

Current distribution and modeling of potential distribution of *Elodea nuttallii* (Planch.) H. St. John at the territory of Ukraine and Europe

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Abstract

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Elodea nuttallii (Planch.) H. St. John – an invasive species that actively expands the boundaries of its secondary range. This work presents the current and predicted future distribution of *E. nuttallii* in Europe. The spread of the species is observed in northern areas with a mild oceanic climate (with mild winters and cool, rainy summers) formed by Atlantic cyclones. *E. nuttallii* occurs in aquatic biotopes throughout the temperate climatic zone and partially occurs in the subtropical. It was established that the most important factors in determining the possibility of a plant's spread are the amount of precipitation in the driest month, the minimum temperature of the coldest month, and altitude above the sea level. According to the data collected, the species is at its ecological optimum in most of Europe. Most of the changes expected in the next 100 years will take place in the next 30–40 years.

Keywords

Elodea nuttallii, macrophytes, secondary range

Introduction

According to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), invasive alien species are the fifth main cause of biodiversity loss (IPBES, 2023) and have become global in our time. Over the last century, human activities have contributed to the increase in invasions, both through the creation of new vectors of introduction and through anthropogenic alteration of the environment. Current invasions are the result of various factors, the main one of which are the climate of the invaded region, the type of environmental disturbance and the non-competitiveness of local species (LONSDALE, 1999).

Water networks are an important pathway for the

introduction and spread of invasive species due to their azonality, a certain homogeneity of ecological conditions. Modern hydro-ecosystems are also characterised by a high degree of transformation, heterogeneity and relative continuity due to the large number of artificial channels linking river basins. The construction of large reservoirs has altered the hydrology of many lotic hydroecosystems on a global scale. The construction of dams on most major rivers has fragmented water flows and significantly increased the number of stagnant freshwater habitats. Reservoirs have acted as a springboard for the spread of invasive species: on the one hand, they have created many new habitats free of native species, and on the other, they have created limnetic biotopes for passively distributed species that

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cannot survive in strong unidirectional flow (HAVEL et al., 2005). For example, Ukraine's largest river – the Dnipro – is now represented by an almost continuous cascade of six large reservoirs, and the majority of freshwater invasions have occurred here (ZHUKINSKIY et al., 2007). Many small and medium-sized rivers of Ukraine are the main canals of reclamation systems (e.g. the upper reaches of the Pripjat River), natural reservoirs and floodplains are transformed in the course of the economic activity, causing the destruction or reconstruction of natural ecosystems. All these factors contribute to the introduction of a new, alien component into the aboriginal hydroecosystem (MOORHOUSE and MACDONALD, 2015; DUDGEON, 2020; STRAYER, 2010; TILMAN, 2004).

A common component of shallow waters are vascular macrophytes – “aquatic photosynthetic organisms large enough to be seen with the naked eye” (CHAMBERS et al., 2007; MURPHY et al., 2019). Macrophytes are important components of freshwater ecosystems and play a major role in structuring aquatic communities (DAVIS, 2009). The invasion of alien macrophytes has the capacity to radically alter the structure and functions of recipient aquatic ecosystems, which can have a significant impact on native hydrobionts (ALAHUHTA et al., 2011; FLEMING and DIBBLE, 2015; LOBATO DE MAGALHÃES et al., 2023; TASKER et al., 2022; DAVIS, 2009). Despite the significant heterogeneity in the reaction of native macrophytes to alien macrophytes, a strong relationship between alien macrophyte invasion and the degradation of native phytocoenoses was revealed (TASKER et al., 2022).

Elodea nuttallii (Planch.) H. St. John is one of the invasive macrophyte species that are actively expanding the boundaries of their secondary range in Europe. It is now of great concern in some European countries, as it is currently spreading very rapidly, especially in anthropogenically transformed or artificial biotopes (PROKOPIUK and ZUB, 2019; ZEHNSDORF et al., 2015). In Europe, the species is considered to have a high ecological impact in invaded areas and is therefore included in the list of invasive alien species of EU concern under 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 (CIR, 2017; EUROPEAN PARLIAMENT and COUNCIL OF THE EUROPEAN UNION, 2014).

E. nuttallii is native to the southeastern part of Canada and the northern states of the USA (from the states of Maine and New York to the states of Minnesota and Oregon, south to the city of Washington, the states of Carolina and Nebraska) (CASPER and KRAUSCH, 1981; DUENAS, 2022). In North America, the species is restricted to low calcium waters, and may occasionally occur in brackish waters (often with *Elodea canadensis* Michx.), but does not tolerate currents as well as *E. canadensis*. Vegetative reproduction is the main method of propagation – fragmentation and division of stems, formation of winter buds on the tops of stems (KUNII, 1984; PRESTON and CROFT, 1997). Entering to a new environment, buds are formed very quickly, as the propagules are in the sediment and grow rapidly.

The secondary distribution ranges of the species covers Europe and Asia (Japan). The first records of *E. nuttallii* in Europe (in Great Britain) dated to 1914, when it was identified as *Hydrilla verticillata* (Lf.) Royle. The species spread: in Belgium – in 1939, in the Netherlands – in 1941 and in Germany – in 1953, in Denmark – in 1974, in Ireland – in 1984, in Sweden – in 1991 and in Norway – in 2006 (JOSEFSSON, 2011). In Europe almost all individuals are female, only in Germany a few sites with male plants are known (PRESTON and CROFT, 1997). Most of the finds of the species in Europe dated to the 1960s and 1970s. In Ukraine, the species was registered for the first time in 2004 in the bay of the Kaniv Reservoir, 100 km downstream from the city of Kyiv (CHORNA et al., 2006).

The wide distribution of *E. nuttallii* in Europe has also been facilitated by a high degree of geoclimatic similarity between the source and host ecozones, which is likely to have had a significant impact on the survival and subsequent wide distribution of the species (LOBATO DE MAGALHÃES et al., 2023). High phenotypic plasticity – the ability to adapt to any stressful environmental situations (presence/absence of current, summer/winter drying of shallow water, etc.) contributed to the active invasion of the species, which provided the species with a competitive advantage over native species (RICHARDS et al., 2006). Summarizing, we have noted that mechanisms of invasion success *E. nuttallii*: Enemy release/EICA, novel weapons/allelopathy, phenotypic plasticity, fluctuating resources/opportunity window (FLEMING and DIBBLE, 2015).

