeferenced in Google Earth 9.186.0.0 [14]. Overly general site information (e.g. identification of a species within a province without specifying a particular locality) and sites from databases that were not confirmed by experts were not taken into consideration. Detailed information on the sites used in the study is given in Chapter 6. In total, data were obtained for 174,704 sites of 40 invasive true bug species.

Some of the sites are in the same location or in close proximity to each other (this usually applies to urban parks, landscape parks, nature reserves or experimental fields and ponds, where observations are most often carried out). Using all such data in ecological niche modeling can lead to a significant overestimation of the result (Boria et al., 2014; Hijmans, 2012; Veloz, 2009). Accordingly, sites (separately for each species) were submitted to spatial autocorrelation reduction using the SDMtoolbox 2.4 tool (Brown et al., 2017; the algorithm randomly selects one site within a 10 km^2 square for a world base map [15] with a spatial resolution of 2.5 arcminutes) in ArcGIS 10.8.2 (ESRI, 2022). The results are summarised in Table 1. Despite this procedure, there may still be a situation where there are significantly more sites in a certain area of the world than in others and this is not due to the range of the species, but to easier access during field observations (e.g. large cities or areas close to access roads). In order to avoid such aggregation of sites, a bias file layer was created for each species using the SDMtoolbox 2.4 tool in ArcGIS, which was then used during the niche modeling - a grid with increased weighting of points having fewer neighbours was generated based on the pre-filtered locations and the Gaussian kernel density estimator (Brown et al., 2017; Elith et al., 2010; Fourcade et al., 2014).

Table 1. Species of invasive true bugs (Hemiptera: Heteroptera) in Europe for which ecological niche modeling (ENM) was performed in this study. The table shows the number of used sites (literature sites, unpublished observations, information from databases; see Chapter 6 for details) and the number of sites after spatial autocorrelation reduction.

Infraorder	Family	Species	Total number of sites	Number of sites after autocorrelation reduction
Cimicomorpha	Anthocoridae	*Amphiareus obscuriceps*	209	123
		Anthocoris butleri	181	101
		Anthocoris sarothamni	417	117
		Buchananiella continua	462	104
	Lyctocoridae	*Lyctocoris campestris*	681	223
	Miridae	*Closterotomus trivialis*	2 661	213
		Deraeocoris flavilinea	5 148	872

Infraorder	Family	Species	Total number of sites	Number of sites after autocorrelation reduction
Cimicomorpha	Miridae	*Dichrooscytus gustavi*	327	110
		Dicyphus escalerae	120	61
		Macrolophus glaucescens	40	28
		Nesidiocoris tenuis	109	81
		Orthotylus adenocarpi	284	136
		Orthotylus caprai	103	35
		Orthotylus concolor	270	153
		Orthotylus virescens	938	352
		Taylorilygus apicalis	2 997	1 004
		Tupiocoris rhododendri	299	106
		Tuponia brevirostris	91	53
		Tuponia elegans	24	18
		Tuponia hippophaes	170	110
		Tuponia mixticolor	125	42
	Reduviidae	*Empicoris rubromaculatus*	742	166
	Tingidae	*Corythucha arcuata*	1 563	555
		Corythucha ciliata	3 773	1 011
		Dictyonota fuliginosa	449	131
		Elasmotropis testacea	104	58
		Stephanitis oberti	1 024	297
		Stephanitis pyrioides	179	125
		Stephanitis rhododendri	444	36
		Stephanitis takeyai	1 254	303
Leptopodomorpha	Saldidae	*Pentacora sphacelata*	278	30
Nepomorpha	Corixidae	*Trichocorixa verticalis*	1 538	139
Pentatomomorpha	Coreidae	*Leptoglossus occidentalis*	69 874	8 496

Infraorder	Family	Species	Total number of sites	Number of sites after autocorrelation reduction
Pentatomomorpha	Lygaeidae	*Arocatus longiceps*	2 416	316
		Nysius huttoni	1 256	260
		Orsillus depressus	1 379	319
	Oxycarenidae	*Oxycarenus lavaterae*	6 746	1 210
	Pentatomidae	*Halyomorpha halys*	38 425	6 233
		Nezara viridula	26 790	4 693
		Perillus bioculatus	814	511
	total:	40 species	174 704	28 931

2.2. Environmental variables

Environmental data are essential in the ecological niche modeling process. Based on the conditions present in known locations of the species, it is estimated where areas of high habitat suitability for the species occur (Pearson, 2007). In this study, continuous and categorical variables with a spatial resolution of 2.5 arcminutes were used (Table 2). Bioclimatic variables based on monthly temperature and precipitation values indicate climate extremes, their seasonal distribution, or annual trends. These data were prepared by the WorldClim team on the basis of climate data from 1970 to 2020 (Fick & Hijmans, 2017). Variables relating to the monthly distribution of minimum, average and maximum air temperature, precipitation, solar radiation (Fick & Hijmans, 2017), elevation [16], climate zones (following the Köppen-Geiger climate classification; Cui et al., 2021) and soil types [17] were also used in the research.

Variables related to elevation, climate zone and soil type were used in the ENM process for each of the species studied (except for the aquatic bug *Trichocorixa verticalis* (Fieber, 1851) (Nepomorpha: Corixidae), for which soil types were not considered). For the remaining predictors, their correlation was checked first, as the use of highly correlated variables can lead to collinearity and overestimation of the modeling result (Warren et al., 2014). To do this, variables were first normalized in ArcGIS software so that predictors with different units of measurement could be compared with each other. Then, using the programming language R ver. 4.2.2 (R Core Team, 2022), the values of the variables were extracted for each of the species' sites and the 10 000 background points. Then, a model (based on the Maxent software algorithm) was first generated using all variables in the MaxentVariableSelection R package (Jueterbock et al., 2016), then those with an effect of less than 5% on the distribution of the species and those with a Pearson correlation coefficient greater than 0.8 were rejected. For the remaining variables, a new model was created and predictors with the previously mentioned parameters were again excluded. The process was repeated until variables with a Pearson correlation coefficient of less than 0.8 and an effect on the distribution of the species of greater than 5% remained. Two coefficients were calculated during each step of the analysis: the Akaike's information criterion (AICc) and the area under the ROC curve (AUC). Finally, variables with the highest AUC (which enhances the model's ability to distinguish where the species is present and where it is not) and the lowest AICc (which enhances the model's ability to identify the fundamental niche of the species) were selected for ecological niche modeling. However, AICc values were treated as more relevant, as relying only on AUC values during variable selection may result in a higher risk of over-fitting the ENM score ([18]; Jueterbock et al., 2016). Predictors that may have been biologically relevant to the distribution of the species, even if discarded in the variable selection process, were also considered in the ENM.

Table 2. Environmental variables used in ecological niche modeling.

Variable symbol	Variable description	Unit	Type of variable (*C* – continuous, *K* – categorical)
BIO1	Annual Mean Temperature	°C	C
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	°C	C
BIO3	Isothermality ((BIO2/BIO7)×100)	dimensionless	C
BIO4	Temperature Seasonality (standard deviation × 100)	°C	C
BIO5	Maximum Temperature of Warmest Month	°C	C
BIO6	Minimum Temperature of Coldest Month	°C	C
BIO7	Temperature Annual Range (BIO5 - BIO6)	°C	C
BIO8	Mean Temperature of Wettest Quarter	°C	C
BIO9	Mean Temperature of Driest Quarter	°C	C
BIO10	Mean Temperature of Warmest Quarter	°C	C
BIO11	Mean Temperature of Coldest Quarter	°C	C
BIO12	Annual Precipitation	mm	C
BIO13	Precipitation of Wettest Month	mm	C
BIO14	Precipitation of Driest Month	mm	C

Variable symbol	Variable description	Unit	Type of variable (*C* – continuous, *K* – categorical)
BIO15	Precipitation Seasonality (Coefficient of Variation)	fraction	C
BIO16	Precipitation of Wettest Quarter	mm	C
BIO17	Precipitation of Driest Quarter	mm	C
BIO18	Precipitation of Warmest Quarter	mm	C
BIO19	Precipitation of Coldest Quarter	mm	C
TMIN01 - TMIN12	Minimum Temperature of Each Month Throughout the Year	°C	C
TAVG01 - TAVG12	Average Temperature of Each Month Throughout the Year	°C	C
TMAX01 - TMAX12	Maximum Temperature of Each Month Throughout the Year	°C	C
PREC01 - PREC12	Precipitation of Each Month Throughout the Year	mm	C
SRAD01 - SRAD12	Solar Radiation of Each Month Throughout the Year	$(kJ/m^2)/day$	C
ELEV	Elevation	metres above sea level [m a.s.l.]	C
CLIMATE	Climate Zones	N/A	K
SOIL	Soil Types	N/A	K

2.3. Model calibration

The aforementioned Maxent software was used to modeling the ecological niche in this study. Leaving the default options in when running the calculations can result in over-fitting the model. It is therefore important to calibrate the model by selecting the appropriate parameters so that it is neither oversimplified nor over-complex - this way it retains the ability to predict independent data (Anderson & Gonzalez Jr, 2011). Maxent offers a selection of features (feature type) that, based on environmental variables, constrain the calculated distribution of habitat suitability levels during modeling. These are: a linear function (L), which forces the selection of predicted sites with identical values of continuous environmental variables to those found in the area of observed sites; a quadratic function (Q) works on the same principle as the linear one, only instead of the specific values of the variables, it takes into account their variance; the product function (P) considers areas where the covariance for each pair of continuous environmental variables is the same as for the input data; the threshold function (T), based on a step function, assigns a value of 0 for parameters below the variable threshold and a value of 1 for parameters above the threshold; the hinge function (H) has the same assumptions as the threshold function, but is based on a linear function. If left at the default settings, Maxent uses the following feature configurations (based on the number of sites of the species): L – 2 to 9 sites, L+Q – 10 to 14 sites, L+Q+H – 15 to 79 sites, L+Q+P+T+H – more than 80 sites (Low et al., 2021; Merow et al., 2013; Phillips & Dudik, 2008; Phillips et al., 2006). Another feature of the software that has an important impact on calibration is the regularization multiplier. It allows the level of regularization of the model to be altered, which is responsible for reducing the level of complexity of the model and avoiding over-fitting (Anderson & Gonzalez Jr, 2011; Phillips et al., 2006; Radosavljevic & Anderson, 2014).

In order to select the optimal settings for the Maxent algorithm, a test modeling of the ecological niche was performed for 20% of randomly selected species, using all possible function configurations for different values of the regularization multiplier (from 0.5 to 5.0, with increments of 0.5). Based on the results obtained (model illustration, AUC values, standard deviation), it was decided to run analyses specific to the following function sets: H+Q+P, L+Q+H+P and L+Q+P, using a regularization multiplier ranging from 0.5 to 2.0 (with increments of 0.5).

2.4. Ecological niche modeling

Ecological niche modeling was performed for each of the 40 invasive true bug species listed in Table 1. The detailed settings selected in Maxent software are described in Table 3.

Table 3. Detailed Maxent software settings selected during ecological niche modeling.

Setting	Description
Samples	list of species sites after reduction of spatial autocorrelation
Environmental layers	selected environment variables
Features	feature types
Create response curves	the generation by the software of graphs showing the dependence of the habitat suitability level on each of the selected environmental variables
Make pictures of prediction	the generation by the software and saving in .png format of images illustrating the result of modeling

Setting	Description
Do jackknife to measure variable importance	checking the relevance of the environmental variable to the modeling result by performing a jackknife test (performing the analysis excluding the selected variable and then the analysis using only the selected variable)
Output format: Cloglog	selected cloglog transformation of the output file
Output file type: asc	selected .asc format for georeferenced output map
Random seed	for each iteration during the bootstrap test, the algorithm used a different, random set of input data
Random test percentage: 20	20% of the sites randomly selected by the algorithm were used as test points and to perform statistical tests (Čengić et al., 2020)
Regularization multiplier	level of regularization multiplier
Max number of background points	number of background points: 10,000 (< 2,500 sites after autocorrelation reduction); 25,000 (2,500 - 5,000 sites); 50,000 (5,000 - 7,500 sites); 75,000 (> 7,500 sites)
Replicated run type: bootstrap	the selected bootstrap method for estimating the distribution of estimation errors (repetition using the random sampling with replacement method)
Replicates: 10	number of bootstrap test repeats
Add samples to background	adding to the background point sites for which the combination of environmental variables was not present
Write plot data	data generated by the software, allowing graphs to be created in external software
Write output grids: unchecked	the generation of a map with georeferenced data (average of all bootstrap repeats)
Write plots	attachment of graphs to the .html file with a summary of the modeling
Append summary results to maxentResults.csv file	saving the parameters and statistical test results for each bootstrap repeat and averaged results
Apply threshold rule: maximum test sensitivity plus specificity	the type of threshold method used when plotting the ROC curve to evaluate the model: maximum sensitivity and specificity of the test (Liu et al., 2005; Liu et al., 2016)
Bias file	the use of a bias file layer during modeling

2.5. Model selection

The final model, whose results for each species are presented in Chapter 3, was selected based on the following parameters: the image of the modeling results, the ROC curve (Receiver Operating Characteristic), the AUC_{train} value (the area under the ROC curve) for the data used during modeling (training points), the AUC_{diff} value (the difference between AUC_{train} and AUC_{test} (calculated for test points)) and the OR_{10} value (the fraction of test points with Maxent suitability results lower than the 10% of training points with the lowest predicted suitability levels). The higher the AUC_{train} value, the better the model is (increasing the model's ability to distinguish where the species is present and where it is not; according to Araujo et al. (2005), models with an AUC between 0.8 and 0.9 are described as good, and models with an AUC > 0.9 as very good), a lower AUC_{diff} (higher values indicate over-fitting of the model) and a lower OR_{10} (higher values indicate limited ability of the model to identify suitable habitats in the study area; Low et al., 2021).

