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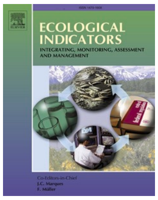

# Native recovery or expansive threat? Past and predicted distribution of *Trapa natans* L. s. l. on northern limit of species' range – Handout for species management

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## ABSTRACT

Global changes are responsible for the movement of species. While many research emphasize the spread of alien or invasive alien species, the rapid spread of rare, native species is poorly study. In our studies, we focused on *Trapa natans*, a species that is considered a strictly protected plant species in Europe, but is considered an alien invasive species in North America and Australia. The aim of the study was to analyze the historical and current occurrence of *T. natans* at the northern range of this species (Poland, Central Europe) and, based on future climate projections (wordClim), to determine its potential spread in Europe by modeling the occupation area of available habitats in Europe. We found a rapid spread of *T. natans* in Poland associated with increasing temperatures. Statistical analyzes showed that the mean temperature of the warmest quarter and precipitation of the driest month are the most important climatic variables determining habitat suitability for *T. natans*. The model for 2021–2040 showed an expansion of habitats suitable for the species to the north (Great Britain and Ireland, Scandinavia), to the east (Germany and Central Europe), to the northeast (Eastern Europe, e.g., Lithuania, Latvia), and to the south (Italy and Southern Europe). In the next two time periods (2041——2060 and 2061——2080), the models showed that the entire European area is suitable for colonization by the species, with the exception of the high mountain regions and Spain. *T. natans* is a representative species whose distribution and recent range changes allow us to track aquatic species feedbacks to climate change in the species' home range and is a good ecological indicator of global warming. The message for conservationists is that the status of species classified as rare needs to be urgently reviewed.

## 1. Introduction

Indisputable evidence of climate change is the increase in the temperature of the Earth's surface and the frequency of extreme weather events (Kundzewicz et al., 2020; IPCC - Intergovermental Panel on Climate Change, 2022). Weather extremes manifest themselves in forest fires, the melting of glaciers, the shortening of the ice sheet and changes in hydrological cycles (IPCC - Intergovermental Panel on Climate Change, 2022). However, global temperature rise is also responsible for the spread of species (Pecl et al., 2017); in particular, the spread and success of invasive species is well documented (Dukes and Mooney, 1999), primarily to northern latitudes. In the United Kingdom, 55 animal species (mainly insects and birds) were found to have expanded their range northward (Pettorelli et al., 2019). While numerous studies emphasized the spread of alien or invasive alien species due to global warming (Turbelin and Catford, 2021), the spread of rare, native species remains insufficiently understood. The spread and rapid colonization of new areas by rare, native species also alters the environment and ecosystem biodiversity.

The effects of species dispersal can vary over time. Species that do not cause harm now may do so in the future. This statement applies to both alien invasive and native species (Davis et al., 2011). The negative impacts of invasive alien species on local biodiversity have been widely recognized and confirmed worldwide. At the same time, native species that are defined as expansive, aggressive and super-dominant can have a negative impact on the natural environment. They can become

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conflicting (problematic native) species whose increase in numbers and changes in range have negative consequences for the human economy (e.g., Cassini, 2022; Dodd et al., 2021; Murphy and van Leeuwen, 2021; Pivello et al., 2018).

Freshwaters are extremely vulnerable ecosystems (Dudgeon, 2019). Among various organisms, macrophytes play an important role in aquatic habitats as they are responsible for numerous ecosystem features, including carbon cycling (Reitsema et al., 2018). They are sensitive indicators of ecosystem health as they are influenced by runoff from agricultural, industrial, or urban areas (Babko et al., 2012; Wilk-Woźniak et al., 2019). Alien invasive macrophyte species are increasingly invading aquatic systems around the world (Bolpagni et al., 2020), causing ecological damage and economic costs (Crystal-Ornelas et al., 2011; https://www.invasive.org/). Nevertheless, an urgent question about what happens to native species that explode in new places and spread rapidly, increases. This phenomenon has been severely neglected, but should be urgently recognized and understood, as ecosystem conservation must also take this aspect into account.