Taking into account the ecological and economic consequences of *E. nuttallii* invasions, the main task of this work is to present the current and future (predicted) distribution of this species in the territory of Ukraine, in particular, and Europe, in general. In order to prevent species from invading new territories, it is necessary to create distribution maps using modern GIS technologies. There have been examples where the risk of invasive species establishment has been successfully determined a priori using climate modeling. Similar ecological studies and predictive models for *E. nuttallii* are an indispensable prerequisite for the future management of this invasive species. Studies on modelling the distribution of this species have already been carried out, but only for the European Union (STEEN et al., 2019), for the territory of Ukraine distribution predictions have never been carried out. It is interesting to compare the data and their distribution in Eastern Europe. We have not only expanded the study area at the expense of Ukraine, but also supplemented the analysis with data from other European countries and updated the points of detection of *E. nuttallii* over the last 5 years, which determines the novelty of our analysis.

Materials and methods

The object of research was an alien invasive species in Europe *Elodea nuttallii* (Planch.) H. St. John., *Hydrocharitaceae* (synonyms: *Anacharis nuttallii* Planch.; *Philotria minor* Small; *Ph. nuttallii* (Planch.) Rydb.; *E. minor*

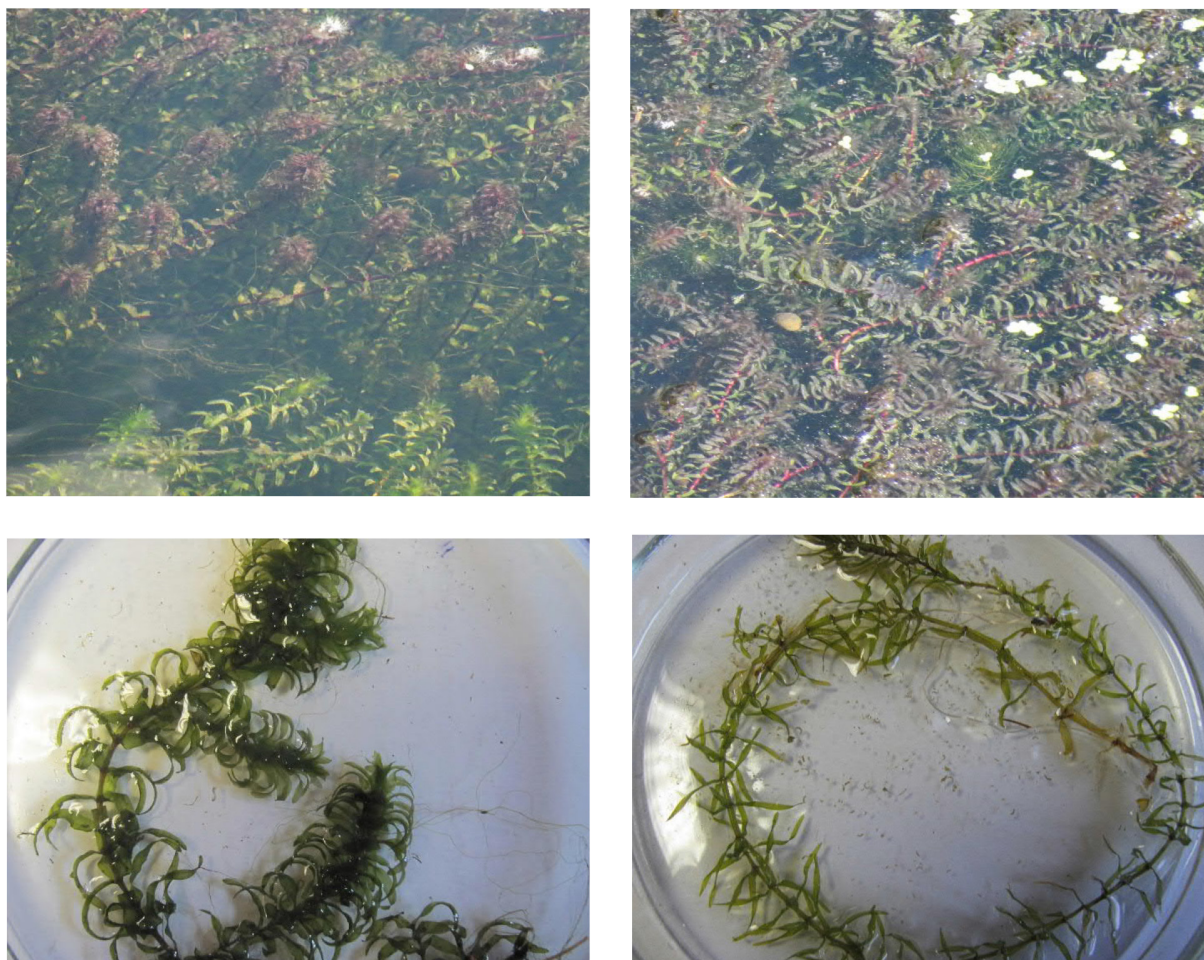


Fig. 1. General view of the *Elodea nuttallii* communities (top row) and its ecomorphs (lentic biotope – on the left, lotic – on the right).

(Engelm.) Farw; *Udora canadensis* var. minor Engelm.; *Philotria occidentalis* House; *E. columbiana* St. John (DUENAS, 2022) (Fig. 1) perennial submerged, rooted or free-floating, a densely leafy, intensively branching plant.

The modelling of the species distribution was performed using the maximum entropy approach (PHILLIPS et al., 2006) the software package Maxent 3.4.4 in the Java Runtime Environment (*Maxent software*, 2023; PHILLIPS, 2017). For a representative presentation of the spatial distribution of the species within the climatic conditions and altitude factor within Europe, a set of observations of *E. nuttallii* was downloaded from the Global Biodiversity Information Facility database (GBIF, 2023), literature (ANDELKOVIC et al., 2016; BUBÍKOVÁ et al., 2016; KIRÁLY et al., 2008; KAMINSKI, 2010) and own observations were also used (PROKOPUK and ZUB, 2020; PROKOPUK and ZUB, 2019). A total of 85,746 sightings of *E. nuttallii* were used for the selected extent of Europe (Fig. 2).