3. Habitat evaluation of european territories for invasive true bug species

3.1. Infraorder Cimicomorpha

3.1.1. Family Anthocoridae

Amphiareus obscuriceps (Poppius, 1909)

Origin	Eastern Palearctic (Rabitsch, 2008)
First record in Europe outside its native range	Bulgaria, 1987 (Rabitsch, 2008)
First record in Poland	Świętokrzyskie Mountains, 2010 (Korcz, 2010; Lis B., 2017)
Number of sites in Poland (as at 03.10.2022)	16 (List no. 1 (Chapter 6); Fig. 41)
The most informative environmental variables	average temperature in February between -5 and +5 °C, minimum temperature in December between -20 and +20 °C

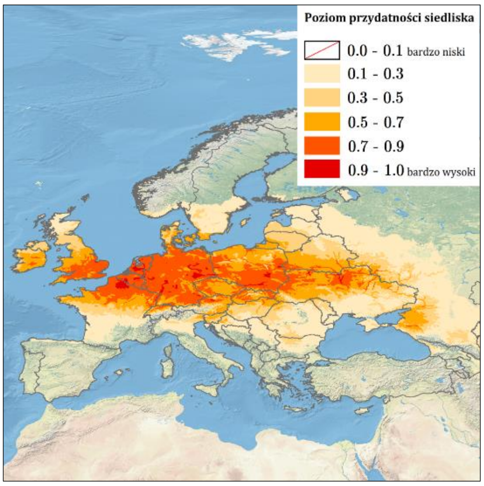


Figure 1. Level of habitat suitability of *Amphiareus obscuriceps* in Europe.

Anthocoris butleri Le Quesne, 1954

Origin	south-west Europe (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	minimum temperature in January between -5 to +6.5 °C, oceanic climate (*Cfb*)

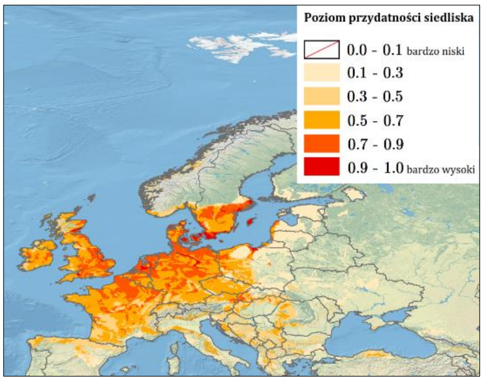


Figure 2. Level of habitat suitability of *Anthocoris butleri* in Europe.

Anthocoris sarothamni Douglas & Scott, 1865

Origin	south-west Europe (Rabitsch, 2008)
First record in Poland	Gdańsk, before 1954 (Bugaj-Nawrocka, 2017)
Number of sites in Poland (as at 04.10.2022)	4 (List no. 3 (Chapter 6); Fig. 42)
The most informative environmental variables	minimum temperature in January above -1 °C, climate types: warm-summer mediterranean climate (*Csb*) and oceanic (*Cfb*)

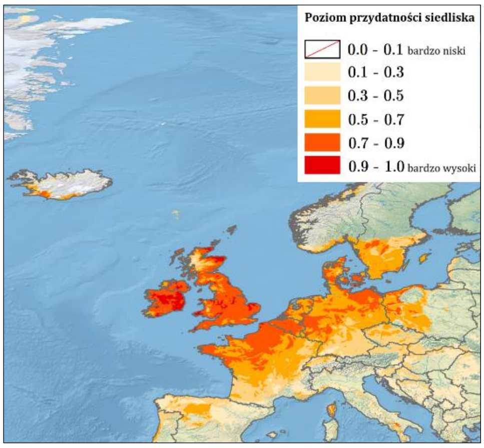


Figure 3. Level of habitat suitability of *Anthocoris sarothamni* in Europe.

Buchananiella continua (White, 1880)

Origin	pantropical (Aukema, 2007)
First record in Europe outside its native range	United Kingdom, 1995 (Aukema, 2007)
First record in Poland	none
The most informative environmental variables	climate types: cold semi-arid climate (*BSk*), warm-summer mediterranean climate (*Csb*), oceanic (*Cfb*)

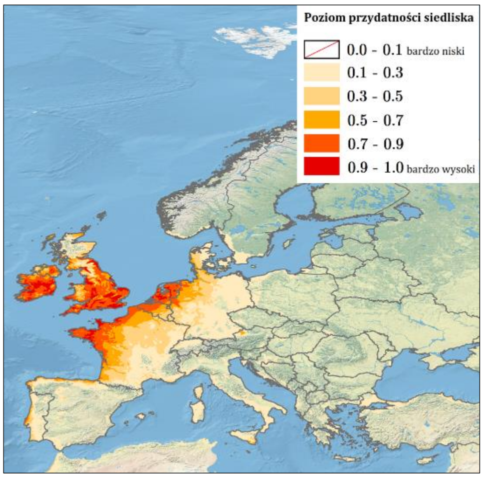


Figure 4. Level of habitat suitability of *Buchananiella continua* in Europe.

3.1.2. Family Lyctocoridae

Lyctocoris campestris (Fabricius, 1794)

Origin	Mediterranean (Fisher et al., 1999; Rabitsch, 2008)
First record in Poland	XIX c. (Nowicki, 1868)
Number of sites in Poland (as at 04.10.2022)	34 (List no. 5 (Chapter 6); Fig. 43)
The most informative environmental variables	average annual temperature from +6.5 to +18.5 °C, climate types: hot desert climate (*BWh*), hot summer mediterranean climate (*Csa*), humid subtropical climate (*Cfa*), oceanic (*Cfb*), subpolar oceanic (*Cfc*), hot summer continental climate (*Dfa*), hemiboreal climate (*Dfb*), typical subarctic climate (*Dfc*), soil types characteristic for the Mediterranean areas native to *L. campestris*

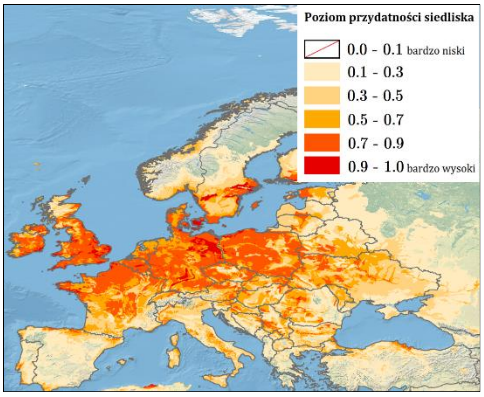


Figure 5. Level of habitat suitability of *Lyctocoris campestris* in Europe.

3.1.3. Family Miridae

Closterotomus trivialis (A. Costa, 1853)

Origin	Mediterranean (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	average temperature in February between -7.5 and +7.5 °C, minimum temperature in January over +1.5 °C, climate types: hot semi-arid climate (*BSh*), hot summer mediterranean climate (typ *Csa*), oceanic (*Cfb*), high altitudes in Mediterranean continental climate zones (*Dsa*)

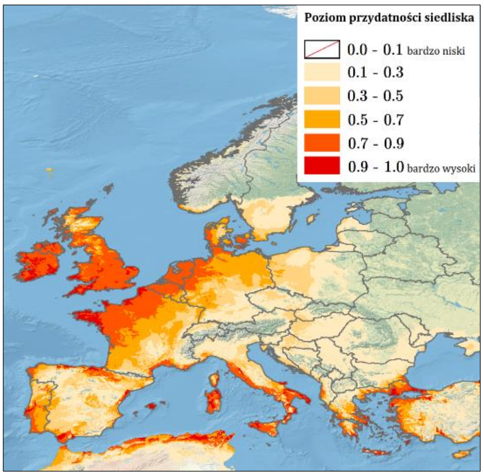


Figure 6. Level of habitat suitability of *Closterotomus trivialis* in Europe.

Deraeocoris flavilinea (A. Costa, 1862)

Origin	Mediterranean (Rabitsch, 2008)
First record in Poland	Gdynia, 2013 (Gierlasiński, 2015)
Number of sites in Poland (as at 21.02.2023)	34 (List no. 7 (Chapter 6); Fig. 44)
The most informative environmental variables	minimum temperature in January above -3 °C, climate types: hot summer mediterranean climate (*Csa*) and oceanic (*Cfb*)

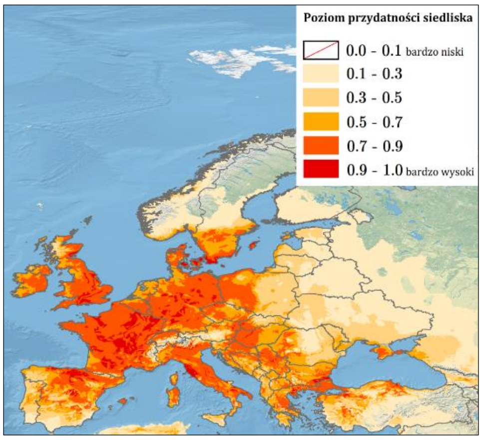


Figure 7. Level of habitat suitability of *Deraeocoris flavilinea* in Europe.

Dichrooscytus gustavi Josifov, 1981

First documented record in Poland	Warszawa, 2015 (Gierlasiński et al., 2019b)
Number of sites in Poland (as at 21.02.2023)	10 (List no. 8 (Chapter 6); Fig. 45)
The most informative environmental variables	minimum temperature in January between -4.5 and +11.5 °C, climate types: warm summer mediterranean climate (*Csb*), oceanic (*Cfb*), hemiboreal climate (*Dfb*)

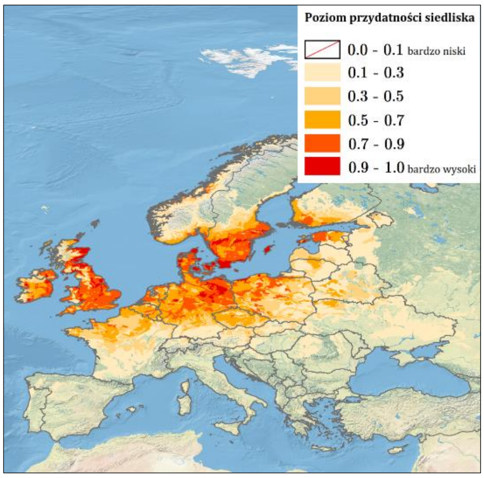


Figure 8. Level of habitat suitability of *Dichrooscytus gustavi* in Europe.

Dicyphus escalerae Lindberg, 1934

Origin	Mediterranean (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	climate types: hot summer mediterranean climate (*Csa*), warm summer mediterranean climate (*Csb*), oceanic (*Cfb*), soil types: dystric cambisols and rendzina soils

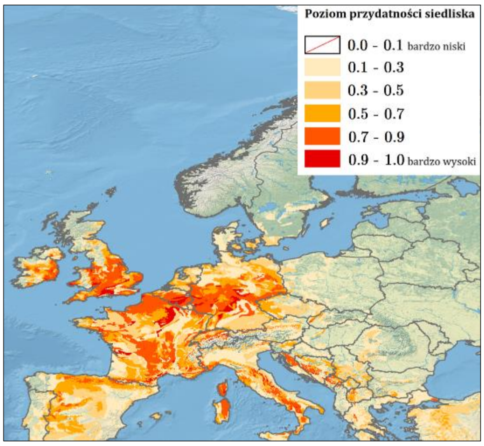


Figure 9. Level of habitat suitability of *Dicyphus escalerae* in Europe.

