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Do climatic requirements explain the northern range of European reptiles? Common wall lizard *Podarcis muralis* (Laur.) (Squamata, Lacertidae) as an example

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Abstract. Climate seems likely to play the key role in determining the northern range limits of reptiles in mid-latitude Europe, as these ectothermic animals are dependent on external conditions. We tested this hypothesis for the example of common wall lizard *Podarcis muralis* (Laur.), and showed that it tolerates a wide range of different climatic factors, therefore could be potentially distributed more to the north from the northern limit of its native range. However, the main factor limiting the occurrence of the lizard in its northern range is the presence of suitable habitats, particularly rocky areas. Human economic activity in mid-latitude Europe resulted in the development of such suitable habitats in areas of advantageous climatic conditions. In this way, humans created niches suitable for the species as well as provided routes of access to these areas, what resulted in the increase the range of this lizard to the north.

Key words: Europe, invasive species, MaxEnt, species distribution modelling.

Introduction

Distribution ranges of species are limited by numerous abiotic and biotic factors (Berglund & Bengtsson 1981), and the different ones operating at different scales, i.e. macro-, meso- and microscale (Suren 1996). Since the Hutchinson's paper (1957), two concepts are distinguished. Fundamental niche is a multidimensional space in which the species could potentially exist. Realized niche is a part of the fundamental niche and indicates where the species really exists. In other words it is the result of the impact of various factors limiting the occurrence of species on their fundamental niche (Soberón & Peterson 2005). At spatial macroscale, the main factors are geographical barriers such as mountains, oceans, rivers and deserts, physiological limitations of organisms resulting from climate, soil and water chemistry (Mott 2010). At meso- and microscale the main factors are dispersal abilities, interspecific competition and presence of suitable habitats (Pearson & Dawson 2003, Peterson 2003).

For reptiles of mid-latitude Europe, factors determining the northern limit of their ranges have still not been specified with few exceptions. Strijbosch et al. (1980) and Bender et al. (1996) explained it by thermal demands. Araújo et al. (2008) argued that the 0 °C isotherm of the Last Glacial Maximum delimits the distributions of narrow-ranging species, whereas the current 0 °C isotherm limits the distributions of wide-ranging species.

In the case of common wall lizard is justified that another factor has a significant impact on the determination of their northern limit of the species native range. The native range of common wall lizard, *Podarcis muralis* (Laur.), covers southern Europe and the southern and western part of the mid-latitude Europe (Sillero et al. 2014). Caught our attention the fact that this species inhabits artificial habitats in mid-latitude Europe far from the north native range. As we think the cause is a human activity. Habitats suitable for this saxicolous lizard, such as quarries, railway embankments, railway stations, ruderal areas, various types of walls in cities or vineyards and etc., are created by humans (Schulte et al. 2008, Langham 2014, Sas-Kovács & Sas-Kovács 2014). Human also provide conditions for the dispersion of this species in intentional introductions and transport via trains or trucks as well as enable spreading of the lizard itself using human infrastructure, e.g. along railways (Covaciu-Marcov et al. 2006, Gherghel et al. 2009, Schulte et al. 2012a,b). To date, we know about 140 populations introduced in Europe (Strugariu et al. 2008, Mačát & Veselý 2009, Schulte et al. 2012b, Wirga & Majtyka 2013, Langham 2014, Sas-Kovács & Sas-Kovács 2014) and should be emphasized that the majority of these populations are located to the north, sometimes even quite far, from the species native range, mainly in England, Germany, Poland, Czech Re-

Table 1. Environmental variables used for ecological niche modelling of the common wall lizard *Podarcis muralis* (Laur.). Z – winter (months: December, January and February), w – spring (March, April and May), l – Summer (June, July and August) and j – autumn (September, October and November).