Due to the repetition and close proximity of a number of observations to each other (typical of observations in England, the Netherlands and Germany), 23,818 records were included in the final analysis. The probability of the finding of the species in a certain area was estimated using the ROC (receiver operating characteristic) curve and determining the AUC (area under the curve) values (PHILLIPS et al., 2006).

Cross-validation was used to determine the uncertainties of the predictive properties of the model and the factors included in it (the sample was divided into four groups without repetition of observations and without quadratic deviation between the estimated initial values of all runs of the mode). Before adding factors to the model, Pearson correlation coefficients were calculated. When moderate levels of closeness of relationships between factors were found ($r > 0.70$), they were removed except for the most generalising and/or practical for further use in modelling.

To predict the distribution of the species, we used climate data from the WorldClim resource (*Global climate and weather data*, 2022). Using correlation analysis for modelling, the following bioclimatic indicators were taken into account: biov_1 – average annual temperature (°C), biov_2 – difference between the average temperature of the warmest and coldest months, biov_5 – maximum temperature of the warmest month, biov_6 – minimum temperature of the coldest month, biov_12 – average annual amount of precipitation (mm), biov_13 – amount of precipitation in the wettest month, biov_14 – amount of precipitation in the driest month, biov_15 – seasonal variability of rainfall (coefficient of variation), and also included in the modelling the terrain (digital terrain model (dem)). In order to predict the impact of climate change on the probable

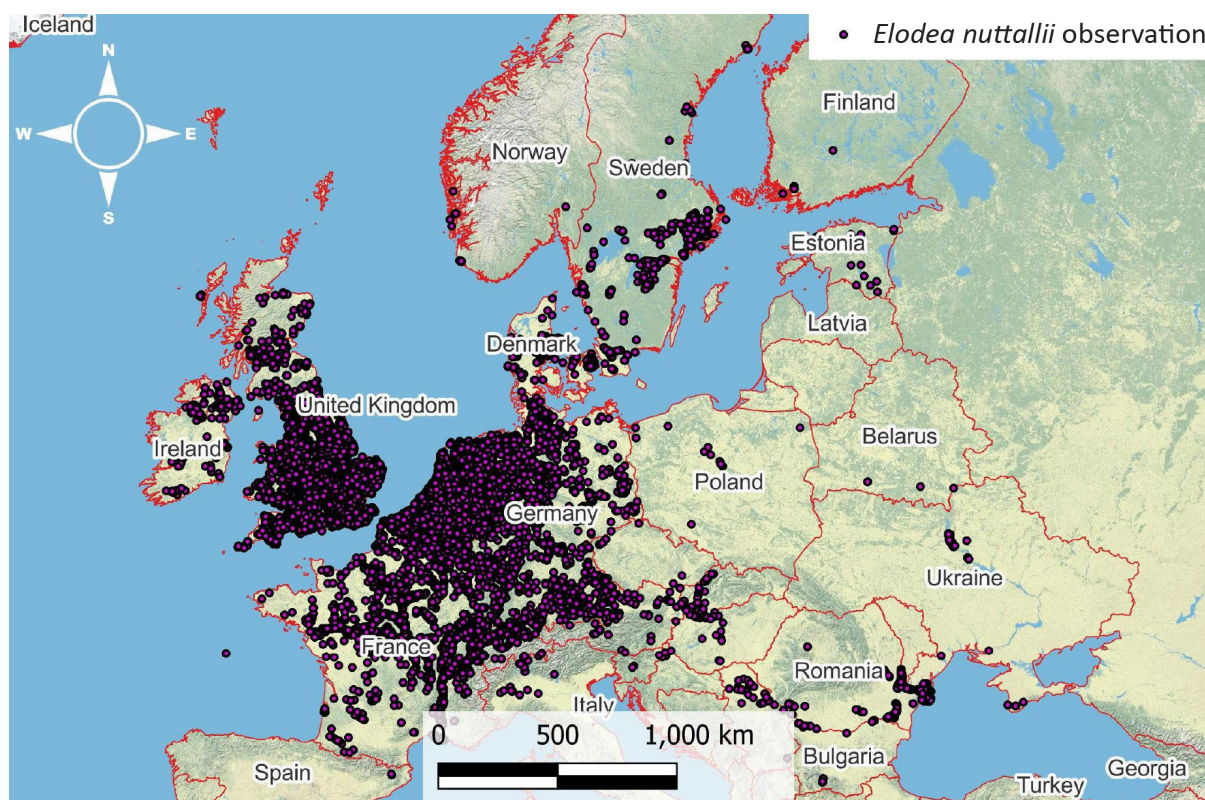


Fig. 2. Spatial distribution of records of *Elodea nuttallii* observations included in the GBIF database, literature and own data (Ukraine).

future distribution of the species in the period 2041–2060 and 2081–2100, the results of climate models were used, depending on the most optimistic and the most pessimistic scenarios of the socio-economic development of society in terms of greenhouse gas emissions and, consequently, the nature of climate change. In the most optimistic version of the development of society, the temperature and other indicators will change according to the ssp126 scenario, in the most negative scenario – ssp585 (*Global climate and weather data*, 2022). For this purpose, averaged data (as an arithmetic mean) from three updated cyclic climate models with 30-second pixel spatial resolution were used: HadGEM3-GC31-LL, IPSL-CM6A-LR and MPI-ESM1-2-HR (*Global climate and weather data*, 2022). These climate models are frequently updated and modified by the scientific teams from European institutes that developed them. They are continually updated to incorporate the latest data, including historical climate observations and forecasts for the future based on various socio-economic development scenarios. These comprehensive and up-to-date models cover the entire surface of the Earth. As a result, scientists widely utilize this data in their research to model various systems of the planet in the future (RIDLEY et al., 2018; GUTJAHR et al., 2019; BOUCHER et al., 2020).

With a significant number of species detection points included in the training sample (23,818 pcs.) and their division into training and test (ratio 75%:25%) during the cross-validation of the model (four runs with random formation of the training and test sample), the criteria evaluated have extremely low variability (less than 1% in rel-

ative values) (Fig. 3 and 4). The areas of uncertainty are hardly visible on the graphs presented (Fig. 3 and 4).

The analysis of the importance of the factors included in the model, optimised by the maximum entropy approach, was carried out taking into account their contribution in the learning process (Percentage contribution) for the parameterisation of the equations and by the method of evaluating the probability of finding a species by changing the values of the indicators of a single factor based on the base values of other indicators (Permutation importance).