Macrolophus glaucescens Fieber, 1858

Origin	Mediterranean (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	minimum temperature in January between -10 and +9 °C, climate types: hot summer mediterranean climate (*Csa*) and oceanic (*Cfb*), soil types: dystric cambisols, rendzina soils, haplic chernozems, chromic luvisols, calcaric phaeozems

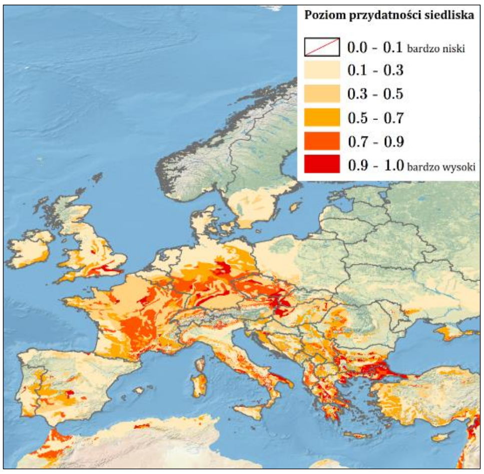


Figure 10. Level of habitat suitability of *Macrolophus glaucescens* in Europe.

Nesidiocoris tenuis (Reuter, 1895)

Origin	tropical (Rabitsch, 2008)
First record in Poland	the only site recorded in south-western Poland in 2020 (Raut & Borowiak-Sobkowiak, 2023; no specific information on the site location)
The most informative environmental variables	solar radiation in December above 6 200 (kJ/m^2)/day, climate types: hot summer mediterranean climate (*Csa*), subtropical highland climates with monsoon influence (*Cwb*)

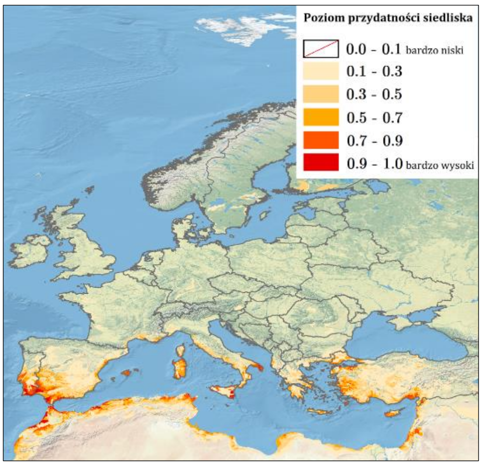


Figure 11. Level of habitat suitability of *Nesidiocoris tenuis* in Europe.

Orthotylus adenocarpi (Perris, 1857)

Origin	western european (Rabitsch, 2008)
First documented record in Poland	Baltic coast, 1960s (Senn & Gierlasiński, 2023)
Number of sites in Poland (as at 02.02.2023)	5 (List no. 12 (Chapter 6); Fig. 46)
The most informative environmental variables	minimum temperature in January between -5 and +6 °C, oceanic climate (*Cfb*)

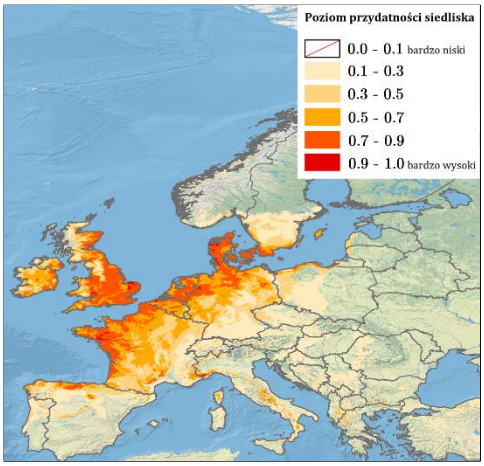


Figure 12. Level of habitat suitability of *Orthotylus adenocarpi* in Europe.

Orthotylus caprai Wagner, 1955

Origin	in Europe, a species native to areas south of the Alps (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	minimum temperature in January between -2 and +14 °C, climate types: humid subtropical climate (*Cfa*) and oceanic (*Cfb*)

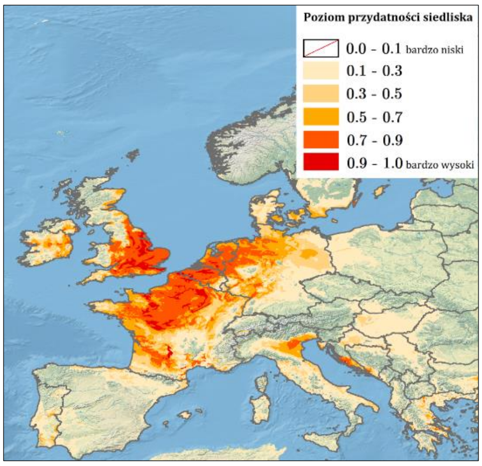


Figure 13. Level of habitat suitability of *Orthotylus caprai* in Europe.

Orthotylus concolor (Kirschbaum, 1856)

Origin	western european (Rabitsch, 2008)
First record in Poland	Nowy Targ Basin, 1960s (Gierlasiński et al., 2021b)
Number of sites in Poland (as at 22.02.2023)	13 (List no. 14 (Chapter 6); Fig. 47)
The most informative environmental variables	minimum temperature in January above -26 °C, average temperature in February between -12 and +12 °C, climate types: cold semi-arid (*Bsk*) and oceanic (*Cfb*)

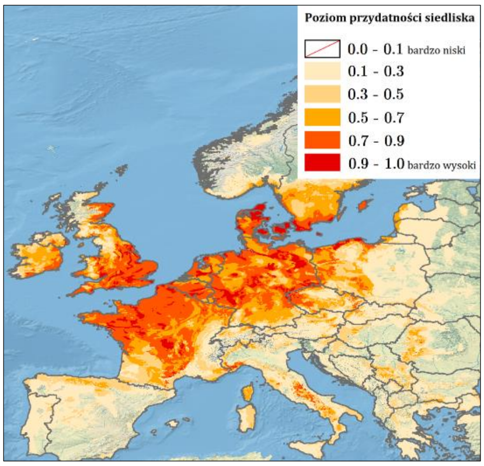


Figure 14. Level of habitat suitability of *Orthotylus concolor* in Europe.

Orthotylus virescens (Douglas & Scott, 1865)

Origin	western european (Rabitsch, 2008)
First record in Poland	Pomeranian Lakeland and Silesia, 1930s (Gorczyca & Chłond, 2005)
Number of sites in Poland (as at 22.02.2023)	15 (List no. 15 (Chapter 6); Fig. 48)
The most informative environmental variables	minimum temperature in January between -7 and +5 °C, climate types: hot summer mediterranean climate (*Csa*) and oceanic (*Cfb*)

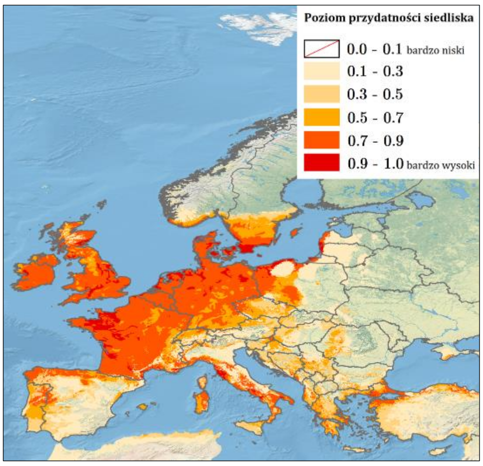


Figure 15. Level of habitat suitability of *Orthotylus virescens* in Europe.

Taylorilygus apicalis (Fieber, 1861)

Origin	pantropical (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	maximum temperature in November between +18 and +26 °C, humid continental climate with dry winters and monsoonal type summer rainfall (*Dwa*)

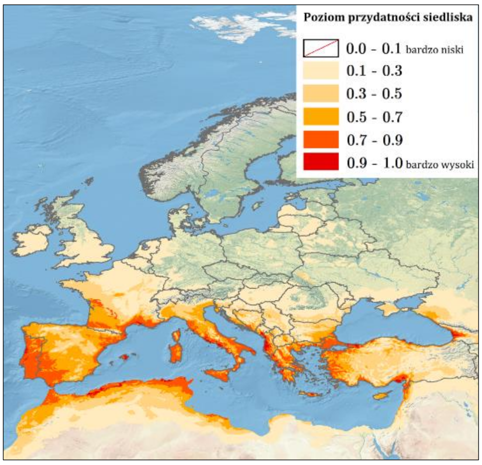


Figure 16. Level of habitat suitability of *Taylorilygus apicalis* in Europe.

Tupiocoris rhododendri (Dolling, 1972)

Origin	the east coast of North America (Rabitsch, 2008)
First record in Europe outside its native range	United Kingdom, 1971 (Rabitsch, 2008)
The single record in Poland (as at 22.02.2023)	Goczałkowice Zdrój in Upper Silesia, 2020 (Rutkowski & Gierlasiński, 2021; Fig. 49)
The most informative environmental variables	oceanic climate (*Cfb*)

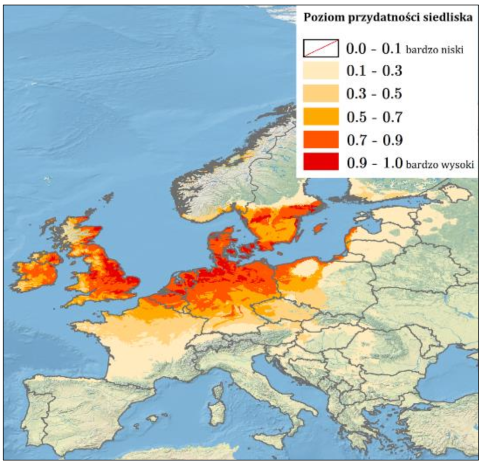


Figure 17. Level of habitat suitability of *Tupiocoris rhododendri* in Europe.

Tuponia brevirostris Reuter, 1883

Origin	Mediterranean (Rabitsch, 2008)
First record in Europe outside its native range	United Kingdom, 1979 (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	climate types: hot summer mediterranean climate (*Csa*) and oceanic (*Cfb*)

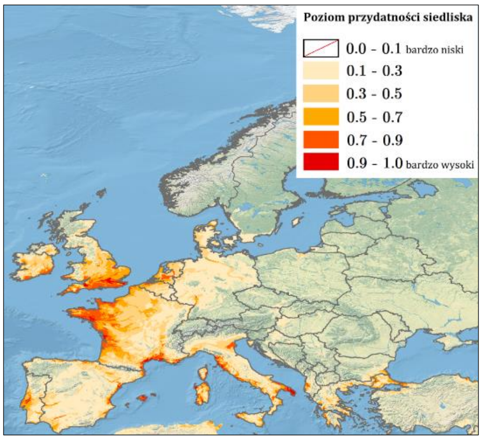


Figure 18. Level of habitat suitability of *Tuponia brevirostris* in Europe.

Tuponia elegans (Jakovlev, 1867)

Origin	central asian (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	soil types: calcaric fluvisols, calcic chernozems, calcaric phaeozems

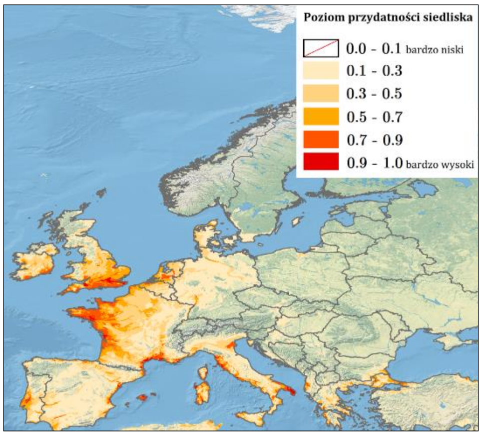
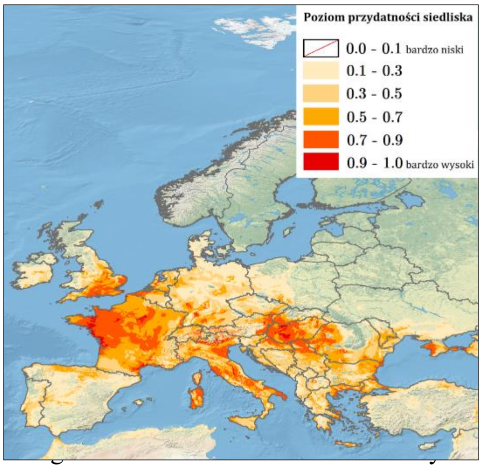


Figure 19. Level of habitat suitability of *Tuponia elegans* in Europe.

Tuponia hippophaes (Fieber, 1861)

Origin	Mediterranean (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	maximum temperature in February above +3 °C, climate types: hot summer mediterranean climate (*Csa*), humid subtropical climate (*Cfa*), oceanic (*Cfb*), tundra climate (*ET*)



Tuponia hippophaes in Europe.

