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**Article**

# Environmental niche modelling of the Chinese pond mussel invasion in Europe under climate change scenarios

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**Abstract**
In this paper, we modelled the Chinese pond mussel distribution in the European subcontinent under the recent climatic conditions and two climate change scenarios. Using species records of *Sinanodonta woodiana* (Bivalvia: Unionidae) in Europe and a set of bioclimatic variables, we applied the maximum entropy approach provided by MaxEnt to build the species distribution models and investigate how each climatic variable affects the species distribution. We found that winter temperatures had the largest contribution to the species distribution in all three scenarios (recent, RCP 4.5, RCP 8.5). We applied the minimum training presence threshold, as a less stringent, and 10th percentile training presence threshold, as more stringent, to map the potential area of the species occurrence. The models show that the climatically optimal range, depicted by the stricter threshold, will be expanded eastwards under all three scenarios. At the same time, the area of minimally suitable environments, represented by the less stringent threshold, will be contracted in the future climate. The species distribution models highlight that the climatic conditions of the British Isles and the Azov-Kuban Lowland are the most suitable, among the uninvaded regions, for further *S. woodiana* invasion.

**Key words** alien species, fundamental niche, MaxEnt, bioclimatic variables, *Sinanodonta woodiana*.

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## Introduction

Biological invasions are one of the most significant ecological disturbances threatening native biodiversity on a global scale (Mollot et al., 2017). Aquatic ecosystems are no exception and have been subject to hundreds of introductions of invasive species (Strayer, 2010), which negatively impact native fauna and entire ecosystems in a variety of ways (Geist et al., 2023; Sousa et al., 2014).

Freshwater mussels of the genus *Sinanodonta* (Bivalvia, Unionidae) are one of the most successful invaders among bivalves along with the Asian clam *Corbicula fluminea* (Mueller, 1774) and the zebra mussel *Dreissena polymorpha* (Pallas 1771). The genus comprises invasive lineages belonging to three species: *S. woodiana* (Lea, 1834), *S. pacifica* (Heude, 1878), and *S. lauta* (Martens, 1877) (Douda et al., 2024). Among these, the Chinese pond mussel *S. woodiana* (also called the "temperate invasive" lineage (Bolotov et al., 2016)), is the most widespread. With native range restricted to China, it has been widely introduced in Europe, Southern Siberia, Central Asia and Southeast Asia (Douda et al., 2024 and references herein), and successfully occupied variety of climatic zones from Myanmar to Northern Europe.

Being subtropical species initially, the Chinese pond mussel has successfully invaded colder temperate and even subarctic areas using anthropogenically heated water bodies as steppingstones (Labecka & Czarnoleski, 2021). It has been shown that initially established viable population of *S. woodiana* in warm waters could successfully spread to natural environments and adapt for surviving and even for recruitment in ice-covered waterbodies (Konečný et al., 2018; Urbańska & Andrzejewski, 2019).

The number of new records of invasive populations of *S. woodiana* in Europe has increased exponentially since it was first discovered in 1979 (Mehler et al., 2024). Such a "hyper-successful" invasion (Sousa et al., 2014) is facilitated by biological and ecological preadaptation of the species leading to outcompeting native mussels (Reichard et al., 2012). The Chinese pond mussel demonstrates a high tolerance to environmental conditions and is able to survive in a wide range of freshwater habitats (Donrovich et al., 2017). The thermal tolerance of glochidia comparable to native species (Benedict & Geist, 2021), relatively higher growth and reproduction rates (Huber & Geist, 2019), resistance to pollution and hypoxia (Sárkány-Kiss et al., 2000), and the ability to use of most fish species as hosts for glochidia (i.e., being a host-generalist; Watters, 1997) have established a broad range of the ecological niche of *S. woodiana*.

The main driver of the invasion is the commercial freshwater fish trade which promotes spread of *S. woodiana* at the glochidial stage (Benedict et al., 2024). Watershed divides loose their role of natural barriers with this type of artificial dispersal, meaning that the species potentially can colonize every habitat regardless of its natural dispersal abilities. In addition to continuing to parasitise aquaculture species, glochidia can parasitise native fish (Donrovich et al., 2017), which subsequently distribute mussels through connected waterways. Studies in Europe have shown that once established, invasive populations can negatively impact the ecosystems by outcompeting native species for food and space and altering biotic composition and abiotic properties (Donrovich et al., 2017; Douda & Čadková, 2018; Reichard et al., 2015).

The high invasion potential of *S. woodiana*, its negative impact on natural ecosystems, and the still vast uncolonized areas in the European subcontinent raise questions about the future direction of invasion and the impact of global climate change on this process. To date, only one study has attempted to answer these questions (Mehler et al., 2024). The authors applied a species distribution modelling technique and showed that the species distribution is controlled by habitat and climate variables. They also forecasted that the area of suitable habitat will decrease at the end of the century.

Species distribution models (SDMs), also called environmental niche models, are a widely used tool for understanding the processes underlying the distribution of species (Da Re et al., 2023; Franklin, 2023). The basis of the whole diversity of SDMs (e.g., generalised linear models, random forest, maxent, etc.) is to find correlations between an observed response variable describing the species distribution and a set of environmental predictors recorded from the species' locations. Thus, the main output of SDM is the estimation of a species' potential niche in a temporal and geographical context (Franklin, 2023).

Global environmental change affects a species distribution through shifting, contracting, expanding and fragmentation of their ecological niches (Chen et al., 2011). The transferability of observed relationships between a species and an environment is an important metric of a SDMs quality which allow a model to be projected in space and time. It is particularly important for tracking and managing invasions, where predictions may help to identify areas with a high probability of invasion and save resources by prioritising the monitoring efforts. At the same time, modelling the distribution of range-shifting species is a more complex task than for species which are in equilibrium with an environment (Elith et al., 2010). Specific suggestions for modelling of invasion are that the overestimation of the geographical area that the alien species could invade is a "desirable property" (Jiménez-Valverde et al., 2011), and the reducing of the model complexity and the overfitting are the key features of a model to avoid the underprediction (Jiménez-Valverde et al. 2011; Jane Elith, Kearney, and Phillips 2010; Santamarina et al. 2019).

The case studies of niche modelling of alien species show that SDM is a powerful spatial analysis tool for predicting the potential distribution of invasions, provided that all necessary precautions regarding the choice of modelling settings are taken into account (Santamarina et al. 2019; Jane Elith, Kearney, and Phillips 2010). One of the main constraint in modelling range-shifting species is the problems of extrapolation due to non-analogous climates in the invaded range compared to the native one (Fitzpatrick & Hargrove, 2009). The approach to overcome this is to calibrate a model using species records from the invaded range (Barbet-Massin et al., 2018).

Among the environmental niche modelling techniques using presence-only data, MaxEnt (Phillips et al., 2008) is the most widely used (Elith et al., 2010, 2011; Fois et al., 2018; Santamarina et al., 2019). Improved predictions are achieved by tuning the default parameters and examination of the complexity of models using different values of MaxEnt (Elith et al., 2010; Radosavljevic & Anderson, 2014; Santamarina et al., 2019).