Results

The averaged initial parameters of the obtained indicators of the models after four runs for *E. nuttallii* are presented in the Table. 1.

The Maxent model for *E. nuttallii* is characterised by a high classification efficiency in explaining the spatial distribution of this species within the secondary range of Europe ($AUC = 0.906 \pm 0.002$). The collected dataset on the localisation of *E. nuttallii* distribution sites has a high homogeneity, due to the concentration of most observations in the countries of Western Europe, and only isolated observations in Central, Eastern and Northern Europe, as well as the absence of data for Southern Europe (Portugal, Spain, Greece, Turkey). With a significant number of species detection points included in the training sample (23,818 pcs.) and their division into training and test (ratio

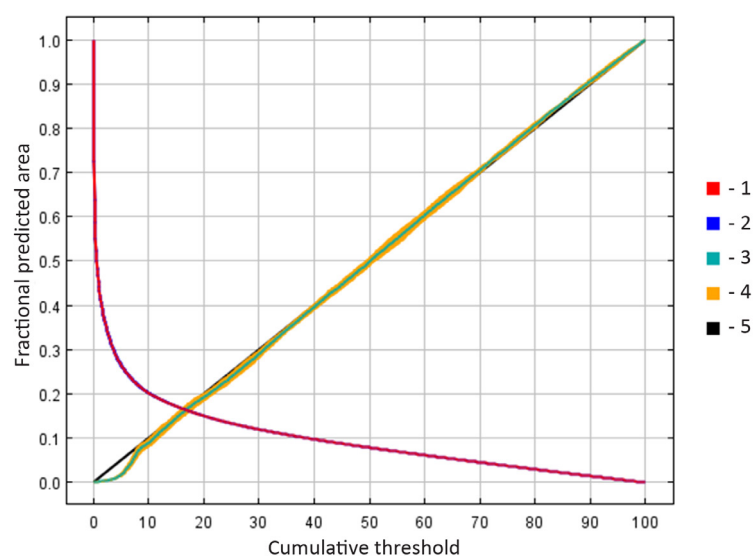


Fig. 3. Dependence of the level of omission and area under the curve (AUC) on the cumulative threshold for test observations of *E. nuttallii*, where: 1 is the arithmetic average of predicted area; 2 is the prediction interval ($\pm$ standard deviation) of predicted area; 3 is the arithmetic average of omission on test data; 4 is the prediction interval ($\pm$ standard deviation) of omission; and 5 is the predicted omission.

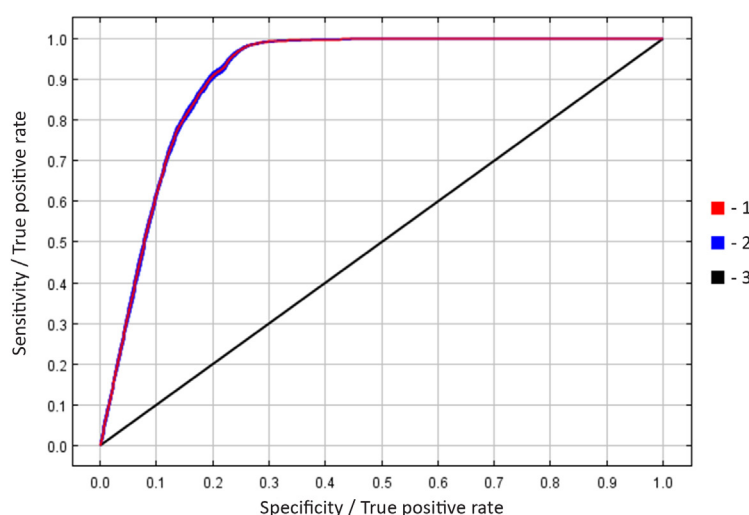


Fig. 4. Receiver operating characteristic (ROC) curve for test observations *E. nuttallii*, averaged over the replicate runs during the cross-validation of the model, where 1 is the arithmetic average of ROC (AUC = 0.906); 2 is the prediction interval ($\pm$ standard deviation) of ROC; and 3 is the random prediction (AUC = 0.5). AUC – area under the curve.

75%:25%) during the cross-validation of the model (four runs with random formation of the training and test samples), the criteria evaluated have an extremely low variability (less than 1% in relative values) (Fig. 3 and 4). The areas of uncertainty are almost invisible visually on the graphs presented (Fig. 3 and 4).

The analysis of the importance of the factors included in the model, optimised by the maximum entropy approach, was carried out taking into account their contribution in the learning process (Percentage contribution) for the parameterisation of the equations and by the method of evaluating the probability of finding a species by changing

Table 1. Initial parameters of the models for the studied species using the maximum entropy approach

Species	Regularized training gain	Unregularized training gain	Iterations	Training AUC	#Test samples	Test gain	Test AUC	AUC SD
<i>Elodea nuttallii</i>	1.33	1.40	290	0.907	5954.5	1.40	0.906	0.002

AUC – area under the curve; SD – standard deviation.

the values of the indicators of a single factor based on the base values of other indicators (Permutation importance). The ranking of the factors involved in the modelling, in descending order of importance for *E. nuttallii* according to the two criteria just mentioned, turned out to be as follows: the amount of precipitation in the driest month (biov_14) – 52.5% and 8.8%, the minimum temperature of the coldest month (biov_6) – 34.7% and 69.9%, height above sea level (dem) – 7.0% and 9.7%, maximum temperature of the warmest month (biov_5) – 2.0% and 7.2%, for percentage contribution and permutation importance, respectively. The importance values of other included bioclimatic indicators were at the level of 0.0–2.6.

The predicted probabilities of finding the species as a function of the values of the independent variables included in the models (Fig. 5) allow us to characterise the optimum and critical values of the factors of existence (in fact the ecological niche) used by *E. nuttallii*.

The amount of precipitation in the driest month – biov_14 – is considered to be the most important factor in the potential spread of the plant (determines the conditions of the biotope – the degree of its watering or the probability of shallowing) and has an ecological optimum at values greater than 40 mm per month (Fig. 5A – biov_14). At lower values, the theoretical probability of the species spreading drops sharply from 0.8 to 0.0.