Tuponia mixticolor (A. Costa, 1862)

Origin	Mediterranean (Gravestein, 1978)
First record in Poland	none
The most informative environmental variables	minimum temperature in January above -1 °C, altitude above sea level less than 200 m, climate types: hot desert climate (*BWh*), hot summer mediterranean climate (*Csa*), oceanic (*Cfb*)

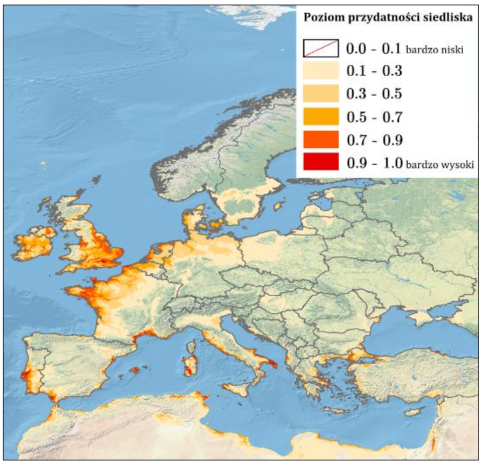


Figure 21. Level of habitat suitability of *Tuponia mixticolor* in Europe.

3.1.4. Family Reduviidae

Empicoris rubromaculatus (Blackburn, 1889)

Origin	pantropical (Putshkov et al., 1999)
First record in Poland	none
The most informative environmental variables	climate types: tropical monsoon (*Am*), hot desert climate (*BWh*), hot semi-arid climate (*Bsh*), cold semi-arid climate (*Bsk*), hot summer mediterranean climate (*Csa*), warm summer mediterranean climate (*Csb*), humid subtropical climate (*Cwa*), subtropical highland climate with monsoon influence (*Cwb*), oceanic (*Cfb*)

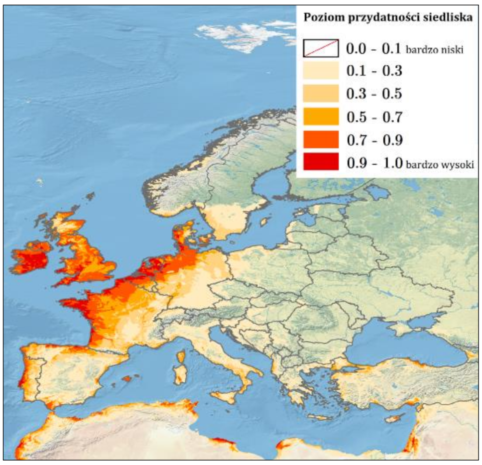


Figure 22. Level of habitat suitability of *Empicoris rubromaculatus* in Europe.

3.1.5. Family Tingidae

Corythucha arcuata (Say, 1832)

Origin	nearctic (Zielińska & Lis B., 2020)
First record in Europe outside its native range	Italy, 2000 (Zielińska & Lis B., 2020)
The single record in Poland (as at 03.06.2023)	Bieszczady Mountains, 2021 (Gierlasiński & Orzechowski, 2023; Fig. 50)
The most informative environmental variables	minimum temperature in January above -11 °C and in March between -3 and +5.5 °C, solar radiation in December between 3 000 and 6 200 (kJ/m^2)/day

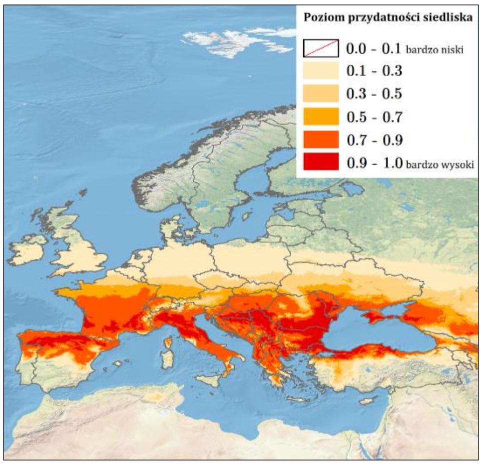


Figure 23. Level of habitat suitability of *Corythucha arcuata* in Europe.

Corythucha ciliata (Say, 1832)

Origin	nearctic (Rabitsch, 2008)
First record in Europe outside its native range	Italy, 1964 (Rabitsch, 2008)
First record in Poland	Wrocław, 2009 (Lis B., 2009)
Number of sites in Poland (as at 24.02.2023)	35 (List no. 24 (Chapter 6); Fig. 51)
The most informative environmental variables	average temperature of the coldest quarter between -4 and +13 °C, average temperature in February between -2.5 and +22.5 °C, and maximum temperature between -11 and +16 °C, climate types: hot semi-arid climate (*Bsh*), hot summer mediterranean climate (*Csa*), warm summer mediterranean climate (*Csb*), humid continental climate with dry winters and monsoonal type summer rainfall (*Dwa*), oceanic (*Cfb*)

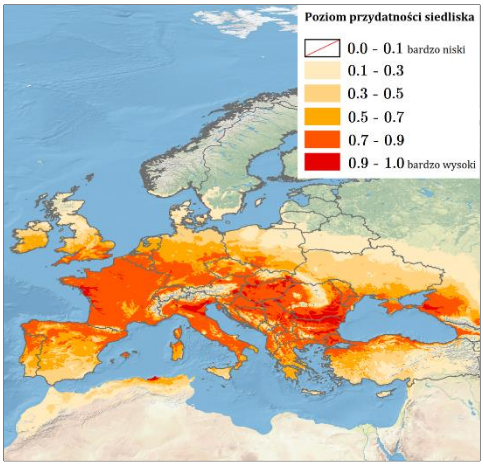


Figure 24. Level of habitat suitability of *Corythucha ciliata* in Europe.

Dictyonota fuliginosa A. Costa, 1853

Origin	Mediterranean (Gierlasiński, 2018)
Records in Poland (as at 25.02.2023)	reported in general from Silesia in the early 20th c. (Gierlasiński, 2018), the only documented site, from 1953, was reported by Heiss et al. (2022; Pustelnik, Łódź Voivodeship ([22], [23], [24]); Fig. 52)
The most informative environmental variables	minimum temperature in January between -12 and +12 °C, oceanic climate (*Cfb*)

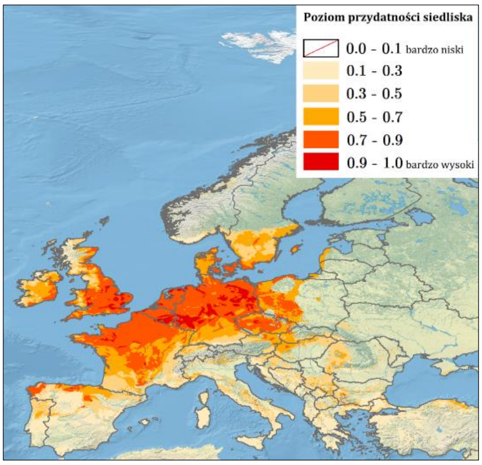


Figure 25. Level of habitat suitability of *Dictyonota fuliginosa* in Europe.

Elasmotropis testacea (Herrich-Schäffer, 1830)

Origin	alien species in countries where the *Echinops* spp. on which it feeds are also considered non-native (Pyšek et al., 2012; Rabitsch, 2008)
Records in Poland	recorded very rarely (4 sites in former Prussia and Roztocze [11]; Lis B., 1999; Strawiński, 1966)
The most informative environmental variables	minimum temperature in January between -8 and +6 °C, climate types: hot summer mediterranean climate (*Csa*), oceanic (*Cfb*), very high altitudes in Mediterranean continental climate zones (*Dsb*)

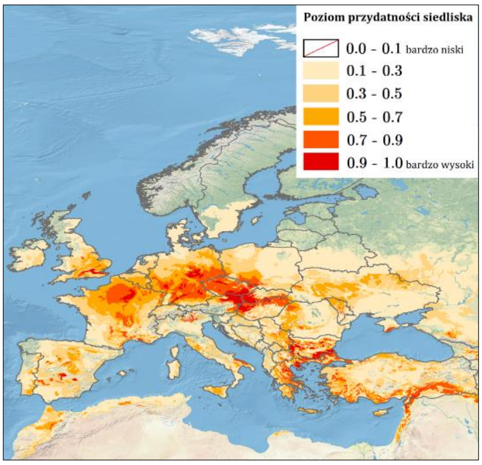


Figure 26. Level of habitat suitability of *Elasmotropis testacea* in Europe.

Stephanitis oberti (Kolenati, 1857)

Origin	Northern Palearctic (Rabitsch, 2008)
First records in Poland	earliest recorded from former Prussia, Silesia and the Baltic coast (Lis B., 1999; [12])
Number of sites in Poland (as at 26.02.2023)	7 (List no. 27 (Chapter 6); Fig. 53)
The most informative environmental variables	precipitation in the driest month between 25 and 60 mm, minimum temperature in January between -10 and +5 °C, soil types matching the soil requirements of the Ericaceae on which they feed (Nestby et al., 2019; Péricart, 1983)

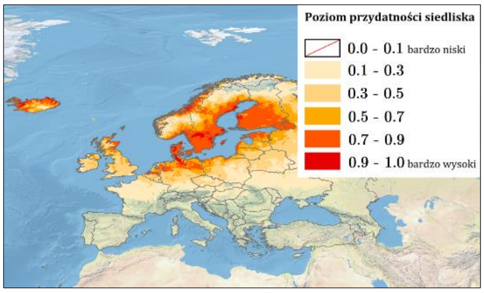


Figure 27. Level of habitat suitability of *Stephanitis oberti* in Europe.

Stephanitis pyrioides (Scott, 1874)

Origin	the Far East (Stonedahl et al., 1992; Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	precipitation in April between 75 and 160 mm, climate types: hot summer mediterranean climate (*Csa*), warm summer mediterranean climate (*Csb*), humid subtropical climate (*Cwa*), humid subtropical climate (*Cfa*), oceanic (*Cfb*), hemiboreal (*Dwb*)

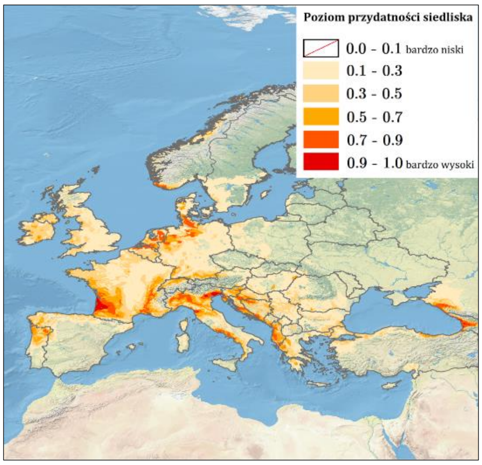


Figure 28. Level of habitat suitability of *Stephanitis pyrioides* in Europe.

Stephanitis rhododendri Horváth, 1905

Origin	nearctic (Rabitsch, 2008)
Records in Poland (as at 26.02.2023)	3 records in Lower Silesia (probably do not survive the winter; Lis B., 1999; Fig. 54)
The most informative environmental variables	oceanic climate (*Cfb*), soil types: humic cambisols, orthic ultisols and podzols

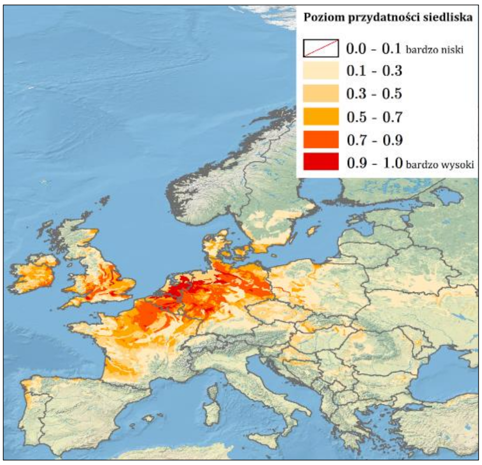


Figure 29. Level of habitat suitability of *Stephanitis rhododendri* in Europe.

Stephanitis takeyai Drake & Maa, 1955

Origin	Japan (Rabitsch, 2008)
First record in Europe outside its native range	Netherlands, 1994 (Rabitsch, 2008)
First record in Poland	Konstancin-Jeziorna on the Mazovian Low-lands, 1998 r. (Soika & Łabanowski, 2000)
Number of sites in Poland (as at 26.02.2023)	9 (List no. 30 (Chapter 6); Fig. 55)
The most informative environmental variables	average temperature of the coldest quarter above +1 °C, maximum temperature in February between +2.5 and +7.5 °C, climate types: oceanic (*Cfb*), subpolar oceanic (*Cfc*), subarctic with severe winters and cool summers, no dry season (*Dfc*)

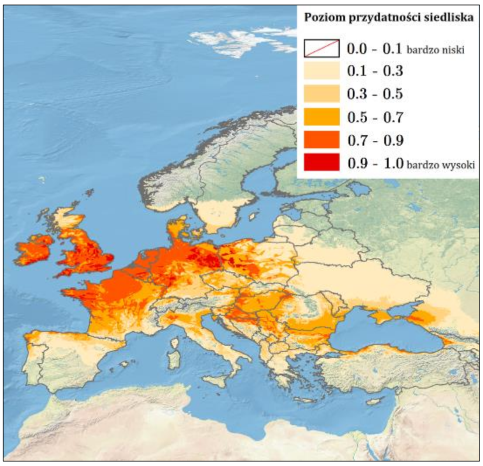


Figure 30. Level of habitat suitability of *Stephanitis takeyai* in Europe.