In this paper, we applied environmental niche modelling to predict the distribution of environmental conditions suitable for *S. woodiana* on the European subcontinent under the historical climate and two scenarios of future climate change. For this, we 1) compiled the dataset of *S. woodiana* occurrences covering its entire invasive range in Europe and 2) used the MaxEnt approach to calculate a set of models of the probability of species presence for the historical climate and two future scenarios.

## Materials and methods

### *Distribution mapping*

The range models of *S. woodiana* were mapped with ESRI ArcGIS 10 software (www.esri.com/arcgis). Free open sources, i.e., Natural Earth Free Vector and Raster Map Data (http://www.naturalearthdata.com), GSHHG (http://www.soest.hawaii.edu/pwessel/gshhg), HydroSHEDS (http://www.hydrosheds.org), and GADM (http://gadm.org) were used to create the base of the maps.

### *Species records*

MaxEnt software (Phillips et al., 2008), used here for SDM, requires presence only data and does not require information about true absence. Georeferenced records of the occurrence of invasive populations of *S. woodiana* in Europe were obtained from the Global Biodiversity Information Facility (GBIF.org (01.05.2020)), from published sources searched in the Web of Science database using key words "*Sinanodonta woodiana*" and "Chinese pond mussel", and "grey" literature. Population records from artificially heated reservoirs were excluded from the search results. The initial dataset contained 325 points after removing repeated records (Figure 1) (dataset on *figshare*: Vikhrev et al., 2024). To avoid model overfitting, the initial dataset was rarified using the SDMtoolbox plugin for ArcGIS 10.4 with a distance of 100 km between closest points (Brown et al., 2017). The final dataset contained 60 records.

### *Environmental data*

Considering the high tolerance of the Chinese pond mussel to biotic conditions and its ability to survive in a wide range of habitats (Benedict & Geist, 2021; Dobler et al., 2022; Konečný et al., 2018), we suggest that climate is a major factor limiting the potential niche of the species.

The range of habitat suitability was modelled using a set of bioclimatic variables for historical (Wouters, 2021) and future (Wouters et al., 2021) climate conditions derived from the Copernicus Climate Change Service (CCS). The recent data cover the industrial period from 1979 to 2018, and the future climate is modelled for the period 2080 – 2100 for two greenhouse gas emission scenarios, i.e., RCP 4.5 and RCP 8.5. The original CCS bioclimatic indicator layers are available for the period 1950 – 2100 with a temporal resolution of 20-year averages. Each layer contains seven bands – one for each 20-year period. We extracted the last seventh band of the period of interest using the Raster Calculator function of QGIS 3.32.3 (QGIS.org, 2022). To improve model performance, it is necessary to exclude areas where species cannot colonise due to geographical barriers or other reasons (Elith et al., 2010). In the case of *S. woodiana*, we know that there are no theoretically unreachable habitats due to human-mediated dispersal, so we only excluded marine waters as a completely unsuitable environment for the strictly freshwater species. All layers of environmental variables were clipped by a coastline mask using ArcGIS 10.4.

SDM results are very sensitive to autocorrelated variables, so removing of multicollinearity is a necessary step in data preparation (Merow et al., 2013; Radosavljevic & Anderson, 2014). We performed an autocorrelation test in the SDMtoolbox plugin for ArcGIS 10.4 to calculate paired Pearson correlations for each of the three sets of variables.

To select which variables to include in the model, we followed Worthington et al. (2016) with our modifications. Highly correlated variables were removed based on the results of permutation test of MaxEnt. First, variables with zero contribution were removed. Then, pairs of variables with higher correlation coefficient were evaluated first and the variable with lower contribution was removed from the model. In the first step, all 19 bioclimatic variables were tested. After reducing the set of variables, the SDM was built with the remaining of variables. Those with zero contribution in the permutation test were not included in the next round of SDM. These steps were repeated until each variable had a contribution to the model greater than zero. After that, the results of a jackknife test were checked, and the variables that disimprove the model performance were removed.

The same approach to variable selection was used for the recent and two forecasting models, meaning that each scenario was projected as an independent model with its own set of variables but the same species records (Worthington et al., 2016). MaxEnt allows the current prediction to be projected to a different environment or geographical extent. However, this approach does not account for potential changes in interactions between variables in space and time, because a decision about variables selection is based on the current correlations between variables. We investigated whether interactions between climatic variables will change in the future against recent data. The Mantel test, implemented in PAST 3.01 (Hammer et al., 2001) was used to calculate correlations between pairs of correlation matrices: recent vs RCP 4.5 and recent vs RCP 8.5.

We examined how each of the environmental variables affects the prediction using response curves provided by MaxEnt. Each curve shows how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Logistic scale does not allow to conclude which values of the predictor are marked suitable habitats, but the probability of presence lover than 50% is considered as not differing from random.

### *Distribution modelling*

Recent and future potential invasion ranges of *S. woodiana* in Europe were build using the maximum entropy algorithm as implemented in MaxEnt software. The default settings, employed for the calibration of the algorithm, were the k-fold cross-validation method, maximum iteration number, the maximum number of background points, and the autofeatures. To reduce the model complexity, different values of the regularization multiplier (β) were tested: 0.1, 0.5, 1, 2, 3, 4, 5 (Elith et al., 2010; Worthington et al., 2016). For each of β-value, 10 model replicates with same settings were built. The averaged model of 10 replicates was used for subsequent analysis and visualization of results. Variables impact on a model was assessed at each β-value using permutation test and response curves generated by MaxEnt. In case if a variable did not affect the prediction, it was excluded from the subsequent modelling.

MaxEnt can generate continuous maps of presence prediction in raw, logistic, and cumulative formats. However, such continuous output is difficult to interpret (Phillips et al., 2008). To evade this constraint, MaxEnt allows to apply threshold rule for the generation of a binary map of presence/absence. The minimum training presence (MP) rule was chosen as the less strict one, which tends to select extreme habitats at the edge of species' niche as suitable. Such approach is useful for invasive range modelling, where overestimation is better than underestimation. The 10th percentile training presence (10P) rule was tested as a more conservative approach. This rule excludes 10 percentages of the most extreme habitats, where species presence was predicted. Of the three output formats, logistic was reported to be less suitable (Merow et al., 2013). The raw format is the most appropriate, but it is impossible to apply a threshold rule to this one. In our modelling, the cumulative format was chosen.

The discriminative ability of the SDMs was assessed using the average evaluation Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve (Elith & Burgman, 2002; Fielding & Bell, 1997). To test for overfitting, the difference between the calibration and the test AUCs (hereafter $AUC_{diff}$) and the average omission rates based on the two selected thresholds were used (Radosavljevic & Anderson, 2014; Santamarina et al., 2019). All these values were extracted or calculated from MaxEnt output files. The model with the optimal β-value was chosen following the consequence of evaluation steps: a) select those with omission rates closer to the theoretical expectations for MP and 10P thresholds (0 and 0.1, respectively), b) among them, select one with a minimal difference between training and test AUCs but still maximal or near maximal observed values for the test AUC. Binary maps of the predictions were generated from the averaged output .asc file using the thresholds values of the selected models.