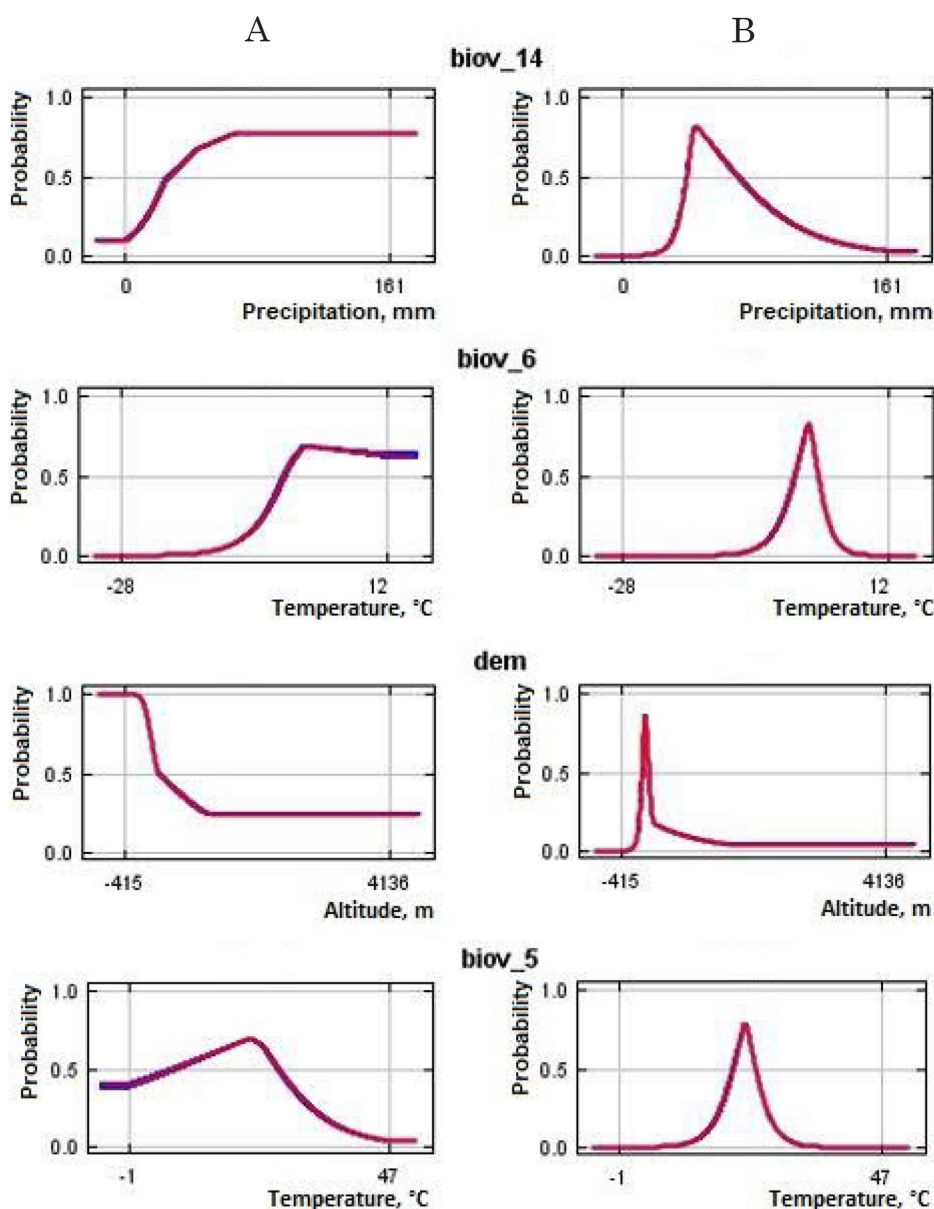


Fig. 5. The predictive probability (complementary log-log function) of the existence of the species *Elodea nuttallii* depending on the values of the "most important" features: A – when all factors are included in the model as independent variables, B – if only one significant factor is involved in the algorithm (biov_14 – amount of precipitation in the driest month, biov_6 – minimum temperature of the coldest month, dem – the modeling the terrain (digital terrain model, biov_5 – maximum temperature of the warmest month)).

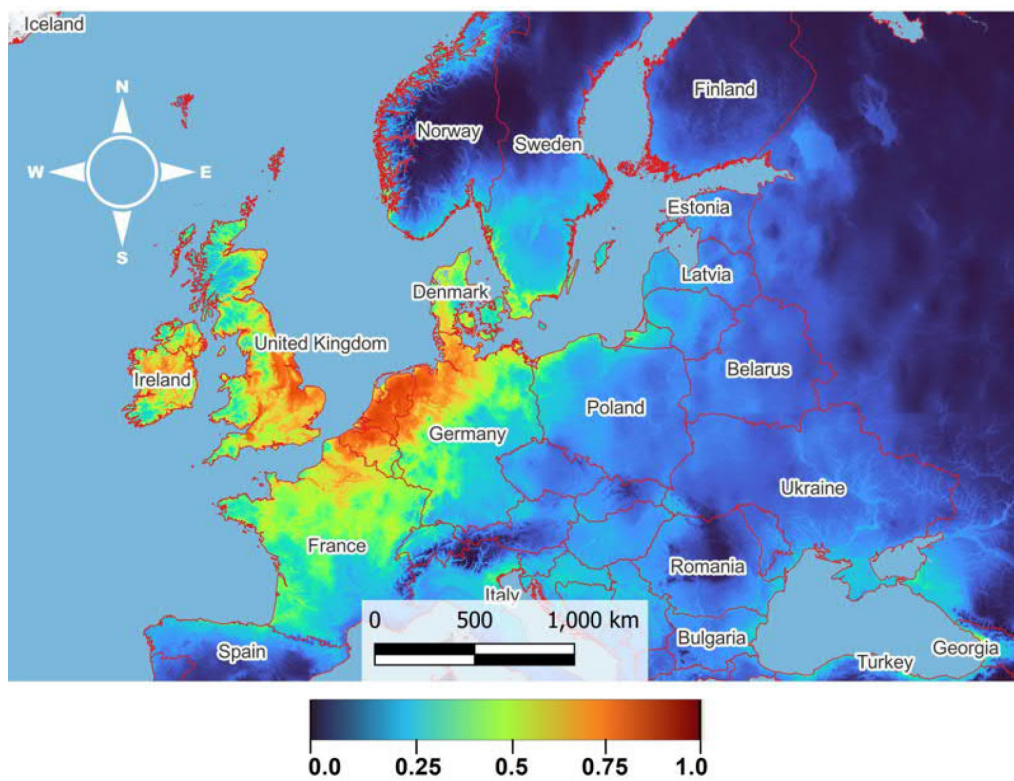


Fig. 6. Map of the current distribution of *Elodea nuttallii* in Europe.