environmental variables	abbrev-iation	definition	interval and unit	source	original resolution
bare rocks	*br*	Presence/absence of bare rocks	binary (1, 0)	calculated using ESDB data	0.0083°
frost days of summer	*fd_l*	average number of summer days where daily minimum temperature < 0°C	1 day	calculated using E-OBS data	0.25°
growing season length of autumn	*gsl_j*	average number of autumn days where daily mean temperature > 5°C	1 day	calculated using E-OBS data	0.25°
growing season length of spring	*gsl_w*	average number of spring days where daily mean temperature > 5°C	1 day	calculated using E-OBS data	0.25°
ice days of winter	*id_z*	average number of winter days where daily maximum temperature < 0°C	1 day	calculated using E-OBS data	0.25°
summer days of summer	*su_l*	average number of summer days where daily maximum temperature > 25°C	1 day	calculated using E-OBS data	0.25°
minimum temperature of summer	*tn_l*	mean of daily minimum temperature (at night) of summer	0.1 °C	calculated using WorldClim data	0.0083°
minimum temperature of winter	*tn_z*	mean of daily minimum temperature (at night) of winter	0.1 °C	calculated using WorldClim data	0.0083°
maximum temperature of summer	*tx_l*	mean of daily maximum temperature (at day) of summer	0.1 °C	calculated using WorldClim data	0.0083°
maximum temperature of winter	*tx_z*	mean of daily maximum temperature (at day) of winter	0.1 °C	calculated using WorldClim data	0.0083°

public and Romania. Thus we think that two important factors form together fundamental niche for this species and we tested the hypothesis that no climate but occurrence of suitable habitats defines the northern limit of the species native range.

We used for this purpose the MaxEnt 3.3.3k software package (Phillips et al. 2004, Phillips et al. 2006), based on the maximum entropy approach for species distribution modelling from presence-only species records. MaxEnt is characterized by several advantages that outperform other similar software. For details, see Phillips et al. (2006) and Elith et al. (2006). After entering data on the presence localities of analysed species and relevant environmental variables, the software produces a continuous probability of presence between 0 and 1 (Phillips & Dudík 2008).

Materials and methods

Study area and environmental variables

Common wall lizard inhabits Europe (Sillero et al. 2014), therefore the entire area of the continent (φ 72.2°N – 33.8°N and λ 24.7°W – 44.7°E) was used in ecological niche modelling. We created a raster map with a 0.0083° (~ 1 km) grid resolution.

We selected 9 climatic variables based on the common wall lizard biology and available data, obtained from WorldClim – Global Climate Data (Hijmans et al. 2005) and E-OBS dataset from the EU-FP6 project ENSEMBLES and data provided in the ECA&D project (Haylock et al. 2008) (Table 1). All these climatic variables directly affect the distribution of the species and are the so-called proximal variables (Austin 2002). Mean values of all climatic variables were calculated from the multi-year period of 1950-2000. To make a habitat variable – *br* (bare rocks) we used *aglim* (limitations to agricultural use), *dr* (depth to rock) and *par-mat-dom* (major group code for the dominant parent material) layers from European Soil Portal – Soil Data and Information Systems (ESDB) (Panagos et al. 2012). In *br* binary variable 1 indicates the presence of bare rocks and 0 indicates the absence of bare rocks. Due to the different resolution data from these sources, we up-scaled E-OBS climatic variables by using the bilinear interpolation to a spatial resolution of 0.0083°. All variables were generated using ArcGIS® (ESRI 2010). We tested climatic variables for correlation by each other using Spearman's rank correlation coefficient in STATISTICA (StatSoft 2011). For all of them, r_s < 0.75. Therefore, the correlation between them was not very high and could be used for modelling in the MaxEnt.

Occurrence Data

A total of 4342 unevenly distributed native records and 123 introduced records of common wall lizard are collected from the available resources (see References: Supplementary documentation). We took into account only those species records that matched the resolution of the variables. In order to minimize potential negative effects caused by sampling bias (Phillips et al. 2006, Merow et al. 2013), we left native records spaced from each other of at least 10 km. We rejected introduced records near the coast because of missing some variable data and these ones which are located within native range. Finally, we used for analysis 2358 native and 85 introduced records. All the above-listed steps were performed in ArcGIS® (ESRI 2010).