3.2. Infraorder Leptopodomorpha

3.2.1. Family Saldidae

Pentacora sphacelata (Uhler, 1877)

Origin	nearctic (Rabitsch, 2008)
First record in Europe outside its native range	Spain, 1953 (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	altitude between -30 and 19 m above sea level, soil types: vitric andisols, haplic phaeozems, calcic cambisols

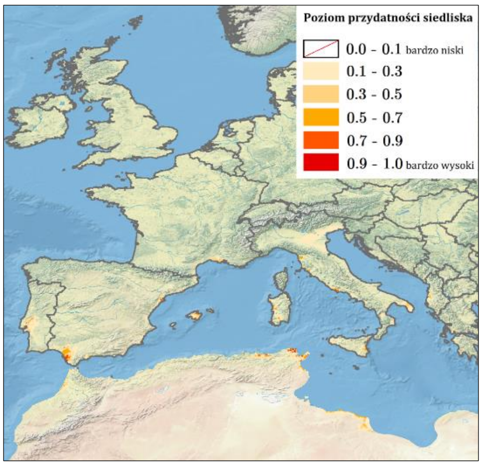


Figure 31. Level of habitat suitability of *Pentacora sphacelata* in Europe.

3.3. Infraorder Nepomorpha

3.3.1. Family Corixidae

Trichocorixa verticalis (Fieber, 1851)

Origin	nearctic (Rabitsch, 2008)
First record in Europe outside its native range	Portugal, 1997 (Rabitsch, 2008)
First record in Poland	none
The most informative environmental variables	altitude below 130 m above sea level, solar radiation in July above 24 200 (kJ/m2)/day, maximum temperature in February between +17.5 and +32 °C

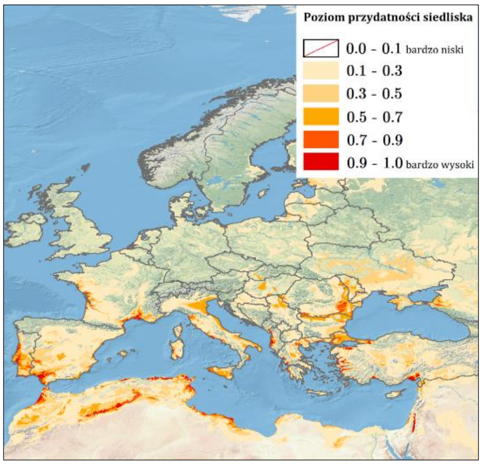


Figure 32. Level of habitat suitability of *Trichocorixa verticalis* in Europe.

3.4. Infraorder Pentatomomorpha

3.4.1. Family Coreidae

Leptoglossus occidentalis Heidemann, 1910

Origin	nearctic (Rabitsch, 2008)
First record in Europe outside its native range	Italy, 1999 (Rabitsch, 2008)
First record in Poland	Wrocław and Miechów near Kraków, 2007 (Lis J.A. et al., 2008)
Number of sites in Poland (as at 26.02.2023)	472 (List no. 33 (Chapter 6); Fig. 56)
The most informative environmental variables	average annual temperature between +3 and +14 °C, maximum temperature in November above +4.5 °C, climate types: hot summer mediterranean climate (*Csa*), warm summer mediterranean climate (*Csb*), oceanic (*Cfb*), hemiboreal climate (*Dfb*)

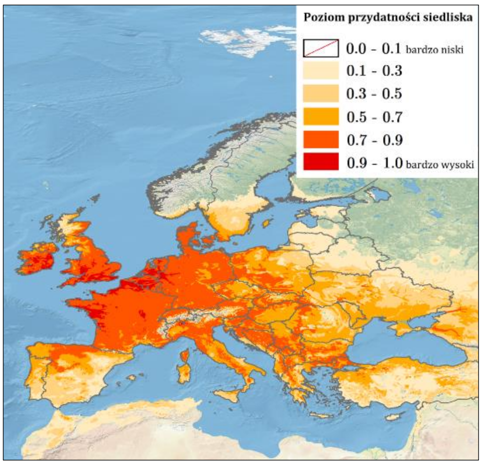


Figure 33. Level of habitat suitability of *Leptoglossus occidentalis* in Europe.

3.4.2. Family Lygaeidae

Arocatus longiceps Stål, 1872

Origin	Pontic-Mediterranean (Rabitsch, 2008)
First record in Poland	Wrocław, 2011 (Gil et al., 2011)
Number of sites in Poland (as at 25.02.2023)	59 (List no. 34 (Chapter 6); Fig. 57)
The most informative environmental variables	solar radiation in December between 1 500 and 3 750 (kJ/m2)/day, minimum temperature in January above -5.5 °C, climate types: hot summer mediterranean climate (*Csa*) and oceanic (*Cfb*)

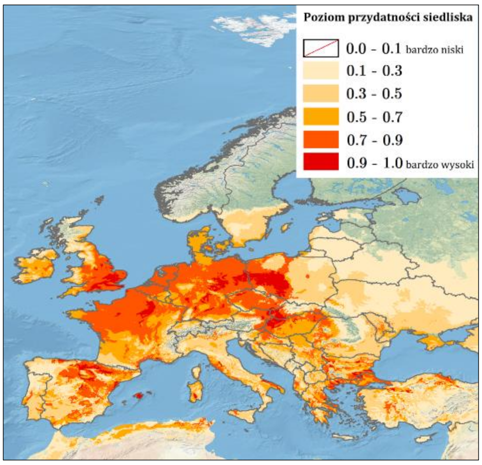


Figure 34. Level of habitat suitability of *Arocatus longiceps* in Europe.

Nysius huttoni F.B. White, 1878

Origin	New Zealand (Aukema et al., 2005)
First record in Europe outside its native range	Belgia i Holandia, 2002-2004 (Aukema et al., 2005)
First record in Poland	none
The most informative environmental variables	average annual temperature between -17.5 °C and +15 °C, precipitation in the driest month between 40 and 260 mm, oceanic climate (*Cfb*)

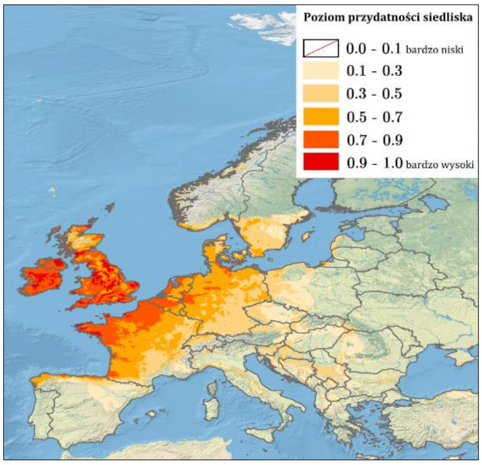


Figure 35. Level of habitat suitability of *Nysius huttoni* in Europe.

Orsillus depressus (Mulsant & Rey, 1852)

Origin	Mediterranean (Rabitsch, 2008)
First record in Europe outside its native range	Niemcy, 1971 (Rabitsch, 2008)
First record in Poland	Poznań, 2004 (Korcz, 2010)
Number of sites in Poland (as at 26.02.2023)	36 (List no. 36 (Chapter 6); Fig. 58)
The most informative environmental variables	minimum temperature in January between -6.5 and +13.5 °C, oceanic climate (*Cfb*)

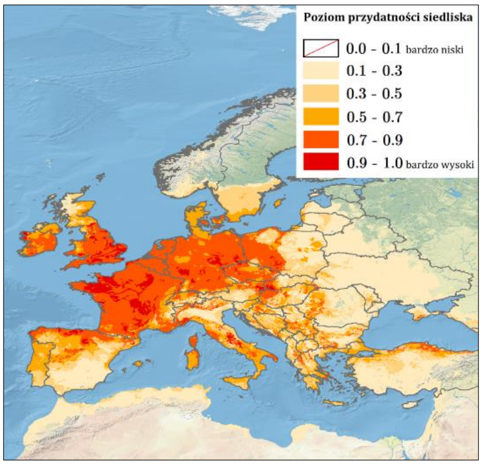


Figure 36. Level of habitat suitability of *Orsillus depressus* in Europe.

3.4.3. Family Oxycarenidae

Oxycarenus lavaterae (Fabricius, 1787)

Origin	Mediterranean (Rabitsch, 2008)
First record in Poland	Rzeszów, 2014 (Hebda i Olbrycht, 2016)
Number of sites in Poland (as at 26.02.2023)	296 (List no. 37 (Chapter 6); Fig. 59)
The most informative environmental variables	average temperature in February between +6 and +17.5 °C, with a minimum above +3 °C, climate types: hot semi-arid climate (*Bsh*), hot summer mediterranean climate (*Csa*), warm summer mediterranean climate (*Csb*), hemiboreal (*Dfb*)

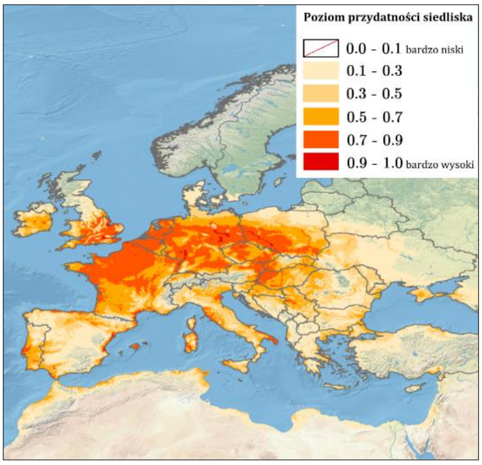


Figure 37. Level of habitat suitability of *Oxycarenus lavaterae* in Europe.

3.4.4. Family Pentatomidae

Halyomorpha halys (Stål, 1855)

Origin	asian (Rabitsch, 2008)
First record in Europe outside its native range	Switzerland, 2007 (Wermelinger et al., 2008)
First record in Poland	Dobczyce, Lesser Poland Voivodeship, 2018 (Claerebout et al., 2018)
Number of sites in Poland (as at 26.02.2023)	26 (List no. 38 (Chapter 6); Fig. 60)
The most informative environmental variables	maximum temperature in November between +5 and +17.5 °C

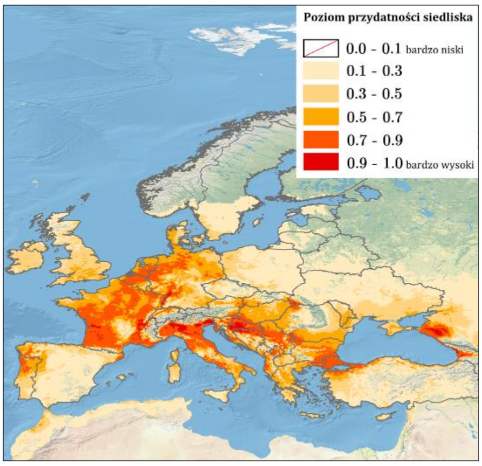


Figure 38. Level of habitat suitability of *Halyomorpha halys* in Europe.

Nezara viridula (Linnaeus, 1758)

Origin	palaeotropical (McPherson, 2018)
First record in Poland	Bielsko-Biała, 2018 (Gierlasiński & Sokołowski, 2019)
Number of sites in Poland (as at 26.02.2023)	7 (List no. 39 (Chapter 6); Fig. 61)
The most informative environmental variables	average annual temperature above +7 °C, average temperature in January between -0.5 and +28 °C, maximum temperature in February between -1 and +29 °C, climate types: hot semi-arid climate (*Bsh*), hot summer mediterranean climate (*Csa*), warm summer mediterranean climate (*Csb*), subtropical highland climate with monsoon influence (*Cwb*), humid subtropical climate (*Cfa*), oceanic (*Cfb*)

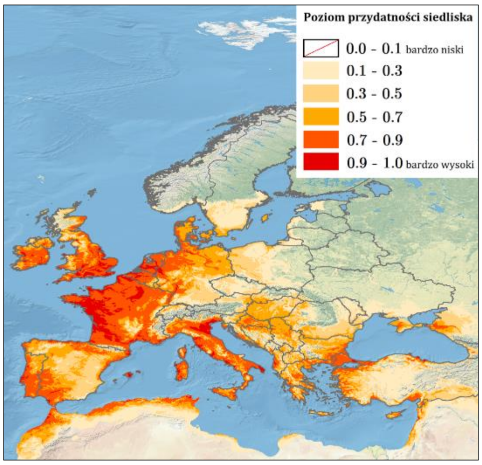


Figure 39. Level of habitat suitability of *Nezara viridula* in Europe.