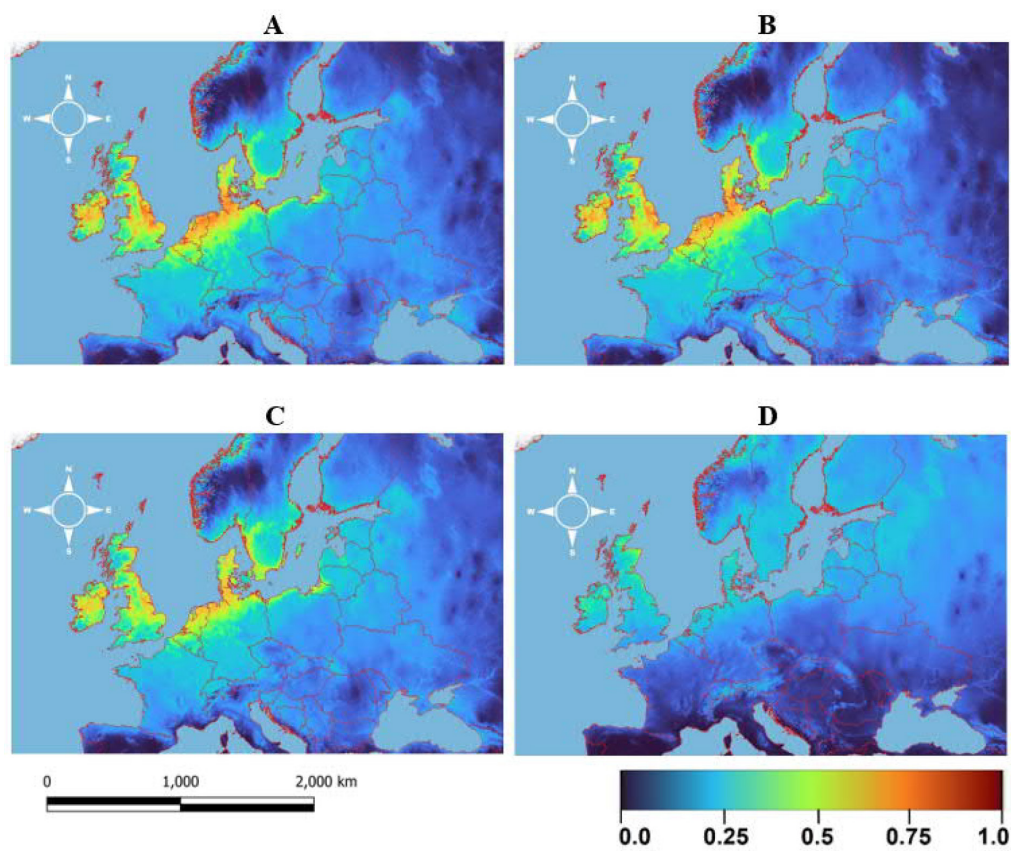


Fig. 7. Distribution map of *Elodea nuttallii* in Europe: A – for 2041–2060 at ssp126, B – at 2081–2100 at ssp126, C – at 2041–2060 at ssp585, D – at 2081–2100 at ssp585.

The next factor influencing the modelling of the probability of occurrence of *E. nuttallii* is the minimum temperature of the coldest month – biov_6. The optimum of the species according to this indicator is around 0.0 °C, with a further decrease in temperature, the probability of its occurrence goes to 0 (Fig. 5A – biov_6), which is explained by the probability of freezing of water bodies and the death of diaspores. At the minimum temperatures of the coldest month of –20 °C, the existence of *E. nuttallii* becomes practically impossible. When the model was trained separately in the Max-ent environment, using only the bioclimatic indicator biov_6, a decrease in the possibility of spreading biov_6, a decline in the possibility of the spread of the species was detected with an increase in temperature after the global extreme (Fig. 5B – biov_6), which is hypothetically related to the probability of droughts, so that range of values is “better” explained by precipitation (Fig. 5A – biov_14) and maximum temperature of the warmest month (Fig. 5A – biov_5).

A change in height above sea level (dem values) from 0 m to 1,000 m leads to a significant decrease in the probability of occurrence of *E. nuttallii* in water bodies (from about 0.8 to 0.28), which may be caused by both climatic factors and the peculiarities of the hydrological regime of high mountain rivers or other water bodies. This requires further research to identify the limiting environmental factors for this species.

The results of the assessment of the likely spatial distribution of *E. nuttallii* are presented in Fig. 6, where shades of red correspond to a high probability of encountering the species (1.0) and blue to a low probability (0.0). According to distribution maps in the secondary range, the species is attracted to northern areas with a mild oceanic climate (with mild winters and cool, rainy summers) formed by Atlantic cyclones. In general, *E. nuttallii* is found in aquatic biotopes throughout the temperate zone, sometimes reaching the subtropical zone.

The predicted future distribution of the species, taking into account climate change under different scenarios, is shown in Figure 7.

Discussion

The spread of *E. nuttallii* through the waterways of Europe has only just begun and is a little more than 100 years old (in contrast to *E. canadensis*, which entered Europe in 1836 with ballast water, by the way, also from Great Britain) (JOSEFSSON, 2011). However, *E. nuttallii* occurs more frequently and replaces *E. canadensis* in many regions (BARRAT-SEGRETAIN, 2001; COOK and URMI-KÖNIG, 1985; PROKOPUK and ZUB, 2019). The vast majority of finds of the species in Europe and Ukraine are confined to river basins and hydro-construction facilities. *E. nuttallii* is a species that today successfully overcomes the natural phytocenotic barrier and began active expansion (DUBYNA et al., 2017).