Ecological Niche Modelling

We generated two models in MaxEnt. First, based only on selected climatic variables. Additionally, we compared mean values of selected climatic variables for the native populations forming the northern range limit and stable introduced populations located to the north from those native populations. Second model was generated based on climatic variables and presence of suitable habitats.

All the MaxEnt parameters were set to default values (Phillips & Dudík 2008), except the maximum number of iterations, which were increased to 5000 to allow adequate time for convergence. Background data were set to 10000 random points taken from the entire analysed area, as suggested by Merow et al. (2013). We used cross-fold validation with 20 replicates. Area under the receiver operating characteristic curve (AUC) was applied to evaluate the model. The AUC value is the probability of presence sites to have higher predicted values than background sites (Elith et al. 2006). The importance of each environmental variable was measured by comparing the difference in the AUC values between the models built respectively with the variable omitted and considered separately (so-called jackknife procedure implemented in MaxEnt). Such processing indicated variables of the greatest importance in the model. MaxEnt was also used to plot graphs showing the relationships between the predicted relative probability of occurrence and values of each environmental variable. In order to generate a binary prediction (suitable versus unsuitable areas), the threshold value was set as first decile of probability of presence of 2358 records from native range.

Statistical analysis of climatic variables

For statistical analysis we used 177 records forming the northern range limit (northern native populations) of common wall lizard and 85 stable introduced records situated to the north from native records (northern introduced populations) (Fig. 1a). We used the Cochran-Cox *t*-test due to the fact that these two groups had normal distributions but different variances. These steps were performed in STATISTICA (StatSoft 2011).

Results

Ecological Niche Modelling

Our model based only on selected climatic variables was typified by average test AUC of 0.854 and average training AUC of 0.857. Model based on climatic variables and presence of suitable habitats was typified by average test AUC of 0.876 and average training AUC of 0.878. The omission rates in both models were closed to the predicted omission.

Suitable areas of model based only on climatic variables covers southern, western and central Europe, with the northern limit extending to central England (particularly its eastern part), western Belgium, the Netherlands (excluding coastal areas), northern Germany, and western Poland. Then the northern limit quite abruptly turns southwards, runs through southern Slovakia, Romania, southern Moldova, Crimea, and reaches the western Ciscaucasia (Fig. 1a). Suitable areas of model based on climatic and habitat variables covers patchy areas more or less to south from northern native populations (Fig. 1b).

Statistical analysis of climatic variables

Average number of frost days in summer (*fd_l*) for populations forming the northern range limit (northern native populations) and for stable introduced populations situated to the north from native populations (northern introduced populations) is 0. Average growing season length for autumn (*gsl_j*) and spring (*gsl_w*) is longer for northern introduced populations (Cochran-Cox *t*-test, respectively $t'_{225} = 4.91$ and $t'_{259} = 3.79$, respectively $p < 0.001$ and $p < 0.001$). Average number of ice days in winter (*id_z*) is less for northern introduced populations (Cochran-Cox *t*-test, $t'_{236} = 4.95$, $p < 0.001$). Average number of summer days in summer (*su_l*) is greater for northern native populations, but the difference is not statistically significant (Cochran-Cox *t*-test, $t'_{222} = 1.97$, $p = 0.049$). Mean of minimum temperature in summer (*tn_l*) and winter (*tn_z*) and mean of maximum temperature in winter (*tx_z*) are higher for northern introduced populations (Cochran-Cox *t*-test, respectively $t'_{260} = 3.91$, $t'_{212} = 5.43$, $t'_{192} = 4.19$, respectively $p < 0.001$, $p < 0.001$, $p < 0.001$). Mean of maximum temperature in summer (*tx_l*) is higher for northern native populations, but the difference is not statistically significant (Cochran-Cox *t*-test, $t'_{200} = 1.73$, p = 0.085) (Fig. 2).