We decided not to use a bias file as we do not expect sampling bias in our dataset. Unevenness of distribution of *S. woodiana* records in Eastern Europe illustrated in the Figure 1 reflects its actual distribution there. Recent publications and our own extensive field work on freshwater bodies across European Russia and Belarus confirm only six populations in the region (Douda et al., 2024; Kondakov et al., 2020; this study).

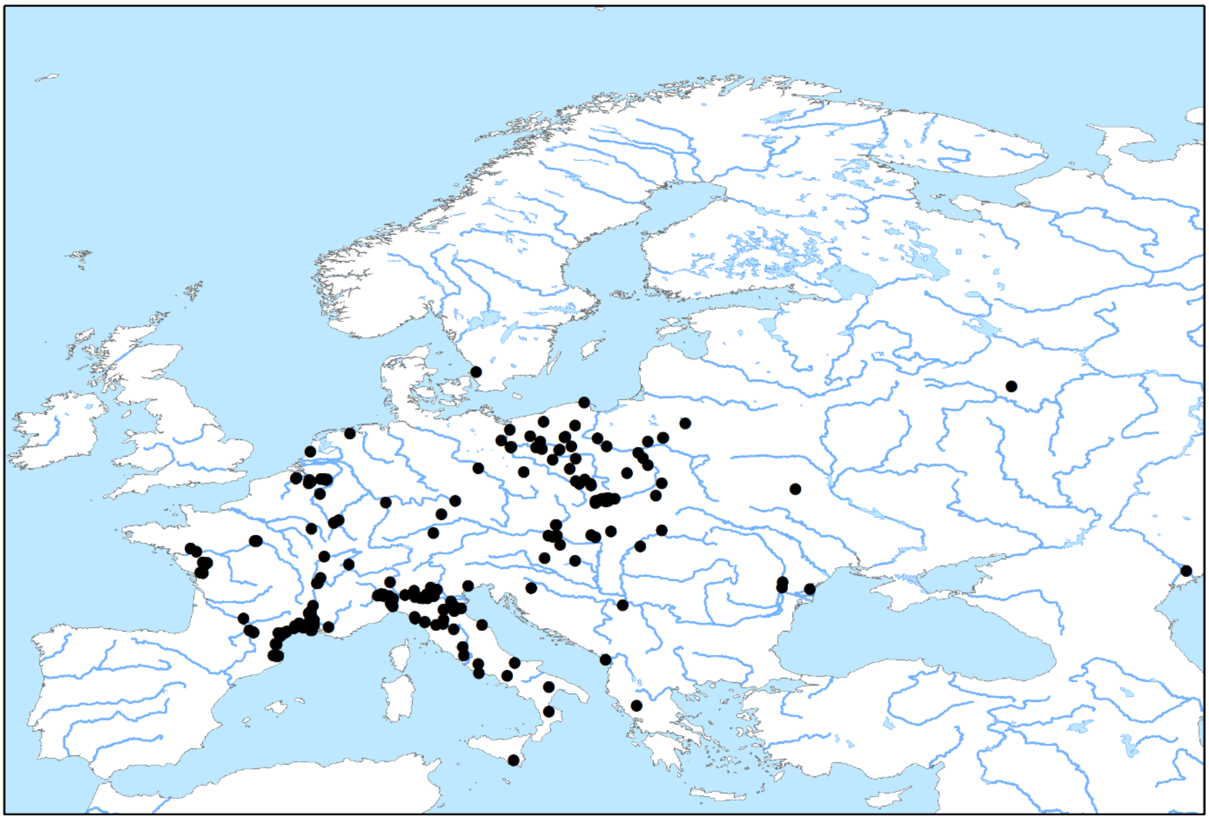

**Figure 1.** Map of records of *S. woodiana* in Europe obtained from GBIF database and published sources (Vikhrev et al., 2024).

## Results

### *Model selection and quality estimation*

The set of models with various β-parameter were built for each climatic scenario (Table 1). Omission levels return the same low values at MP and 10P thresholds in all models. Therefore, the choice of the optimal β-parameter was based on AUCdiff and testAUC. The lowest AUCdiff for each of the scenarios were reached when β=5. In all cases testAUC value at β=5 was lower than the highest (recent: 0.865 vs 0.878; RCP 4.5: 0.861 vs 0.884; RCP 8.5: 0.871 vs 0.887), but still high enough (>0.8) to consider the good discrimination ability of each selected model.

**Table 1**. Parameters from MaxEnt output used to evaluate the quality of *S. woodiana* distribution models (β-parameter – regularization multiplier; $AUC_{diff}$ = ${}_{train}AUC$ - ${}_{test}AUC$; minimum training presence (MP) and 10th percentile training presence (10P) omissions), and to draw maps of probability of presence. The best quality models are shown in grey.

| Model | β-parameter | $AUC_{diff}$ | ${}_{train}AUC$ | ${}_{test}AUC$ | MP omission | 10P omission | MP threshold | 10P threshold |
|---|---|---|---|---|---|---|---|---|
| Historic | 0.1 | 0.065 | 0.937 | 0.871 | 0.000 | 0.094 | 0.901 | 19.211 |
| | 0.5 | 0.035 | 0.912 | 0.877 | 0.000 | 0.094 | 1.711 | 20.752 |
| | 1 | 0.027 | 0.905 | 0.878 | 0.000 | 0.094 | 1.965 | 23.438 |
| | 2 | 0.024 | 0.900 | 0.876 | 0.000 | 0.094 | 3.572 | 29.942 |
| | 3 | 0.020 | 0.895 | 0.876 | 0.000 | 0.094 | 4.928 | 34.285 |
| | 4 | 0.017 | 0.889 | 0.871 | 0.000 | 0.094 | 6.208 | 36.328 |
| | 5 | 0.014 | 0.879 | 0.865 | 0.000 | 0.094 | 7.774 | 35.587 |
| RCP 4.5 | 0.1 | 0.068 | 0.934 | 0.866 | 0.000 | 0.094 | 3.645 | 12.200 |
| | 0.5 | 0.033 | 0.917 | 0.884 | 0.000 | 0.094 | 3.054 | 14.695 |
| | 1 | 0.030 | 0.910 | 0.880 | 0.000 | 0.094 | 4.970 | 18.177 |
| | 2 | 0.025 | 0.901 | 0.876 | 0.000 | 0.094 | 8.076 | 23.111 |
| | 3 | 0.022 | 0.893 | 0.872 | 0.000 | 0.094 | 10.026 | 28.124 |
| | 4 | 0.017 | 0.885 | 0.868 | 0.000 | 0.094 | 11.945 | 32.221 |
| | 5 | 0.014 | 0.876 | 0.861 | 0.000 | 0.094 | 13.444 | 33.786 |
| RCP 8.5 | 0.1 | 0.053 | 0.922 | 0.869 | 0.000 | 0.094 | 1.542 | 14.827 |
| | 0.5 | 0.023 | 0.909 | 0.885 | 0.000 | 0.094 | 2.472 | 17.145 |
| | 1 | 0.018 | 0.906 | 0.887 | 0.000 | 0.094 | 3.922 | 20.249 |
| | 2 | 0.015 | 0.902 | 0.887 | 0.000 | 0.094 | 7.038 | 24.318 |
| | 3 | 0.014 | 0.897 | 0.883 | 0.000 | 0.094 | 9.940 | 26.564 |
| | 4 | 0.013 | 0.891 | 0.878 | 0.000 | 0.094 | 12.282 | 28.047 |
| | 5 | 0.012 | 0.883 | 0.871 | 0.000 | 0.094 | 14.695 | 29.747 |