Perillus bioculatus (Fabricius, 1775)

Origin	nearctic (Rabitsch, 2008)
First record in Europe outside its native range	intentionally introduced in France (1929), followed by other European countries, including Poland in 1959 (very high mortality rate; Gerber & Schaffner, 2016; Schaefer & Panizzi, 2000)
The most informative environmental variables	solar radiation in December between 3 300 and 9 200 (kJ/m2)/day, minimum temperature in January between -15 and 0° C

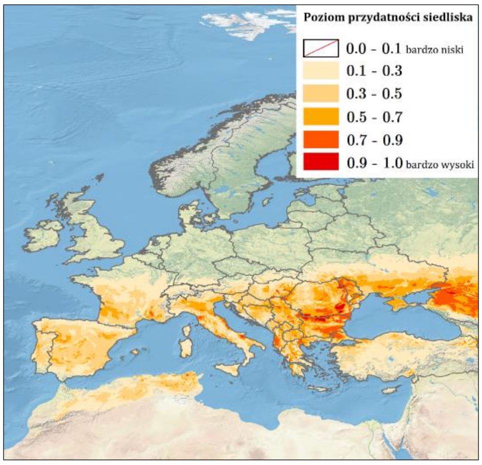


Figure 40. Level of habitat suitability of *Perillus bioculatus* in Europe.

4. Discussion

Chapter 3 discusses the results of the ecological niche modeling for 40 species of invasive true bugs. For all species, a result with an AUC_{train} value (i.e. the ability of the model to distinguish between where the species is present and where it is not) greater than 0.9 was obtained, which, according to Araujo et al. (2005), defines the model as very good (with an AUC > 0.99 for 19 species and an AUC between 0.98 and 0.99 for 11 species).

According to the results obtained, species for which the level of habitat suitability is very high in a large part of the European continent, and therefore – the risk of successful invasion in Europe (or increasing the current range) is high, are: *Amphiareus obscuriceps* (mainly central-western part of Europe), *Lyctocoris campestris* (mainly central-western part of Europe), *Deraeocoris flavilinea* (mainly central-western and south-western part of Europe), *Orthotylus concolor* (mainly central-western part of Europe), *Orthotylus virescens* (mainly Western Europe and the coasts of Southern Europe), *Taylorilygus apicalis* (coast of Southern Europe), *Corythucha arcuata* (between 40 and 48 °N), *Corythucha ciliata* (mainly Southern Europe), *Dictyonota fuliginosa* (mainly central-western part of Europe), *Stephanitis oberti* (mainly Northern Europe), *Stephanitis takeyai* (mainly Western Europe), *Leptoglossus occidentalis* (mainly Western Europe and northern part of Southern Europe), *Arocatus longiceps* (mainly central-western part of Europe), *Orsillus depressus* (mainly Western Europe and the northern part of Southern Europe), *Oxycarenus lavaterae* (mainly central-western part of Europe and coast of Southern Europe), *Halyomorpha halys* (mainly the centre of Western Europe and the coast of Southern Europe) and *Nezara viridula* (Western and Southern Europe). The species with the highest habitat suitability in Poland are: *Amphiareus obscuriceps* (mainly the centre, west, east and south of the country), *Lyctocoris campestris* (all voivodeships), *Deraeocoris flavilinea* (west of the country), *Orthotylus concolor* (mainly the South Baltic Coast), *Orthotylus virescens* (mainly the South Baltic Coast and the west of the country), *Tupiocoris rhododendri* (mainly the South Baltic Coast), *Corythucha ciliata* (mainly the south-west of the country), *Dictyonota fuliginosa* (west of the country), *Elasmotropis testacea* (mainly the south-west of the country), *Stephanitis oberti* (mainly the South Baltic Coast), *Stephanitis takeyai* (in the west of the country), *Leptoglossus occidentalis* (mainly in the south and west of the country and the South Baltic Coast), *Arocatus longiceps* (in the western part of the country), *Orsillus depressus* (in the western part of the country) and *Oxycarenus lavaterae* (in the south and southwest of the country).

For 36 of the 40 species discussed in this paper, the variable that significantly influenced the model was the temperature of the late autumn/winter months, namely: minimum temperature in January (*Anthocoris butleri, A. sarothamni, Buchananiella continua, Lyctocoris campestris, Deraeocoris flavilinea, Dichrooscytus gustavi, Macrolophus glaucescens, Orthotylus adenocarpi, O. caprai, O. virescens, Tupiocoris rhododendri, Tuponia brevirostris, T. elegans, T. mixticolor, Empicoris rubromaculatus, Dictyonota fuliginosa, Elasmotropis testacea, Stephanitis oberti,* *S. rhododendri, Arocatus longiceps, Nysius huttoni, Orsillus depressus*), minimum temperature in January and average temperature in February (*Closterotomus trivialis, Orthotylus concolor*), average temperature in January and maximum temperature in February (*Nezara viridula*), minimum temperature in January and February (*Perillus bioculatus*), maximum temperature in February (*Tuponia hippophaes*), average and maximum temperature in February (*Corythucha ciliata*), minimum and maximum temperature in February (*Stephanitis takeyai*), minimum temperature in January and March (*Corythucha arcuata*), average temperature in February and minimum temperature in December (*Amphiareus obscuriceps*), maximum temperature in November (*Taylorilygus apicalis, Leptoglossus occidentalis*), maximum temperature in January, February, November and December (*Trichocorixa*), minimum temperature in January, minimum and average temperature in February, minimum temperature in December (*Oxycarenus lavaterae*), minimum temperature in January, February and December, maximum temperature in November (*Halyomorpha halys*). The appropriate temperature is probably related to the ability of individuals to survive the winter in a given area, which is a necessary condition for the invasive species to spread beyond its current range. It can be assumed that with climate change and increasingly warmer winters, the mentioned invasive species will increase their ranges towards the north and north-east in Europe.

Of the species studied, the most economically important are, above all, phytophagous pests that feed on trees, crops and ornamentals. *Closterotomus trivialis* is a pest of olive, citrus, peach and apricot orchards, *Dichrooscytus gustavi* feeds on the fruit of common juniper and species of the family Cupressaceae, *Dicyphus escalerae* sucks the sap of the common snapdragon, *Orthotylus adenocarpi*, *O. concolor*, *O. virescens* and *Dictyonota fuliginosa* feed on the common broom but also prey on arthropods on it, *Taylorilygus apicalis* feeds on Asteraceae, *Tupiocoris rhododendri* feeds mainly on the sap of various *Rhododendron* species, but also attacks aphids, *Tuponia brevirostris*, *T. elegans*, *T. hippophaes* and *T. mixticolor* feed on plants of the tamarisk family, *Corythucha arcuata* is a pest of oaks, *C. ciliata* feeds mainly on the undersides of leaves of plane trees, *Elasmotropis testacea* feeds on various species of *Echinops*, *Stephanitis oberti*, *S. pyrioides*, *S. rhododendri* and *S. takeyai* are pests of heather family, *Leptoglossus occidentalis* feeds on cones and needles of conifers, *Arocatus longiceps* is found on plane trees, maples, hornbeams, chestnuts, lindens and alders, *Nysius huttoni* is a pest of many crops and grasses, *Orsillus depressus* feeds primarily on the cypress family species, *Oxycarenus lavaterae* feeds on young leaves of lindens, *Halyomorpha halys* is one of the most important economic pests, feeding on more than 175 species of fruit and ornamental, shrubs and vegetables, while *Nezara viridula* causes significant damage to legumes, herbaceous plants, fruit, nut and ornamental trees. Other species, which are zoophagous, can be a threat to native species of small arthropods, but at the same time can have a positive economic impact by attacking pests of crops and ornamental plants. *Anthocoris butleri* attacks *Psylla buxi* bugs that feed on the common box, *A. sarothamni* preys on the common broom bugs, *Deraeocoris flavilinea* feeds on aphids, *Nesidiocoris tenuis* is used to control pests of tobacco, tomato and other greenhouse vegetables, and *Perillus bioculatus* preys on the Colorado potato beetle. A zoophagus negatively affecting the economy is *Lyctocoris campestris*, which can infest clothing and bedding, attacking humans while they sleep, parasitise animals and damage silkworm farms.

Rapid detection of invasive species is important both for economic reasons (e.g. early application of pesticides) and for the conservation of biodiversity, as discussed in Chapter 1. The results presented in this paper may be helpful in identifying areas for more frequent inspections by phytosanitary services, e.g. specialists from the State Plant Health and Seed Inspection Service and personnel from the Regional Directorate for Environmental Protection. However, monitoring on such a large scale is very difficult to achieve, even taking into account the faunistic studies of entomologists. An invaluable support in such cases is the so-called citizen science, where volunteers participate in field surveys, while at the same time enlisting the help of specialists for species determination (Gierlasiński et al., 2019a). In Poland, a series of faunistic data on true bugs is published. These data were collected in cooperation with amateurs as part of citizen science. Another example is the study of the spread of *Halyomorpha halys* in northern Italy and southern Switzerland, where a large amount of data has been collected by amateurs and students (Maistrello et al., 2016). Access to online databases also has a significant impact on the speed of IAS detection, but also carries the risk of publishing site information for a misidentified species. Therefore, caution should be taken when using information from databases where coordinates can be published by amateurs and records are not checked by specialists.

Many Heteroptera species can only be identified by careful observation of, for example, the structure of the male reproductive system (e.g. in *Tuponia* spp.), but sometimes clear identification is not possible. In such cases, DNA barcoding can be used to identify the species based on the sequence of one or more loci, regardless of developmental stage (Skuza et al., 2015). In animals, the gene encoding cytochrome c oxidase subunit I (Skuza et al., 2015) or mini-barcodes, i.e. sequences of 125-257 bp in length, are used for this purpose (Piper et al., 2021). Barcode sequences are stored in the BOLD database (The Barcode of Life Data System; Ratnasingham and Hebert, 2007), but it is not error-free (Lis J.A. et al., 2016).

The correct identification of the species for which the location information is given is one of the most important factors influencing the outcome of ecological niche modeling - the use of incorrect data can significantly distort the picture of the model. It is also recommended to provide specific data on the site - geographical coordinates or the name of the locality (however, it should be remembered that in Poland many names of localities are repeated, therefore the description should allow unambiguous identification of the place where the species was observed). It is equally important to carry out faunistic studies in places that have not yet been visited - a very large number of reported sites concern the same place or places close to each other, especially in towns and parks (during the preparation of this thesis data on a total of 174 704 sites were collected, but after applying the reduction of spatial autocorrelation (Chapter 2) only ⅙ of them, that is 28 931 sites, could be used for modeling in Maxent). The implementation of the above recommendations when publishing information, whether by a specialist or by an amateur within the citizen science movement, will allow for more accurate ecological niche models in the future. This in turn will allow for a more realistic evaluation of habitat suitability of invasive species of true bugs in Europe.

The above conclusions can be observed, among others, when comparing the locations of invasive true bugs in Poland with the obtained habitat suitability maps (Figs. 41-61). The results also confirm the possibility of occurrence of such rare species in Poland as *Anthocoris sarothamni* on the Baltic coast, *Corythucha arcuata*, *Dictyonota fuliginosa*, *Orthotylus adenocarpi*, *Stephanitis oberti* in the north of Poland and *Tupiocoris rhododendri*. On the other hand, the more common species were found in areas of high habitat suitability (*Arocatus longiceps*, *Amphiareus obscuriceps*, *Lyctocoris campestris*, *Leptoglossus occidentalis*, *Orsillus depressus*, *Oxycarenus lavaterae*). However, for many species, single sites occur in areas with very poor or poor environmental conditions for their survival (e.g. *Nezara viridula*, *Orthotylus concolor*, *Orthotylus virescens*, *Stephanitis oberti* (offshore)). This may mean that these species have been misidentified and need to be re-examined by specialists, or that the individuals have arrived at the site as a result of accidental introduction and are unlikely to survive in the local environment. It would therefore be advisable to recheck these areas for the presence of the species. As mentioned above, it is important to extend faunal studies to areas that have not yet been checked. This is especially important in areas with high habitat suitability for the species. Close cooperation of citizen science amateurs with specialists, especially in the case of species that are difficult to identify, may lead not only to a more accurate knowledge of the spread of invasive Heteroptera species in Poland, but also to faster detection of the presence of rare species or those appearing in the country for the first time.

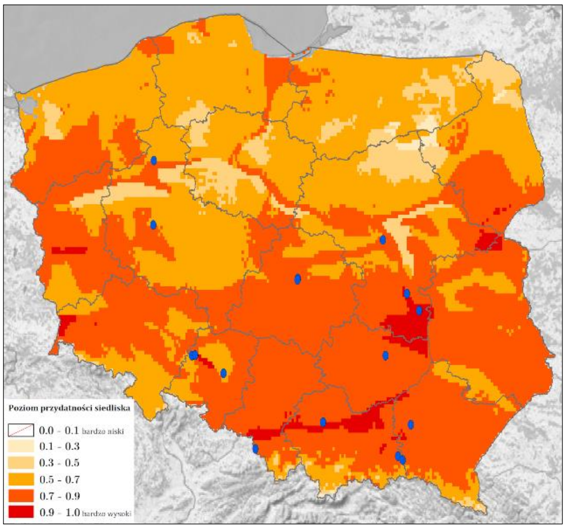


Figure 41. Distribution in Poland and level of habitat suitability of *Amphiareus obscuriceps*.