Discussion

As values close to 0.500 indicate a fit no better than that expected by random while a value of 1.000 indicates a perfect fit, AUCs of our models can by described as good following Baldwin (2009) (for more, see Supplementary material – available exclusive online).

Range limits of organisms are determined by numerous factors, most important of which include climate, geographical barriers, competitive

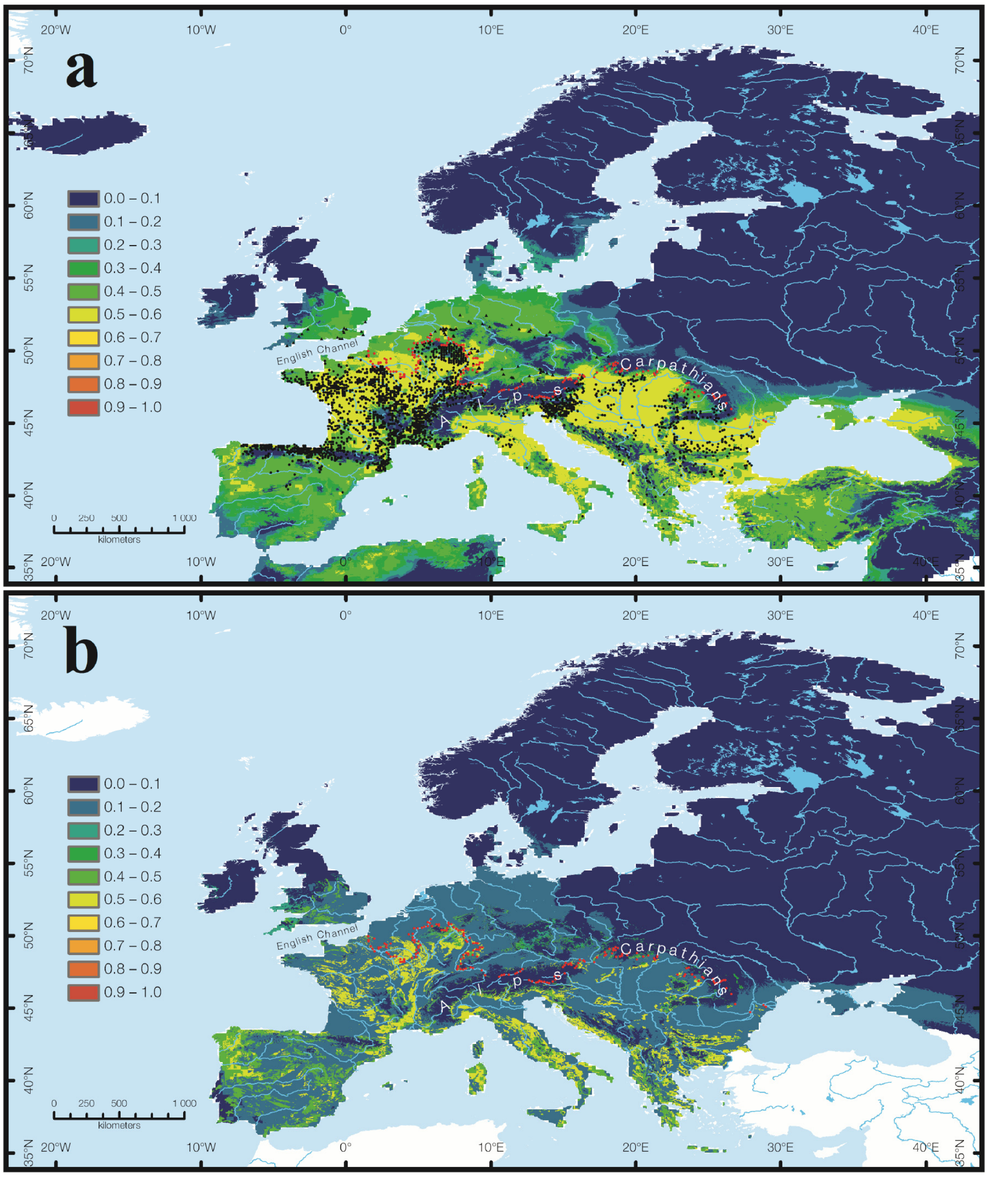

Figure 1. Climatic suitability map based solely on climatic variables (a), and environmentally suitability map based on climatic and habitat variables (b) for common wall lizard, *Podarcis muralis* (Laur.). Colour scheme corresponds to the MaxEnt logistic output, where values of ca. 0.500 indicate typical presence sites, 1.000 – best suitable areas and 0.000 – unsuitable areas; white areas indicate lack of data. Suitable areas are marked as logistic value ≥ 0.3 – 0.4 for a, and logistic value ≥ 0.4 – 0.5 for b. Black dots = native populations, red dots = native populations forming the northern range limit, triangles = introduced populations.

exclusion and presence of suitable habitats (Hardin 1960, Pearson & Dawson 2003, Peterson 2003, Mott 2010). The northernmost recorded native population (50.85 °N) is found at the locality of Maastricht (Netherlands) (Strijbosch et al. 1980), while the so far