### *Climatic variables contribution*

Mantel test returned absence of correlation between pairs of correlation matrices of environmental variables: recent vs RCP 4.5 ($r$=-0.008, $p$>0.05) and recent vs RCP 8.5 ($r$=-0.06, $p$>0.05). This result indicates significant changes in interactions between climatic variables in future against recent data. Considering this, two different sets of six environmental variables were retained for prediction of *S. woodiana* distribution under the recent climatic conditions and future RCP 4.5 scenario, and four variables explain prediction of the Chinese pond mussel distribution under the RCP 8.5 scenario (Table 2). The majority of them are temperature-related, and only two, i.e., Bio 15 and Bio18, refer to precipitation.

MaxEnt returned minimal temperature of the coldest month (Bio6) as the variable with highest contribution to the recent climate model (Table 2). The probability of presence is skyrocketed with rise of a minimal temperature of the coldest month over -5 ºC and the model does not show the temperature value which drops the MaxEnt prediction (Figure 2D). Probability of presence became non-random when cross 50% threshold at values of 5.6 ºC. Bio6 was also included in the RCP 4.5 model but with much lower contribution than in the recent one (Figure 3C). The variable crossed 50% threshold at the similar value of 4.3 ºC, but response curve demonstrates much smoother distribution. Second high variable in the recent model is the temperature seasonality (Bio4), which refers to the variability of temperature within the year (Figure 2C). Lower values correspond to more stable climate over year. In the model, the variable maximizes the probability of presence at the value 6.5 degrees of standard deviation of mean temperature change. Lower values decrease the probability faster than higher values.

**Table 2.** Environmental variables selected for prediction of *S. woodiana* distribution under three climate change scenarios and variables contribution to each model. Highest contribution values are marked in bold.

| Variable | Contribution to the model, % | | |
|---|---|---|---|
| | Recent | RCP 4.5 | RCP 8.5 |
| Bio2 (Mean diurnal range) | 0.3 | 17.4 | n/a |
| Bio3 (Isothermality) | 1.4 | 6.2 | 10.5 |
| Bio4 (Temperature seasonality) | 25.2 | n/a | 0.4 |
| Bio6 (Minimum temperature in coldest month) | **46.5** | 6.9 | n/a |
| Bio7 (Temperature annual range) | 7.4 | n/a | n/a |
| Bio8 (Mean temperature in wettest quarter) | n/a | 4.3 | n/a |
| Bio11 (Mean temperature of coldest quarter) | n/a | **56.8** | **48.8** |
| Bio15 (Precipitation seasonality) | n/a | 8.3 | n/a |
| Bio18 (Precipitation in warmest quarter) | 19.2 | n/a | 40.3 |

The future distribution will be the most contributed from another climatic variable as forecasted by both models. Mean temperature of coldest quarter (bio11) will share the highest contribution in the model under both future scenarios (Figures 3E and 4C). Response curves are almost identical for RCP 4.5 and RCP 5.8, but with plus two-degree shift in extreme scenario.

Bio18 is the only variable in the recent and RCP 8.5 models related to precipitation (Figures 2F and 3D). It indicates averaged volume of precipitations during the warmest quarter across the referenced period. The contribution to the future model is two times higher (40.3 vs 19.2), and the maximum values are significantly differed. The value of the variable that maximize the recent prediction is 113.8 mm, and 81.7 mm in the future. Lower values drop probability dramatically in both cases, while higher values leave it almost constant in the recent model but decrease rapidly in the future. Prediction under the moderate future scenario RCP 4.5 is affected by precipitation in a much less degree (Figure 3F). Precipitation seasonality (Bio15) has low contribution to the model (8.3%) and decrease the probability of presence across the whole range of values.

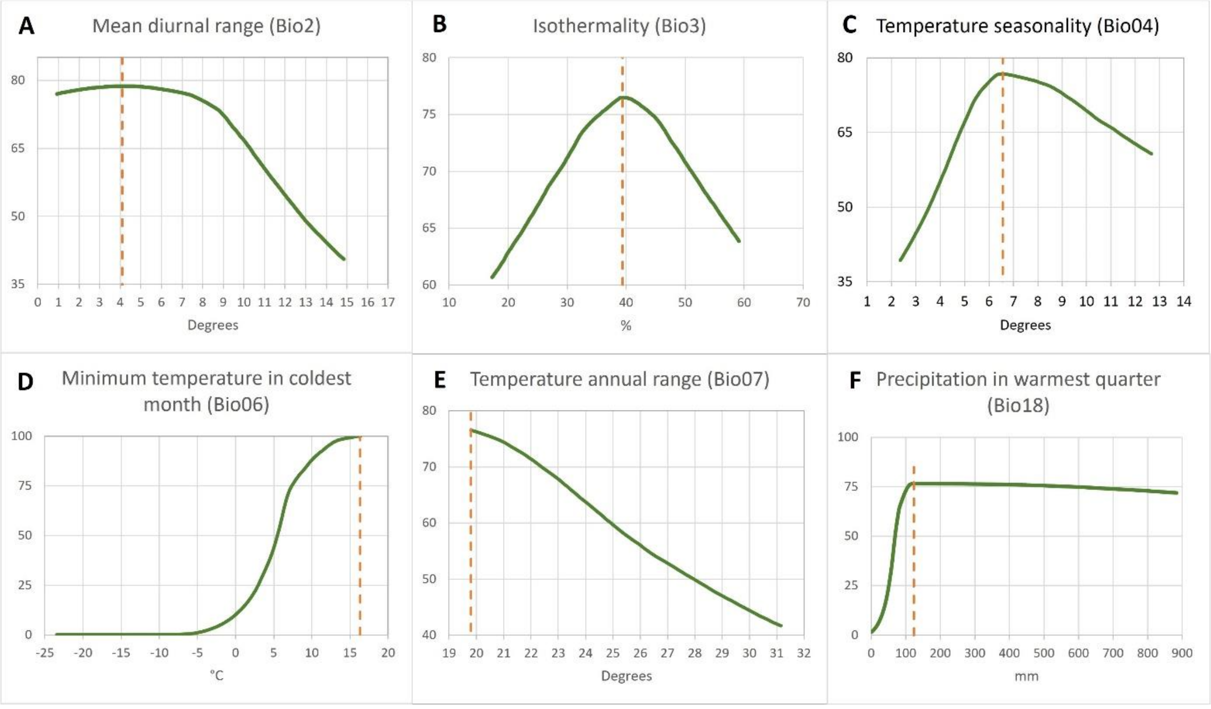

**Figure 2.** Response curves of the environmental variables selected for prediction of *S. woodiana* distribution under the recent climate scenario. Each curve (green line) shows how the logistic prediction changes as each environmental variable is varied. The orange dashed line crosses the maximum value of the variable.