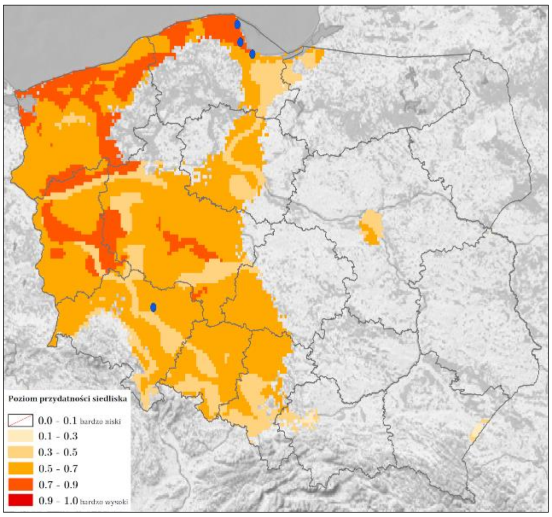


Figure 42. Distribution in Poland and level of habitat suitability of *Anthocoris sarothamni*.

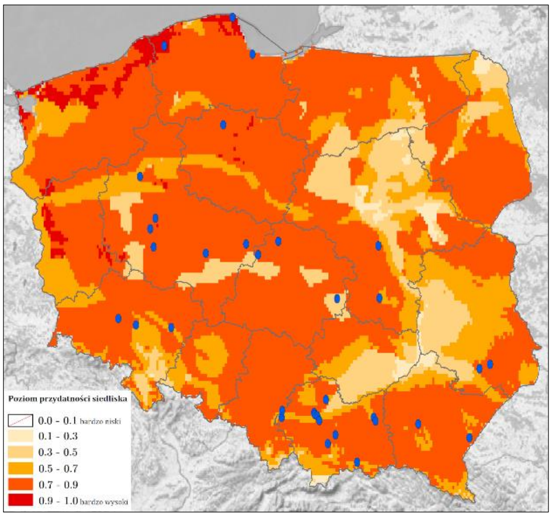


Figure 43. Distribution in Poland and level of habitat suitability of *Lyctocoris campestris*.

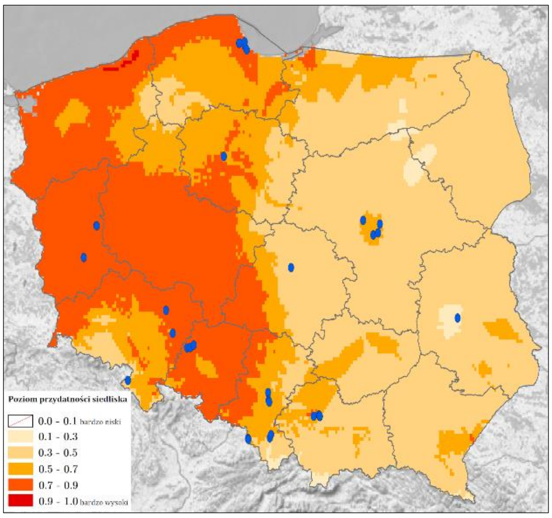


Figure 44. Distribution in Poland and level of habitat suitability of *Deraeocoris flavilinea*.

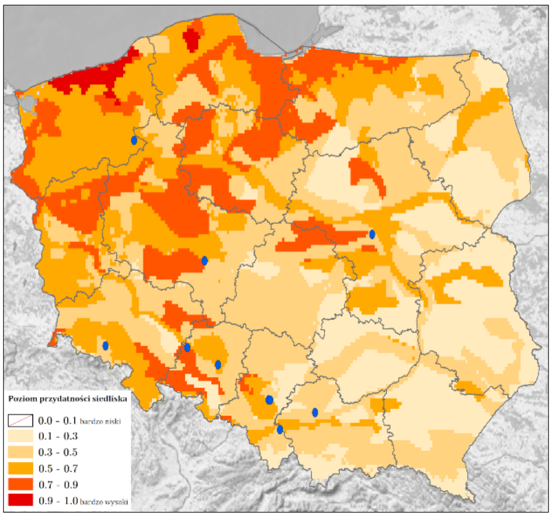


Figure 45. Distribution in Poland and level of habitat suitability of *Dichrooscytus gustavi*.

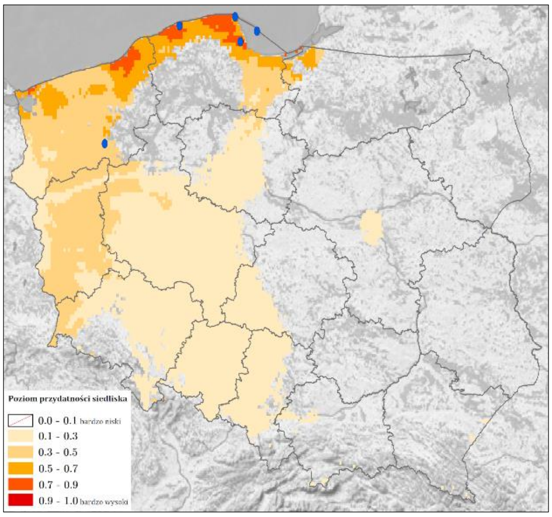


Figure 46. Distribution in Poland and level of habitat suitability of *Orthotylus adenocarpi*.

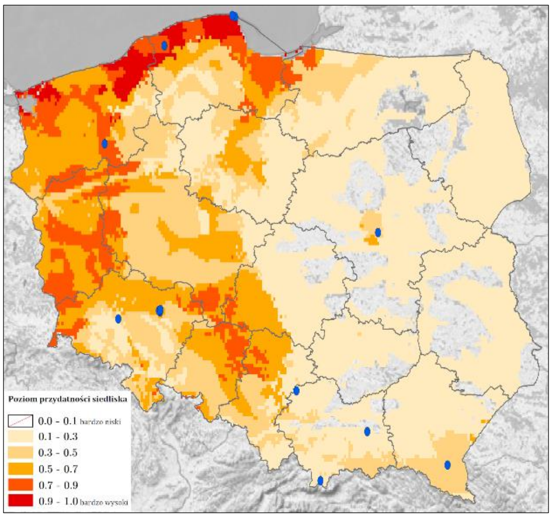


Figure 47. Distribution in Poland and level of habitat suitability of *Orthotylus concolor*.

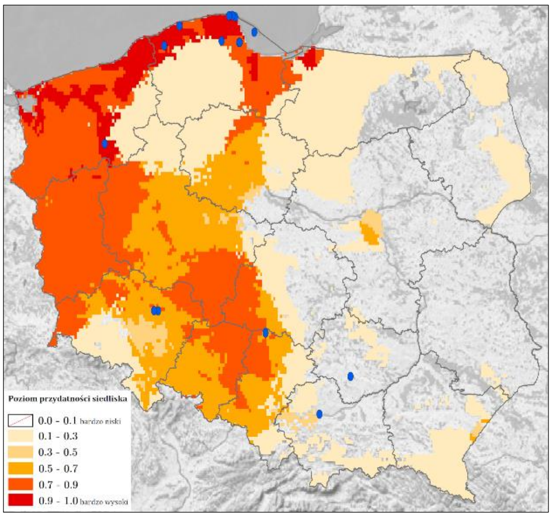


Figure 48. Distribution in Poland and level of habitat suitability of *Orthotylus virescens*.

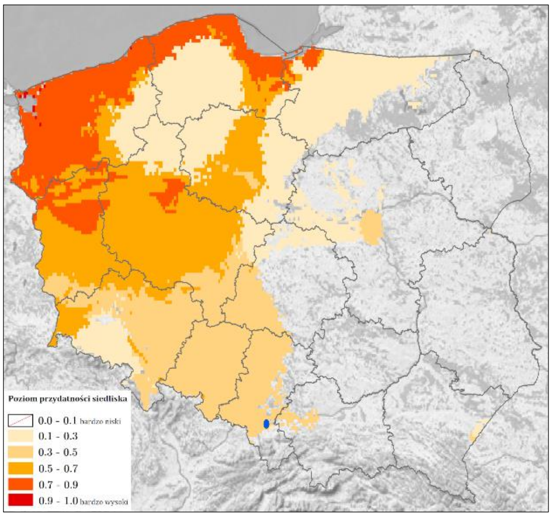


Figure 49. Distribution in Poland and level of habitat suitability of *Tupiocoris rhododendri*.

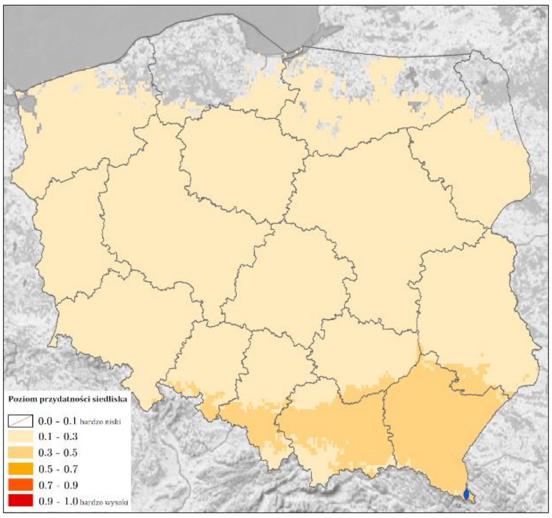


Figure 50. Distribution in Poland and level of habitat suitability of *Corythucha arcuata*.

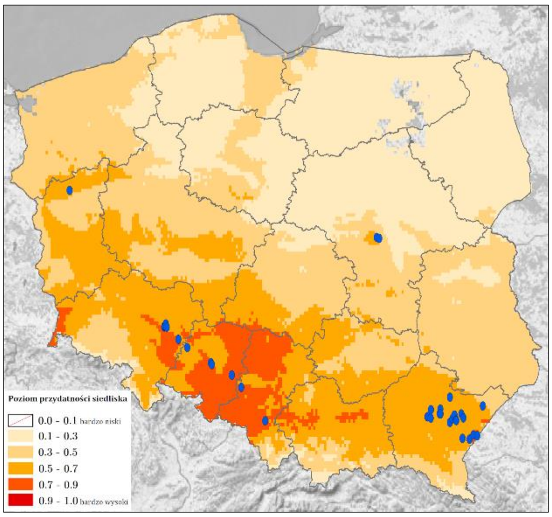


Figure 51. Distribution in Poland and level of habitat suitability of *Corythucha ciliata*.

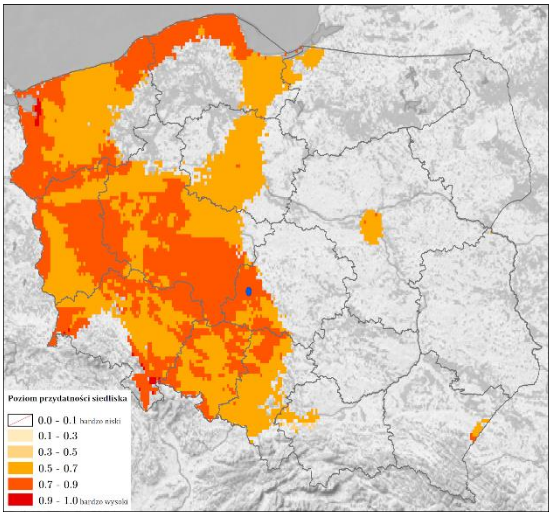


Figure 52. Distribution in Poland and level of habitat suitability of *Dictyonota fuliginosa*.

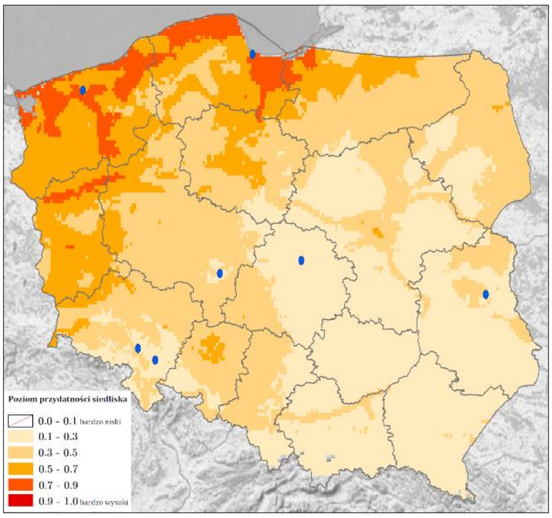


Figure 53. Distribution in Poland and level of habitat suitability of *Stephanitis oberti*.