The changes that can currently be observed in ecosystems are expressed in changes in species diversity and structure of habitats, as some species retreat and others emerge in new locations. Changes in the distribution ranges (contraction vs. expansion) of plant species are a natural process. These processes are mainly determined by the dispersal mode, the availability of optimal habitats and climatic conditions. They are also driven by anthropogenic factors that can enhance the natural dynamics of native species dispersal. One of the freshwater macrophyte species that is currently expanding its range is water caltrop (*Trapa natans* L. s. l.). It is a thermophilic, annual macrophyte that reproduces naturally by seed and is capable of extensive clonal growth (Groth et al., 1996). It inhabits eutrophic waters in sluggish areas of stagnant or slow-moving water with pH between 6.7 and 8.2 and alkalinity of 12 to 128 mg/L calcium carbonate (Hummel and Kiviat, 2004).

*T. natans* has a wide native distribution spanning southern, central, and eastern Europe, eastern and southern Asia, and northern and eastern Africa (Phartyal et al., 2018; POWO - Plants of the World On-line, 2023). The northern limit of its range is in waters where the temperature reaches 22 °C for at least 2 months of the year (Hegi, 1965).

To date, *T. natans* is considered a strictly protected plant species (Appendix I of the Bern Convention, Convention on the Conservation of European Wildlife and Natural Habitats. Standing Committee, 1997). In Poland, in its northern range, it is considered an vulnerable (VU) (Kaźmierczakowa, 2016). In Lithuania and Spain, it has been classified as an extinct species (IUCN - International Union Conservation of Nature, 2022). Worldwide it has the status of least concern (IUCN - International Union Conservation of Nature, 2022) and at the same time is considered an invasive species in North America and Australia (https://www.invasive.org/; Naylor, 2003; Toma et al., 2021). According to various publications and personal observations, this species has started to increase its presence in Europe in the last two decades, e.g., in Serbia (Marković et al., 2015), in the Lower Oder Valley (Ławicki et al., 2017; Kowalski et al., 2018), in Germany (Armin Hermann, pers. comm.), in Ukraine (Merzlikin and Savitsky, 2021).

Since *T. natans* is considered a rare species in many European countries, its rapid spread may not be considered a threat. However, in fact, it can lead to sudden spread and overgrowth of aquatic habitats, causing various problems. Dense, floating mats of *T. natans* restrict light availability, reduce oxygen levels which affects fish and invertebrates communities (Hummel and Kiviat, 2004), and suppress other emergent and floating vegetation (du Plessis, 2019). Its dense populations also restrict boating, fishing, swimming, and other recreational activities (O'Neill et al., 2006). The suppression of submerged plants by *T. natans* leads to a reduction in species diversity and could promote the occurrence of non-native species (Hummel and Kiviat, 2004).

On the other hand, water caltrop is able to remove nitrogen from the water and accumulate heavy metals. The nuts of the species are valued for their nutritional and medicinal properties (Hummel and Kiviat, 2004).

We considered *T. natans* because of its expansive character. It is an aquatic, thermophilic species, visibly changing in abundance and expanding in range. It has been recognised as a rare species, protected in Europe and is also an invasive species in North America and Australia. With increasing temperatures and hydrological changes, this species can become a model species to show how species respond to climate change. There's incomplete data about the size and trends of population of *T. natans*, particularly within its native range. There is a marked decline in some regions, but overall trends remain unclear due to confusion as to where it may have come from and taxonomic ambiguity. In many European countries, it has declined until the beginning of the 21st century, typically due to loss and degradation of habitats. However, currently in Central Europe a noticeable increase in the *T. natans* populations and its recolonization of historical localities is observed.

It's worth emphasizing that temporal and spatial fluctuations in the range of *Trapa* sp. in Central and Northern Europe have been well documented and linked to climate changes during the Quaternary period. *Trapa* sp. achieved its maximum range during the Atlantic and subboreal periods of the Holocene, as evidenced by the presence of fossilized nuts and pollen, covering a vast portion of Europe including southern England, central Sweden and central Finland towards the north (Ahlqvist, 2007; Flenley et al., 1975; Korhola and Tikkanen, 1997).