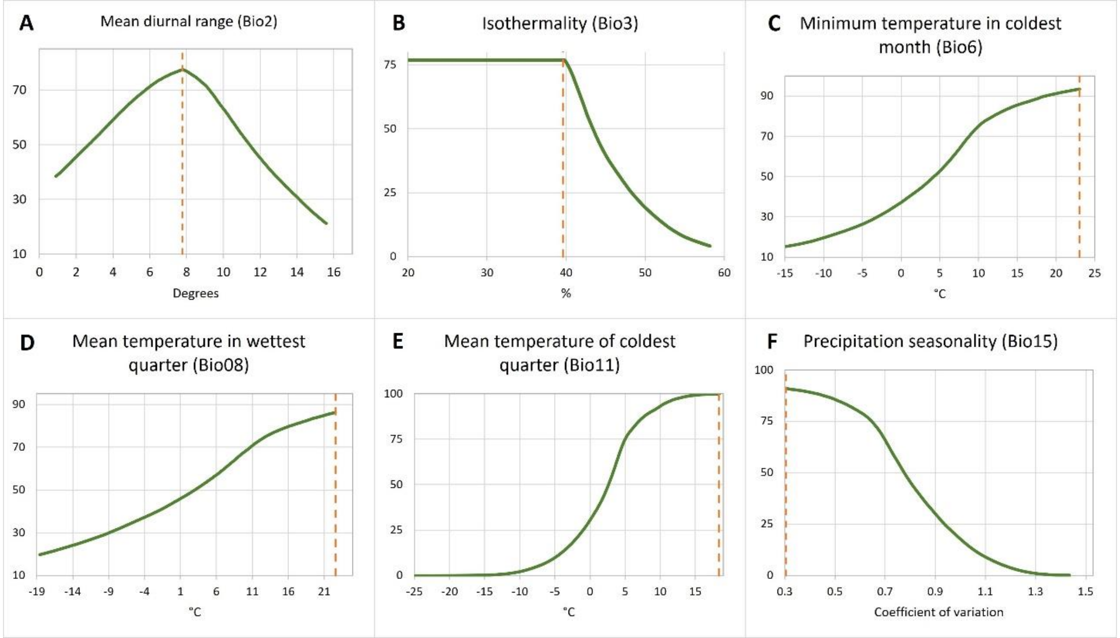

**Figure 3.** Response curves of the environmental variables selected for prediction of *S. woodiana* distribution under the RCP 4.5 scenario. Each curve (green line) shows how the logistic prediction changes as each environmental variable is varied. The orange dashed line crosses the maximum value of the variable.

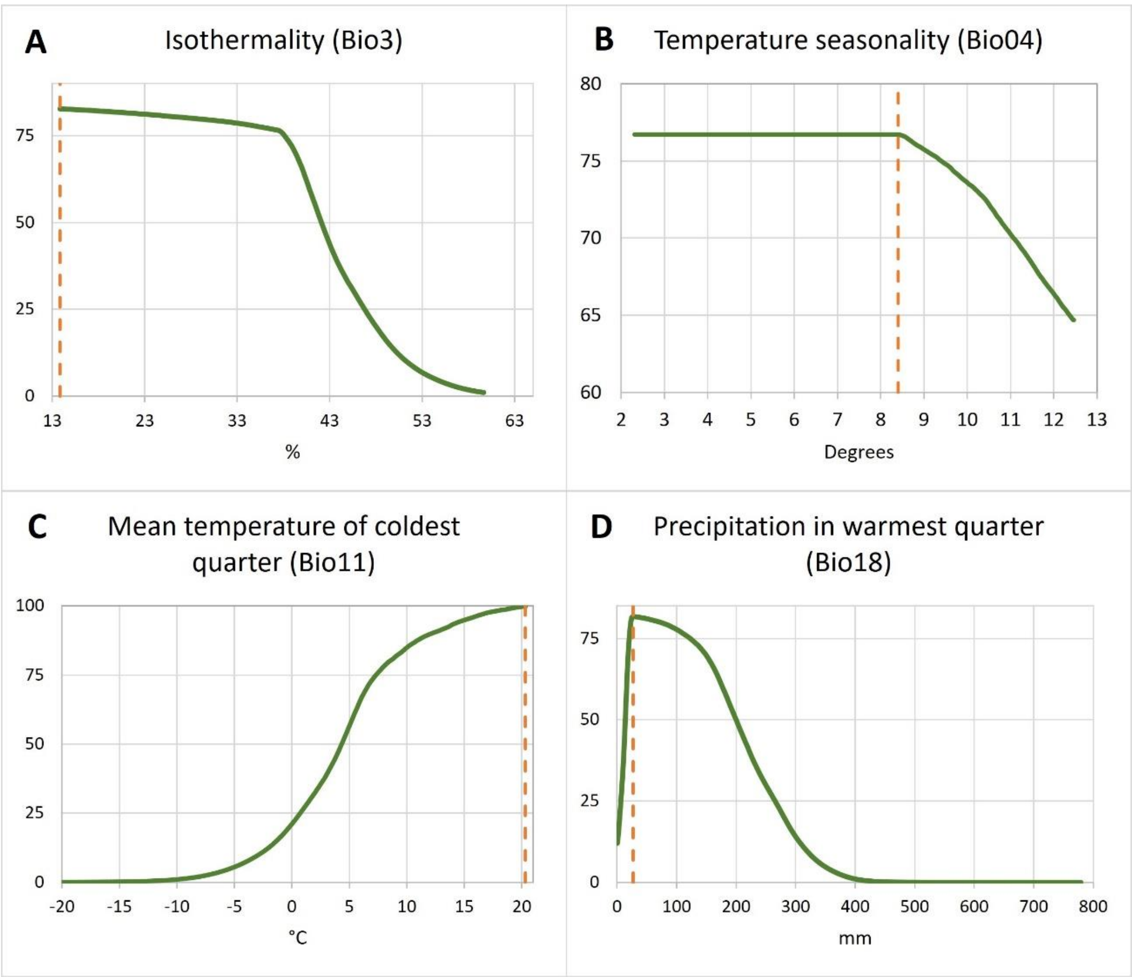

**Figure 4.** Response curves of the environmental variables selected for prediction of *S. woodiana* distribution under the RCP 8.5 scenario. Each curve (green line) shows how the logistic prediction changes as each environmental variable is varied. The orange dashed line crosses the maximum value of the variable.

Isothermality (Bio3) is the only variable that presents in all models (Figures 2B, 3B, and 4A). The contribution of the predictor grows from 1.4% in recent model to 10.5% in RCP 8.5 but stays on low levels.