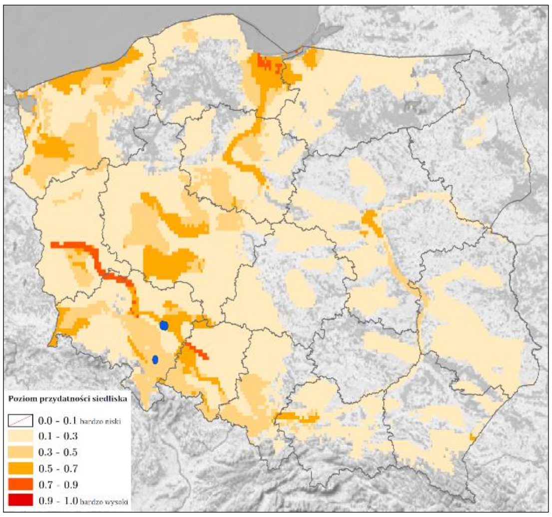


Figure 54. Distribution in Poland and level of habitat suitability of *Stephanitis rhododendri*.

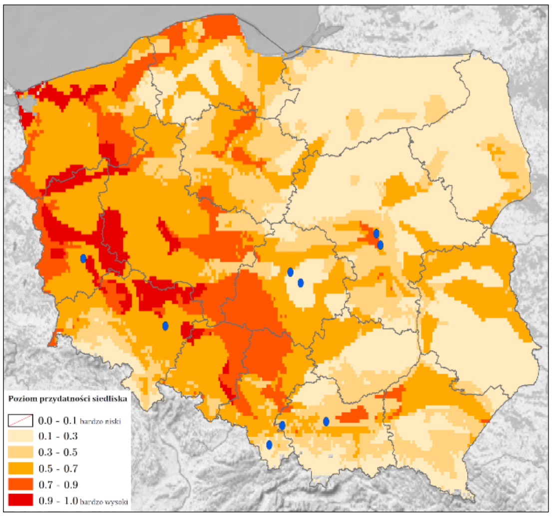


Figure 55. Distribution in Poland and level of habitat suitability of *Stephanitis takeyai*.

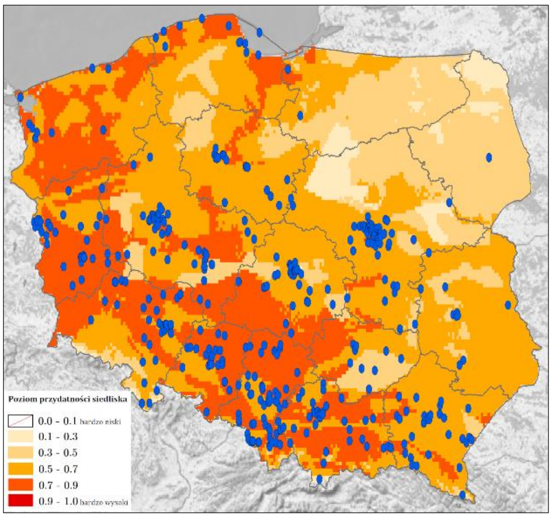


Figure 56. Distribution in Poland and level of habitat suitability of *Leptoglossus occidentalis*.

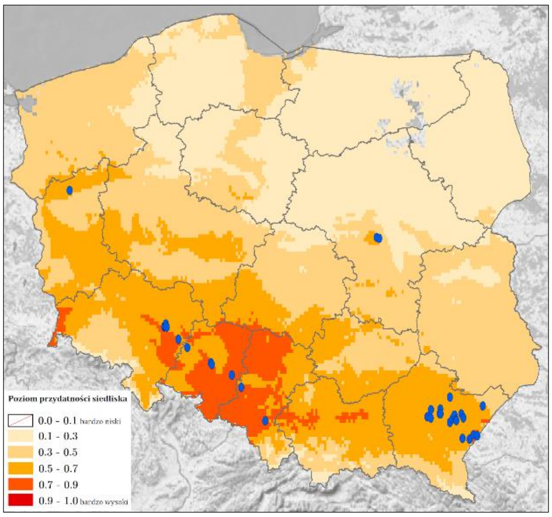


Figure 57. Distribution in Poland and level of habitat suitability of *Arocatus longiceps*.

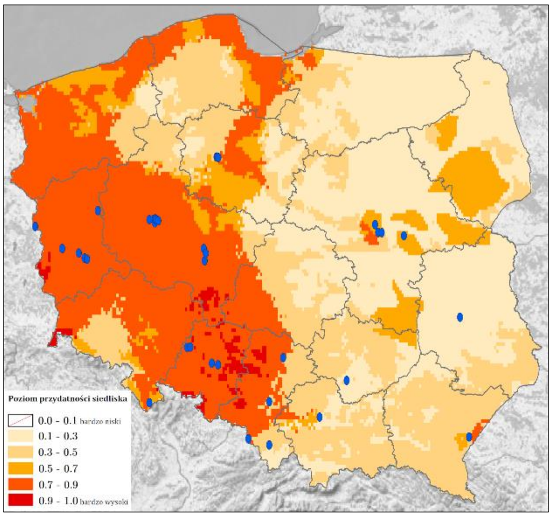


Figure 58. Distribution in Poland and level of habitat suitability of *Orsillus depressus*.

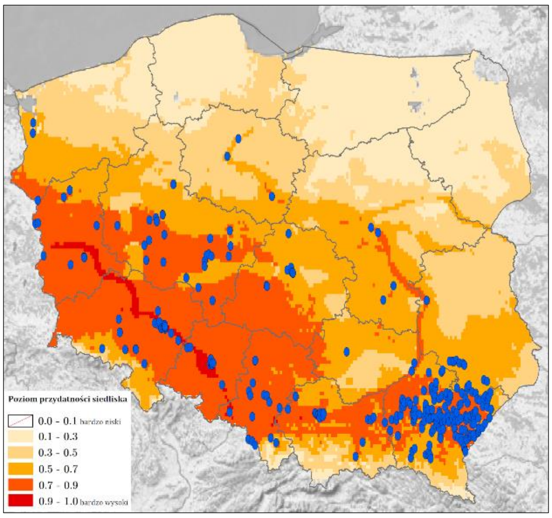


Figure 59. Distribution in Poland and level of habitat suitability of *Oxycarenus lavaterae*.

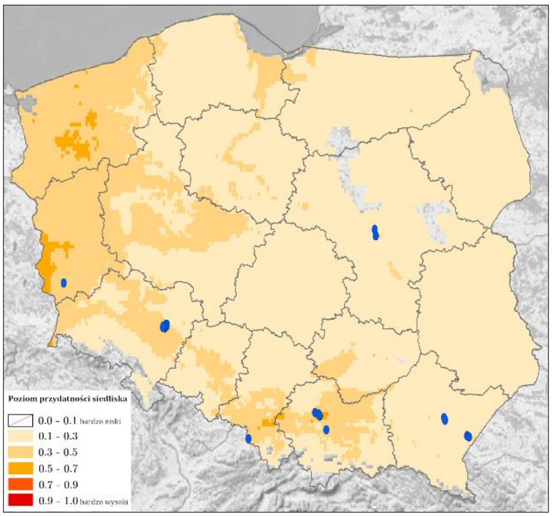


Figure 60. Distribution in Poland and level of habitat suitability of *Halyomorpha halys*.

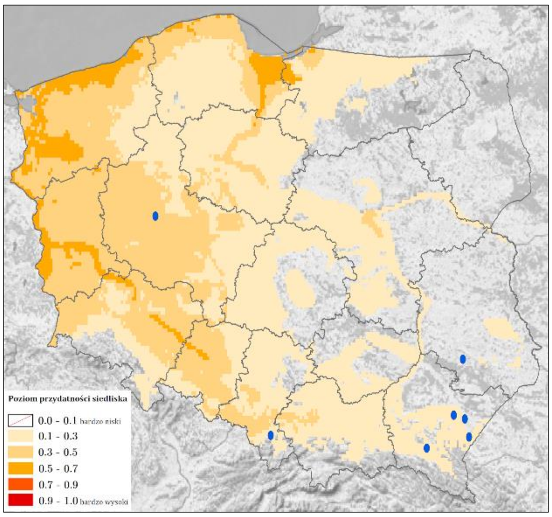


Figure 61. Distribution in Poland and level of habitat suitability of *Nezara viridula*.

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6. List of sites used during the ENM

No. of list	*Description*	*Access*
1.	List of *Amphiareus obscuriceps* sites used during the ENM (as at 03.10.2022).	https://doi.org/10.5281/zenodo.8366241
2.	List of *Anthocoris butleri* sites used during the ENM (as at 08.06.2022).	https://doi.org/10.5281/zenodo.8366283
3.	List of *Anthocoris sarothamni* sites used during the ENM (as at 04.10.2022).	https://doi.org/10.5281/zenodo.8366318
4.	List of *Buchananiella continua* sites used during the ENM (as at 04.10.2022).	https://doi.org/10.5281/zenodo.8366323
5.	List of *Lyctocoris campestris* sites used during the ENM (as at 04.10.2022).	https://doi.org/10.5281/zenodo.8366347
6.	List of *Closterotomus trivialis* sites used during the ENM (as at 22.07.2022).	https://doi.org/10.5281/zenodo.8366353
7.	List of *Deraeocoris flavilinea* sites used during the ENM (as at 21.02.2023).	https://doi.org/10.5281/zenodo.8366358
8.	List of *Dichrooscytus gustavi* sites used during the ENM (as at 21.02.2023).	https://doi.org/10.5281/zenodo.8366364
9.	List of *Dicyphus escalerae* sites used during the ENM (as at 30.07.2022).	https://doi.org/10.5281/zenodo.8366391
10.	List of *Macrolophus glaucescens* sites used during the ENM (as at 13.08.2022).	https://doi.org/10.5281/zenodo.8366401
11.	List of *Nesidiocoris tenuis* sites used during the ENM (as at 19.08.2022).	https://doi.org/10.5281/zenodo.8366414
12.	List of *Orthotylus adenocarpi* sites used during the ENM (as at 02.02.2023).	https://doi.org/10.5281/zenodo.8366433
13.	List of *Orthotylus caprai* sites used during the ENM (as at 24.08.2022).	https://doi.org/10.5281/zenodo.8366548
14.	List of *Orthotylus concolor* sites used during the ENM (as at 22.02.2023).	https://doi.org/10.5281/zenodo.8366551
15.	List of *Orthotylus virescens* sites used during the ENM (as at 22.02.2023).	https://doi.org/10.5281/zenodo.8366557
16.	List of *Taylorilygus apicalis* sites used during the ENM (as at 29.08.2022).	https://doi.org/10.5281/zenodo.8366565
17.	List of *Tupiocoris rhododendri* sites used during the ENM (as at 22.02.2023).	https://doi.org/10.5281/zenodo.8366575
18.	List of *Tuponia brevirostris* sites used during the ENM (as at 30.08.2022).	https://doi.org/10.5281/zenodo.8366580
19.	List of *Tuponia elegans* sites used during the ENM (as at 22.08.2022).	https://doi.org/10.5281/zenodo.8366596
20.	List of *Tuponia hippophaes* sites used during the ENM (as at 02.09.2022).	https://doi.org/10.5281/zenodo.8366600

No. of list	*Description*	*Access*
21.	List of *Tuponia mixticolor* sites used during the ENM (as at 02.09.2022).	https://doi.org/10.5281/zenodo.8366610
22.	List of *Empicoris rubromaculatus* sites used during the ENM (as at 06.09.2022).	https://doi.org/10.5281/zenodo.8366619
23.	List of *Corythucha arcuata* sites used during the ENM (as at 03.06.2023).	https://doi.org/10.5281/zenodo.8366677
24.	List of *Corythucha ciliata* sites used during the ENM (as at 24.02.2023).	https://doi.org/10.5281/zenodo.8366776
25.	List of *Dictyonota fuliginosa* sites used during the ENM (as at 25.02.2023).	https://doi.org/10.5281/zenodo.8366787
26.	List of *Elasmotropis testacea* sites used during the ENM (as at 25.02.2023).	https://doi.org/10.5281/zenodo.8366798
27.	List of *Stephanitis oberti* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8366800
28.	List of *Stephanitis pyrioides* sites used during the ENM (as at 07.09.2022).	https://doi.org/10.5281/zenodo.8366806
29.	List of *Stephanitis rhododendri* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8366822
30.	List of *Stephanitis takeyai* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8366830
31.	List of *Pentacora sphacelata* sites used during the ENM (as at 09.09.2022).	https://doi.org/10.5281/zenodo.8366836
32.	List of *Trichocorixa verticalis* sites used during the ENM (as at 22.09.2022).	https://doi.org/10.5281/zenodo.8366843
33.	List of *Leptoglossus occidentalis* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8366860
34.	List of *Arocatus longiceps* sites used during the ENM (as at 25.02.2023).	https://doi.org/10.5281/zenodo.8366989
35.	List of *Nysius huttoni* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8367000
36.	List of *Orsillus depressus* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8367011
37.	List of *Oxycarenus lavaterae* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8367021
38.	List of *Halyomorpha halys* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8367031
39.	List of *Nezara viridula* sites used during the ENM (as at 26.02.2023).	https://doi.org/10.5281/zenodo.8367037
40.	List of *Perillus bioculatus* sites used during the ENM (as at 28.09.2022).	https://doi.org/10.5281/zenodo.8367049