According to the latest data (BUTKUVIENĖ et al., 2022), *E. nuttallii* (with an indication of the first record) occurs in 26 European countries: England (1914), Belgium (1939), the Netherlands (1941), France (1950), Germany

(1953), Ireland (1960), Belarus (1964), Austria (1970), Denmark (1974), Luxemburg (1980), Switzerland (1980), Slovakia (1986), Czech Republic (1988), Hungary and Sweden (1991), Italy and Poland (1994), Romania (1997), Ukraine (2001), Bulgaria (2002), Serbia (2005), Croatia and Norway (2006), Slovenia (2007), Albania (2017). This species is rarely found in Scandinavia and Eastern European countries (BUTKUVIENĖ et al., 2022) (Fig. 6), however, rapid spread and climate change with warmer temperatures during the growing season will encourage *E. nuttallii* to continue to spread in the north and northeast (Fig. 7). Today, *E. nuttallii* is already widespread in the region of north-eastern Poland, north-eastern Belarus and southern Lithuania and will continue to spread north and northeast directions (BUTKUVIENĖ et al., 2022). Extreme values of temperature and humidity limit the survival of populations and thus set the ultimate limits of potential geographic range as determined by climate (SUTHERST, 2003).

E. nuttallii can be considered as a species of northern climatic preference (optimum of the species according to – minimum temperature of the coldest month – around 0.0 °C (see Fig. 5), however, nowadays the species shows a tendency to sub-Atlantic distribution in Europe and, in particular, to expansion in France (GREULICH and TRÉMOLIÈRES, 2006) (see Fig. 5). Our research confirms the results obtained in modelling hot spot areas for the invasive alien plant *E. nuttallii* in the EU (STEEN et al., 2019), which also showed that most of the EU is suitable for the establishment of this species. The rapid spread of *E. nuttallii* and closely related water bodies in Europe suggests that these areas are likely to be invaded in the near future. In the present study, the temperature of the driest quarter was the most important determinant. According to our data, the amount of precipitation in the wettest month and the minimum temperature of the coldest month were also the most important determinants, which is in line with the results of (KELLY et al., 2014), who also identified the minimum temperature of the coldest month as a determining factor. Our results are therefore consistent with previous studies, using species distribution modelling and global climatic models, in that climatic variables are more important than nutrient loads.

E. nuttallii is actively expanding the boundaries of its secondary distribution range in Ukraine (Fig. 8): in contrast to the ten localities of the first records of this species in 2001–2004, our research (2010–2022) revealed 38 localities (PROKOPUK and ZUB, 2020; PROKOPUK and ZUB, 2019). And these were not isolated finds. Formed monodominant communities of the species (mainly with total soil cover (TSC) up to 100%) were recorded in reservoirs of Kyiv and Cherkasy regions, in rivers, bays, and lakes. A trend of *E. nuttallii* moving up the Dnipro River is observed, the highest downstream points were recorded downstream from the mouth of the Desna River. In the coming years, we predict the advance of this species in the hydrological networks of the Desna and Pripyat rivers, as well as in the upper reaches of the Kyiv Reservoir. The lowest six localities of *E. nuttallii* were found in 2020 in the Lower Dnipro River (Kherson Region) within the ter-

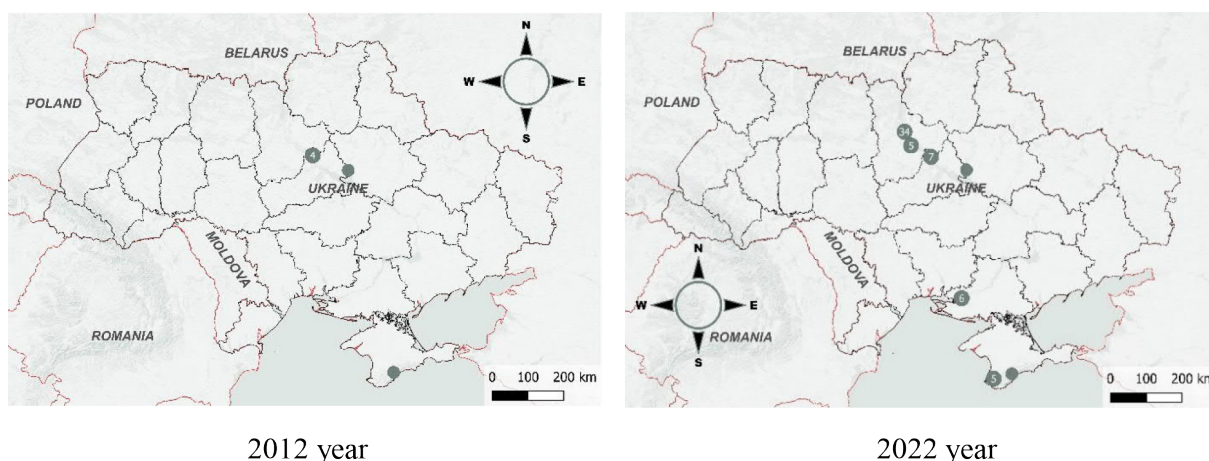


Fig. 8. Dynamics of distribution of *Elodea nuttallii* in Ukraine.

ritory of Nyzhniodniprovskiy National Nature Park. These are the first verified records of this alien aquatic plant (native to North America) in the Steppe Zone of Ukraine (DAVYDOVA et al., 2021).

The species prefers fresh waters, especially floodplains, but it is also found in ditches, canals and oxbow lakes (HAROLD, 1965). *E. nuttallii* can grow in muddy, highly eutrophic waters (COOK and URMI-KÖNIG, 1985; OZIMEK et al., 1993; THIÉBAUT and MULLER, 1999), and in transparent oligo-mesotrophic waters (THIÉBAUT et al., 1997) and in waters with some organic pollution (BEST et al., 1996), and is adapted to low light (ANGELSTEIN and SCHUBERT, 2009). Our research in Ukraine confirmed the well-known fact that the growth of *E. nuttallii* is stimulated by an excess of nitrogen (DENDENE et al., 1993), but under conditions of significant anthropogenic eutrophication (hypertrophic, polysaprobic waters), the communities of *E. nuttallii* become thinned to 5% of TSC and the production indicators of the coenopopulation is declining (PROKOPUK and ZUB, 2019). *E. nuttallii*, preferring meso-eutrophic and eutrophic, low-flow reservoirs, grows on a depth of up to 1.5 m and slightly silted sandy bottom sediments. It can occur to depths of 3 m (SIMPSON, 1990) – and 5 m (IKUSIMA, 1970), where the plant forms dense mono-dominant thickets. The fact that the plant prefers shallow water biotopes (with depths of up to 1 m), which are the first to respond to temperature changes (desiccation in case of warming, freezing – in conditions of cooling) and identified as the main factors: the amount of precipitation and the minimum temperature of the coldest month (see Fig. 5).