### *Predictions of presence*

The map of the potential invasion range of *S. woodiana* in Europe under the recent climatic conditions was drawn using MP and 10P thresholds (Figure 5). The MP threshold defines as suitable the wide range from the southern part of Finland in the north to the southern edge of the Iberian Peninsula in the south, and from the British Isles in the west to the Volga Delta in the east. All species records, that used in the model, are fall within the predicted distribution. Moreover, large areas with no records are also predicted as suitable for the species presence, i.e., the British Isles, the Iberia, the basins of the Dnieper, Don, and Kuban rivers, the rivers of the Finnish Gulf Basin, and waterbodies of Southern Scandinavia. The 10P threshold depicts a much narrower range, excluding areas with 10% of the most extreme environmental conditions. However, even in this case most of the British Isles' territory, coastal areas of the Iberian Peninsula and the Black Sea, and the Kuban River basin are considered to be regions with a high probability of presence. At the same time, there are many records of the species in the eastern part of the invasive range, which are outside the predicted distribution. This finding illustrates that invasive species have successfully adapted to environmental conditions at the edge of their potential niche.

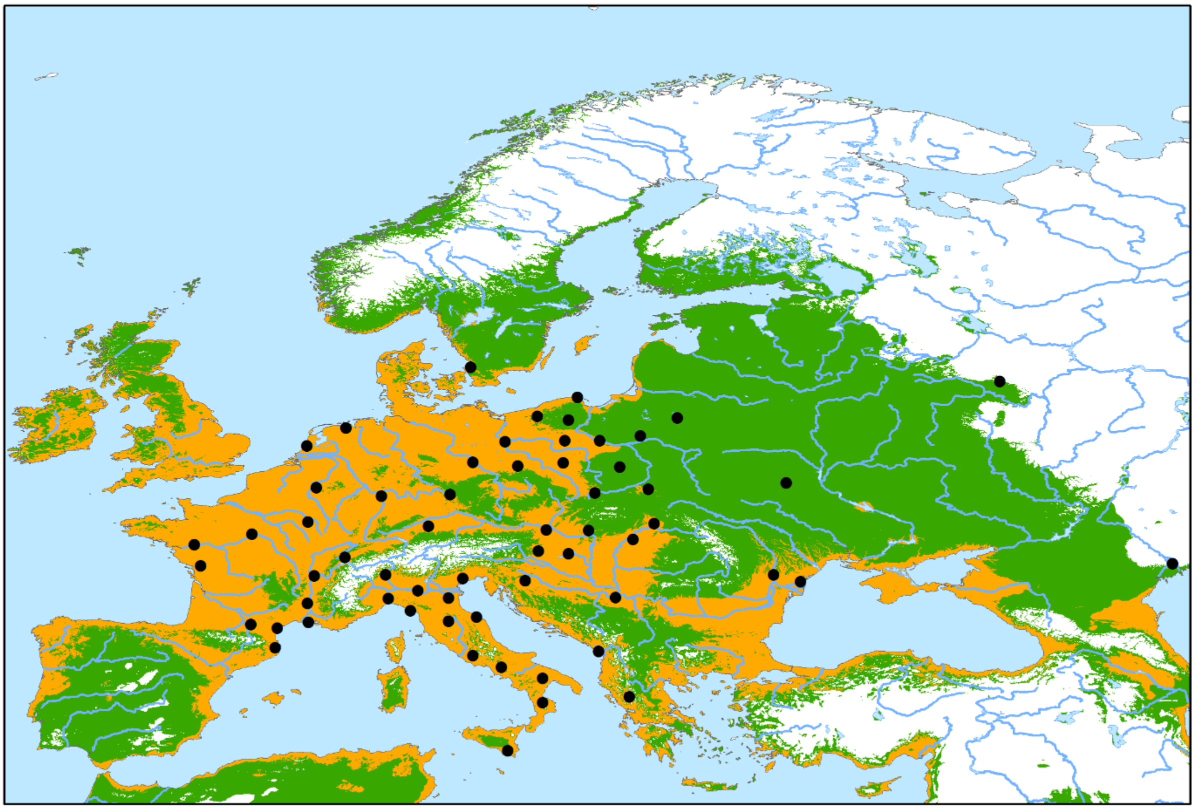

**Figure 5.** Map of potential invasion range of *S. woodiana* in Europe under the recent climate conditions: green filling indicates areas defined as suitable using minimum presence (MP) threshold; orange filling indicates areas defined as suitable using 10th percentile presence (10P) threshold. Black dots indicate species record used for SDM.

Maps of prediction of *S. woodiana* presence in Europe under future climate change scenarios show a controversial picture of the forecasted species distribution. The area of presence of the species will be contracted according to the MP threshold of the RCP 4.5 model (Figure 6) compared with the recent climatic model. The eastern boundary of the range will be shifted westwards to the Dnieper and Daugava basins, and only scattered areas of the Iberian Peninsula will be depicted as suitable. At the same time, the presence range under the 10P threshold of the RCP 4.5 model (Figure 6) will be extended eastwards from that shown in the recent model.