identified northernmost introduced population (52.44 °N) inhabits the locality of Bramsche (Germany) (Schulte et al. 2012b). Therefore, the distribution range appears to be shifted at about 1.59 ° (ca. 177 km) to the north. Moreover, our model based only on climatic variables shows that northernmost localities may ex-

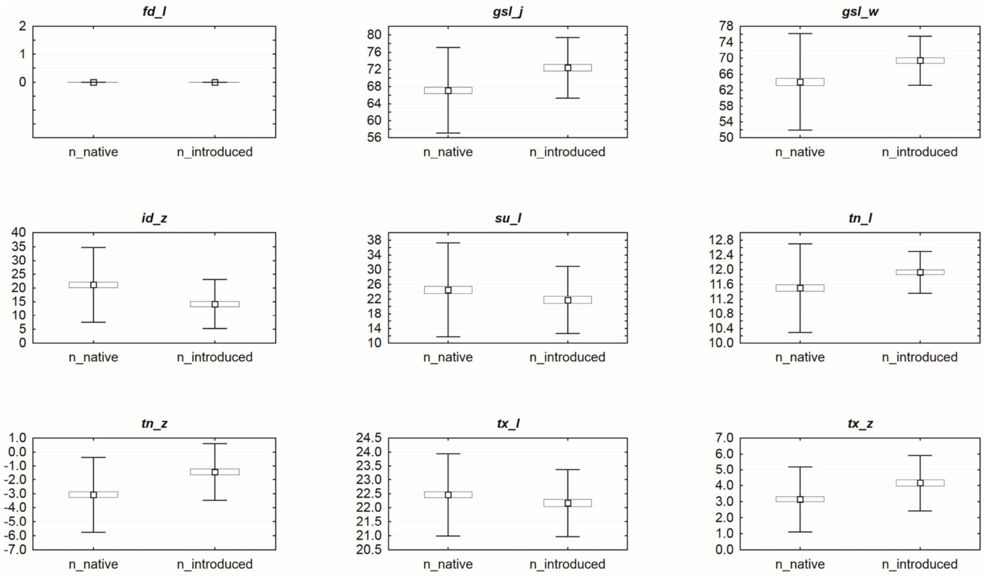

Figure 2. Comparison of the values of 9 climatic variables for the two groups: northern native populations (n_native) and northern introduced populations (n_introduced). Shown are means (squares), standard errors (boxes) and standard deviations (whiskers). See Methods for definitions of variables and groups.

tend up to even 54.00 °N, providing a shift of ca. 350 km, in relation to native localities (Fig. 1a). Analysis of particular climatic variables indicated that most of them displayed slightly different mean values for northern introduced populations and northern native populations, in favour those first ones (Fig. 2). This means that introduced populations north of English Channel, Alps and Carpathians are located in more favourable climatic conditions - longer growing season, smaller number of ice days and a higher average minimum and maximum temperatures during the summer (incubation of eggs) and winter (hibernation) than populations forming the northern limit of the native range.