According to meteorological observations over the last 130 years, total precipitation has remained close to normal or slightly above normal, but seasonal variations are pronounced and snowfall has decreased (*Climate change and security in Eastern Europe, ..., 2016*). Modern climate models predict the greatest warming in Southern Europe in summer and in Northern Europe in winter (*Climate change and security in Eastern Europe, ..., 2016*) as shown by our forecast maps (see Fig. 7). Most of the changes expected in 2081–2100 will already occur in 2060. Within Ukraine, the probability of species expansion ranges from 35% – in

2060 and the same – in 2100 with ssp126 (the most optimistic scenario) and 35% in 2060 and 20% – in 2100 ssp586 (the most negative scenario – see Fig. 7).

The CMIP6 climate models predict warming of around 0.4 °C this century (*Carbon brief, 2019*). Changes in several drivers of climate change have already been observed in all regions of Europe: an increase in average temperature and extreme heat, and a decrease in cold (GUTIÉRREZ et al., 2021; SENEVIRATNE et al., 2021). The freezing of lakes and rivers has decreased (FOX-KEMPER et al., 2021; GUTIÉRREZ et al., 2021), and the average amount of precipitation increased (DOUVILLE et al., 2022; GUTIÉRREZ et al., 2021), in Northern European and Eastern European. All this will contribute to the expansion of the “European” range of *E. nuttallii* to more continental and eastern territories, primarily Belarus and the north of Ukraine (in the case of a pessimistic scenario with the highest emissions, see Fig. 7D). And extreme water levels, coastal flooding and sandy shoreline subsidence, which are predicted to increase along many European coastlines (GUTIÉRREZ et al., 2021) may explain the decline in the species’ distribution in West-Central Europe (the most negative scenario of climate change, see Fig. 7C, D).

E. nuttallii is included in the List of Invasive Alien Species of Union Concern (EUROPEAN PARLIAMENT and COUNCIL OF THE EUROPEAN UNION, 2014). The species is expanding the boundaries of its secondary range: in contrast to several reservoirs – localities of the first detections of this species since 2004, in the course of 18 years it has spread to more than 30 water bodies of Ukraine both downstream and upstream of the Dniro, has penetrated into the water network of the rivers Desna, Trubizh, Sula (see Fig. 8) (PROKOPUK and ZUB, 2019). In addition to climatic factors, the widespread deterioration of the ecological condition of water bodies and their anthropogenic eutrophication is crucial for the spread of the species (PROKOPUK and ZUB, 2019).

Such a rapid spread of *E. nuttallii* requires the development of effective control and management measures. The best known biological control method that can significantly reduce the biomass of the plant is extensive grazing

of fish and waterfowl on *E. nuttallii* in shallow temperate lakes (ZEHNSDORF, 2015). In the Netherlands, for example, the introduction of large numbers of rudd (*Carassius* sp.) as part of lake biomanipulation has been blamed for the sudden disappearance of *E. nuttallii* (VAN DONK and OTTE, 1996). The challenges and potential benefits of managing submerged aquatic vegetation with white cupids (*Ctenopharyngodon idella*) have been reviewed and summarised by ZEHNSDORF (2015). For the chemical control of *E. nuttallii* there are no methods for chemical control in Europe (NEWMAN, 2010).

The best physical/chemical control method is cutting before July. This is because during June the roots of this species die and in September the plant attains maximum biomass (NEWMAN, 2010). Remove as much of the plant as possible by mechanical means after the end of June and before the end of August (NEWMAN, 2010). Water level drawdown refers to the exposure of aquatic vegetation to winter frost or summer dryness by reducing the water level, and the lowered water level can then be used for easy mechanical removal of *Elodea* (CHAPMAN et al., 1974). The use of biodegradable jute mats to cover *E. nuttallii* has been investigated, but so far with effects on growth for only one growing season, after which the mats were damaged and ineffective (HOFFMANN et al., 2013). Shade can also be provided by planting trees on the south side of water bodies or by using a floating sheet of opaque material (NEWMAN, 2009).

Another method to control *E. nuttallii* invasion is to maintain/achieve good quality of natural waters and prevent their anthropogenic eutrophication: according to our research, *Elodea* actively invades only transformed habitats (PROKOPUK and ZUB, 2019).

Conclusions

The potential distribution of the species based on the climatic suitability of the region of origin based on 23,818 observations of *E. nuttallii* showed that most of Europe is suitable for the expansion of the species (with the exception of high mountain areas). The species prefers northern areas with a mild oceanic climate with mild winters and cool, rainy summers caused by Atlantic cyclones. *E. nuttallii* occurs in aquatic biotopes throughout the temperate climatic zone, partially entering the subtropical.

The most important factors limiting the distribution of the species are the amount of precipitation in the driest month, which has an ecological optimum with values greater than 40 mm per month; at lower values, the theoretical probability of the spread of the species decreases sharply. The optimum of the species according to the minimum temperature of the coldest month is around 0.0 °C, with a further decrease in temperature the probability of its occurrence goes to 0. At minimum temperatures of –20 °C the existence of *E. nuttallii* becomes practically impossible. And also altitude and maximum temperature of the warmest month for percentage contribution and permutation importance, respectively. The values of importance

of other included bioclimatic indicators were at the level of 0.0–2.6.

The eurytopic nature of *E. nuttallii*, its origin from a region with a temperate climate, and the speed of its modern aquatic spread give reason to consider *E. nuttallii* within the borders of Europe (including Ukraine) as an aggressive species capable of rapidly expanding its secondary range. Due to its invasive strategy, ability to spread rapidly and significantly and to form dense monodominant populations, this species is of concern. The species is at an ecological optimum in its wider European range. The whole of Eastern Europe, including the territory of Ukraine, is suitable for its spread. *E. nuttallii* is actively expanding the boundaries of its secondary range in Ukraine, mostly forming dense monodominant thickets.

Considering the rapid spread of the species, the closely connected hydrographic networks of Western and Eastern Europe, and current climate change, it is likely that this species will significantly increase its distribution range in the near future. Most of the changes will take place already in 2060. In the case of a pessimistic scenario of the largest emissions of climate change, we predict the expansion of the “European” range of *E. nuttallii* into more continental and eastern territories, primarily Belarus and northern Ukraine, and a decrease in the distribution of the species in West-Central Europe.

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