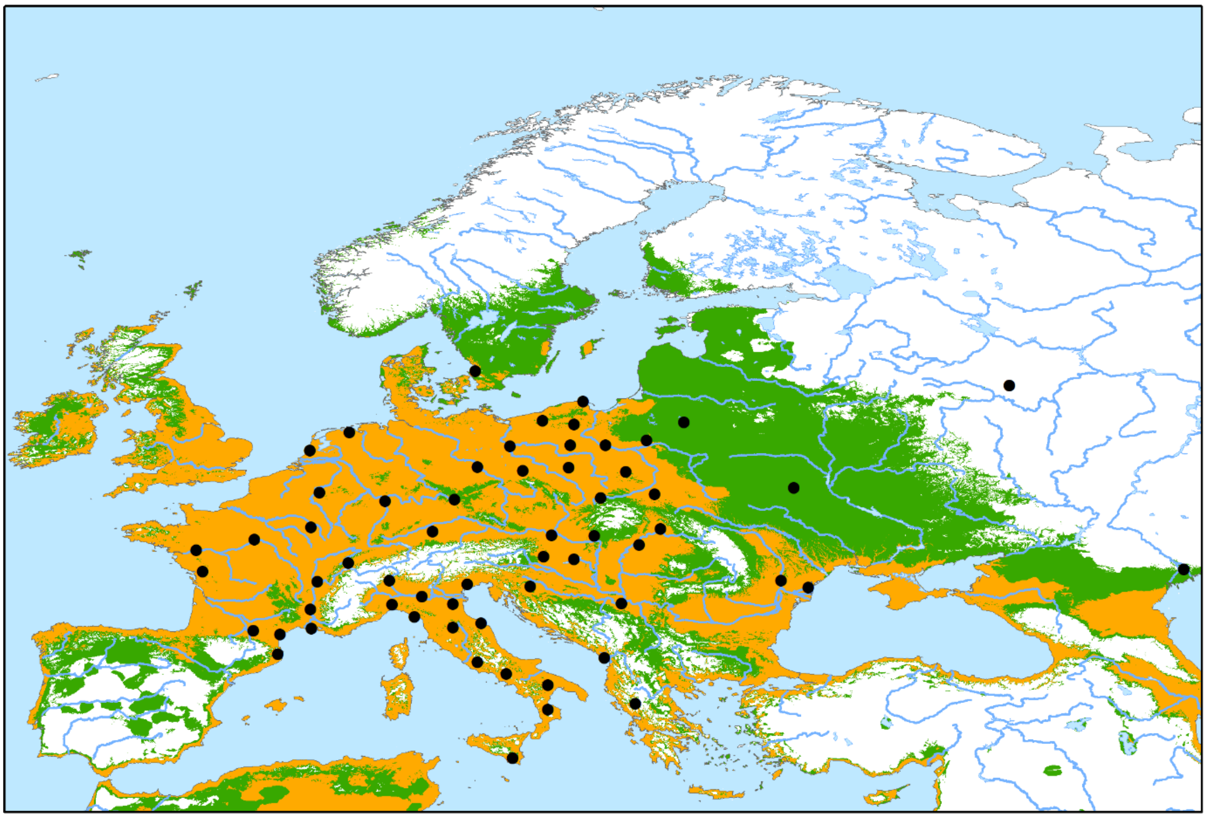

**Figure 6.** Map of potential invasion range of *S. woodiana* in Europe under the RCP 4.5 climate change scenario at 2080-2100: green filling indicates areas defined as suitable using minimum presence (MP) threshold; orange filling indicates areas defined as suitable using 10th percentile presence (10P) threshold. Black dots indicate species record used for SDM.

The most significant changes that predicted by the RCP 8.5 model (Figure 7) relate to the south-eastern part of the invasive range. The probability of presence in this area is higher than both thresholds and its boundary will be shifted northwards at least to the Lower Don and Volga (10P threshold) or up to the Middle Volga including almost the entire Don River basin (MP threshold).

All scenarios of MaxEnt prediction warn that among the areas not yet colonized, the Azov Lowland and the south of the British Isles share the most suitable climatic conditions for successful invasion. Notably, the probability of presence in Southern Scandinavia will be below 10P threshold in the RCP 8.5 model, while the remote Arctic island of Kolguev in the Barents Sea is predicted to be suitable for invasion.

## Discussion

### *Effect of climatic variables on the modelled distribution*

Environmental niche models of *S. woodiana* predict that temperature variables have the greatest contribution to the shaping of the potential distribution range currently and in the future. In particular, we found that winter temperatures play the most important role. This is not surprising considering subtropical origin of the species and previous results of the species SDM (Mehler et al., 2024). Probability of presence in all our models decreases with decreasing temperature, whereas examples of successful adaptation to colder environments in the invasion range (Domagała et al., 2007; Kondakov et al., 2020) and even overwintering in ice-covered waterbodies (Urbańska et al., 2021) demonstrate that the Chinese pond mussel is quite resistant to the temperature decrease. The probability of presence in the recent climate model became non-random at the value of about 5 °C of the minimum temperature of the coldest month. It is likely that this temperature threshold is not related to the survival as such, but to the reproductive success of the species. It has been shown that the survival rate of glochidia of *S. woodiana* is the highest at the 5 °C and significantly higher than that of the native *Unio crassus* Philipsson, 1788 (Benedict & Geist, 2021). Together with the ability to year-round reproduction (Labecka & Domagala, 2018), it gives a significant reproductive advantage to the Chinese pond mussel. Additionally, this temperature threshold is a robust indicator of the length of the growing season, and the productivity of aquatic ecosystems is directly dependent on water temperature (Downing, 2014). The Chinese pond mussel prefers nutrient-rich water (Kraszewski & Zdanowski, 2007), and a lack of food resources may limit the species survival in colder environments. Such environmental conditions are currently at the edge of the fundamental niche of *S. woodiana*, and adaptation to them may be more costly than that for native species (Lurman 2014).

Precipitation influences prediction of occurrence in lesser degree than temperature in our models. However, in the future climate under the extreme scenario, the precipitation in the warmest quarter is the variable with the second highest contribution to the model. The same predictor has a relatively high contribution in the recent climate model. Both scenarios demonstrate that lower values of variables, associated with precipitation deficits and possibly droughts, are less favourable conditions for the species than higher values of precipitation. Examples of massive die-offs caused by temperature extremes or long-term droughts are not rare under current climatic conditions (Bódis et al., 2014; Cilenti et al., 2019; White et al., 2015), and it is predicted that future climate change will multiply the duration and frequency of such extreme events, especially in temperate and Mediterranean areas (Schneider et al., 2013; van Vliet et al., 2013).