Geographical barriers, associated with the dispersal abilities of organisms, prevent them from reaching their suitable areas. In its northern boundary, the native range of the discussed species is limited by barriers such as the English Channel and large mountain systems of the Alps and the Carpathians (Fig. 1a, b), which are the spreading barrier for another species of reptiles (Joger et al. 2007, Sillero et al. 2014).

As saxicolous species common wall lizard requires rocky habitats. Large areas of bare rocks are present in southern Europe ranging from low altitudes. Most of the mid-latitude Europe is either flat or hilly covered by thick layer of sediments. Rocky habitats are present mostly at higher altitudes. Lowlands in this part of Europe provide suitable climate, however are devoid of advantageous habitats. In contrast, mountains of this region provide suitable habitats (rocky terrains), however are typified by climate too cold for this species (Fig. 1a, b). Human activity disturbed this relationship and, in part of lowlands, created suitable habitats and various routes of their access, enabling colonization by common wall lizard.

In the southern part of its range, if common wall lizard competes with other lacertid lizards than occupies narrower ecological niches. However, at sites devoid of competitors this species expands its ecological niches and range (Arnold 1987). The northern part of common wall lizard native range is co-inhabited by only two other lacertid species, namely the sand lizard, *Lacerta agilis* (L.), and common lizard, *Zootoca vivipara* (Licht.). Observations described by Mole (2008), Schulte et al. (2008) and Heym et al. (2013) indicate that common wall lizard either co-occurrences with these species or displaces them. Therefore, in its northern part the distribution range of common wall lizard is not limited by other lizards.

According to the EEA Report (2012), in the period of 2002 – 2011 the average temperature for European land area increased by 1.3 °C comparing to the pre-industrial level. The frequency and length of heat waves increased as well. Precipitation did not show such a clear trend as temperature, however generally increased (especially in winter) in northern Europe and decreased in the southern part of continent since the 1950s. The SRES A1B emission scenario predicts an increase in land temperature between 1.0 ° and 2.5 °C by 2021 – 2050 and between 2.5 ° and 4.0 °C by 2071 – 2100, particularly during winters in eastern and northern Europe and during summers in southern Europe. Heat waves should become more frequent and last longer across Europe, which will be also marked by further changes in rainfall, increasing particularly during winter in the northern part of continent and declining during summer in the southern part. Such events would improve conditions for the existence of the discussed heliothermic lizard in the northern part of its range and enable extension of its potential distribution further to the north.

Conclusion

The northern limit of common wall lizard native range is determined by the presence of suitable habitats or geographical barriers, however not climate or competitors (Fig. 1a, b). Human activity, resulting in the development of habitats advantageous for the species in mid-latitude Europe, enabled its expansion into new regions of suitable climate, located to the north from its native range (Schulte et al. 2012a,b). As defined in our model, based solely on climatic variables, the northern range limit was shifted by ca. 3 °, i.e. ca. 350 km, further to the north from the native northern range limit. Additionally, in mid-latitude Europe reported successful introductions of several species of lizards north of their native ranges, e.g. *Lacerta viridis* (Laur.) in England (Mott 2010), *Podarcis liolepis* (Blngr) in Germany (Schulte et al. 2012a) and *Darevskia armeniaca* (Méh.) in Ukraine (Ananjeva et al. 2006). This means that the climate in these species probably does not play a major role in the determination of their northern limit ranges too.

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