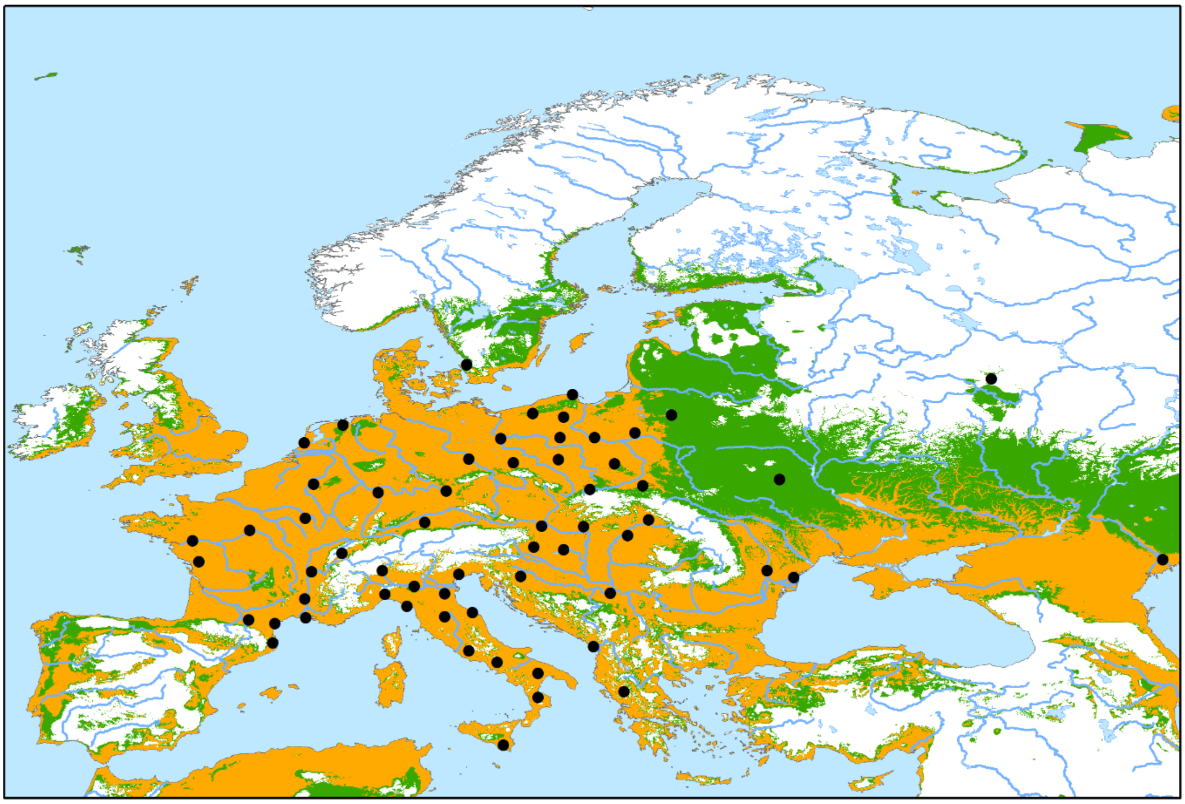

**Figure 7.** Map of potential invasion range of *S. woodiana* in Europe under the RCP 8.5 climate change scenario at 2080-2100: green filling indicates areas defined as suitable using minimum presence (MP) threshold; orange filling indicates areas defined as suitable using 10th percentile presence (10P) threshold. Black dots indicate species record used for SDM.

### *Recent modelled distribution*

The modelled recent distribution indicate that climatically suitable areas occupy a broad range of waterbodies across Europe. Compared to the recently published *S. woodiana* SDM, our model predicts a much wider distribution of the species (Mehler et al., 2024). The differences in results are likely to be due to different sets of the species records used in the model and different approaches to model tuning and evaluation.

The distribution of minimally suitable environmental conditions, where the probability of presence of *S. woodiana* is higher than the most tolerant threshold (MP), includes all known records in Europe and, in addition, large uninvaded areas in Eastern Europe and Southern Fennoscandia. The Chinese pond mussel is a species with the high tolerance to environmental conditions, owing to its ability to inhabit lotic and lentic habitats with a variety of substrates (Douda et al., 2024 and references herein). In this context, the predicted range appears feasible. Application of the less tolerant threshold reduces the predicted distribution of the species to Central, Western, and Southern Europe, and to the coastal areas of the Black Sea region. This threshold excludes habitats with the most extreme conditions. Thus, the depicted areas provide optimal climate for *S. woodiana* distribution. Most of the optimal range coincides with known records of the species, however, the British Isles and the Azov-Kuban Lowland are not invaded. The vulnerability of the Lower Kuban and Don river basins to the Chinese pond mussel invasion has been noted previously (Kondakov et al., 2020), and our SDM confirms this concern.

The differences between the predicted distributions under different thresholds indicate areas where species can invade by adapting to new environments. There are several records of *S. woodiana* (Figures 1, 6) from this area and even from the edge of the suitable range. Using heated waterbodies as refugia in the colder environment, the species can gradually adopt thanks to the temperature gradient between warm and cold waters (Konečný et al., 2018). At the same time, the Chinese pond mussel from the Lower Volga River, located at the edge of the modelled distribution, was able to establish a viable (naturally reproducing) population in the absence of thermal refugia (Kondakov et al., 2020). We suppose that the founder of this population was already adapted to the non-native environment and was transferred from analogues habitat somewhere in Kazakhstan or Southern Siberia (Kondakov et al., 2020).

### *Future modelled distribution*

Under both scenarios of the future climate change, there was a contraction of minimally suitable areas and an expansion of areas with optimal environmental conditions. The latter trend is consistent with previous findings that alien species benefit from climate warming, especially in moderate and high latitudes (Rahel & Olden, 2008). The explanation for the future decline of minimally suitable areas is not so straightforward. Considering winter temperatures as the factor that most controls the distribution of the species, it is logical to assume that the northeastern boundary of the invasive range of *S. woodiana* will continue to shift as winter temperature increase. However, our models predict the opposite. The decrease in precipitation in the future is reported as a significant threat to terrestrial and aquatic ecosystems as discussed above and has been suggested as a cause for the future decline of *S. woodiana* (Mehler et al., 2024). The distribution model under the most extreme scenarios reveals that the probability of presence in areas affected by droughts is very low (Figure 5D). However, this fact is also a poor explanation for the future contraction of the potential species range in the east. An increase in drought events is predicted for all of Europe, but especially for the south (van Vliet et al., 2013), which could explain the decrease of suitable environments in Iberia in the future scenarios (Figures 6, 7).

The given sets of environmental variables do not allow us to explain the decline of minimally suitable habitats in Northern and Northeastern Europe in the future. The answer may lie in the interactions between environmental variables and the species' response to them, which will require additional research efforts in the framework of a future study.

### *Models' shortcomings and limitations*

The quality assessment criteria for SDMs used in this study revealed that the models obtained have good predictive power and transferability, but as the models are addressed to range shifting species, they have shortcomings and limitations.

We have done our best to include in SDMs all the range of habitats currently invaded by the Chinese pond mussel in Europe. Our initial species records dataset is smaller than that in analogous research (Mehler et al., 2024), but includes records from a wider geographical extent and significantly expands the range of environmental conditions used in SDM. Rarefaction of the initial dataset reduces the number of records mainly in Central and Southern Europe, but records from the Central Pyrenees were missing in the initial one. Potentially, these records could improve our SDM locally and specify the predicted presence in the particular region.

Our SDM is based on bioclimatic variables that are widely used in this kind of studies (Barbet-Massin et al., 2018; Bazzato et al., 2021; Fourcade et al., 2018; Mehler et al., 2024). However, other-than-climate predictors, like land use, vegetation cover, distance to the nearest waterbody, etc., are also influence species distribution and can strengthen the predictive power of SDMs (Mehler et al., 2024; Thuiller et al., 2004). We decided not to include such type of variables for several reasons. We assume that current association of *S. woodiana* distribution with anthropogenically affected environments (Sîrbu & Benedek, 2018) does not reflect its fundamental niche, but linked with human-mediated invasion. The dynamic of this predictor at the local scale under the future climate changes is the subject of special research efforts (Arfasa et al., 2023; Lukas et al., 2023; Zhang et al., 2022). The dispersal of the Chinese pond mussel with fish stocks, independent of direct connections between watercourses, makes useless predictors related to river network density and watershed divides. Potentially, the distribution of fish farms, fishponds, and heated waterbodies could serve as variables that significantly contribute to the *S. woodiana* SDM.

Projecting of the current species distributions in space and time is a major challenge for SDM (Franklin, 2023: see the review in the section 2.5; Wenger & Olden, 2012). We have used different sets of environmental variables for both future SDMs, but predictions of distribution are based on current relationships between species records and environments, and do not take into account the potential evolution of these relationships through time. One of the techniques to improve the extrapolation ability of environmental niche models is to generate an ensemble of predictions using several modelling methods (Araujo & New, 2007).

The above criticism does not significantly affect the predictive power of SDMs presented here, and we suppose that these models could be used as risk maps for assessing of further invasions of *S. woodiana*. However, the *Sinanodonta* species complex comprises several invasive lineages that are distributed globally. Forecasting of multi-species invasions on a global scale, using improved modelling techniques, is of great importance and should attract special research efforts.

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