The aim of this study was to analyze the historical and current occurrence of *T. natans* in the northern range of this species (Poland, Central Europe) and to determine its potential range in Europe based on future climate projections (wordClim; projections for the periods 2021–2040, 2041–2060, 2061–2080, https://www.worldclim.org/) by modeling the range of available habitats in Europe. *T. natans* is a representative species whose distribution and recent changes in its range enable to track aquatic species feedbacks to climate changes in the species' home range.

## 2. Materials and methods

All data visualizations and statistical analyzes were performed using R v. 4.2.2 and RStudio (R Core Team and Team, 2022). The distribution of historical and current occurrences of *T. natans* was visualized using the 'ggplot2′ package (Wickham et al., 2016). Exploratory analysis of the dataset was performed using hierarchical clustering based on the 'Manhattan' distance and 'Complete' agglomeration methods. To measure the connectivity of the population, we analyzed the mean Euclidean distance to the nearest neighbor in the studied periods. Calculations of the parameter were performed using the 'nndist()' function from the 'spatstat.geom' package (Baddeley et al., 2015).

The distribution of *T. natans* in Poland was presented using historical and current data. We derived the distribution of water chestnut in 4 time periods from the following publications and databases: a) data collected until 1950 (Hryniewiecki, 1950); b) data collected between 1950 and 1980 (Piórecki, 1980); c) data collected between 1980 and 2000 (Kaźmierczakowa and Zarzycki, 2014; Kaźmierczakowa, 2016); d) current data collected between 2000 and 2023 (https://www.iop.krakow.pl/kotewka, Supplement 1).

The future habitat suitability of *T. natans* was assessed using the 'Maxent' model of the 'dismo' package (Hijmans et al., 2017) based on presence-only data for the species' current distribution in Europe. The occurrences of *T. natans* were derived from the GBIF database (https://www.gbif.org/; https://doi.org/10.15468/dl.t5ygyj). Within the Maxent model, the occurrences were compared with site-characteristic bioclimatic variables and then used to predict the species' entire range in Europe (Elith et al., 2011). Recent climate data were downloaded from the global climate database WorldClim (https://www.worldclim.org/), and climate database and climatic projections included in Coupled Model Intercomparison Project Phase 6 (CIMP6 https://esgf-node.llnl.gov/search/cmip6/). Bio-climatic variable used in MaxEnt model were: BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal

Range (Mean of monthly (max temp - min temp)), BIO3 = Isothermality (BIO2/BIO7) (×100), BIO4 = Temperature Seasonality (standard deviation × 100), BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range (BIO5-BIO6), BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO16 = Precipitation of Wettest Quarter, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter, BIO19 = Precipitation of Coldest Quarter. Mentioned bio-climatic variables control habitat suitability for aquatic plants, mediating the length of the growing season, physico-chemical features of water, such as water level, water velocity (in lotic ecosystems), alkalinity, conductivity and pH, availability of nutrients (Gillard et al., 2020). The response curves for the environmental variables were extracted from the Maxent model and used to interpret how habitat suitability for *T. natans* is influenced by bio-climatic factors.

The distribution of species was predicted in Shared Socio-economic Pathway 3 – 7.0, the Regional Rivalry scenario, which precisely depicts the current trends in the global economy facing various challenges (COVID-19-mediated shifts in national economies, local armed conflicts, increasing tensions between the largest states worldwide, migration crisis). The prediction was established for three periods: 2021–40, 2041–60, and 2061–80, with a resolution of 2.5 min per degree.

## 3. Results

Analysis of historical and current data on the occurrence of *T. natans* in Poland revealed that before 1950 the range of the species included localities in southern Poland to the central part of western Poland (Odra and Warta rivers; Fig. 1a). The species was also found along the San and Vistula rivers (southern part of Poland) and in isolated localities in northeastern Poland (around Suwałki). In the following period between 1950 and 1980, the range decreased and the species was present only in southern Poland (Fig. 1b). Between 1980 and the end of the 20th century, *T. natans* was recorded only in the regions of the upper and middle Odra river and the upper Vistula river, as well as in isolated localities in southeastern Poland (Fig. 1c). Since ca. 2010, the species appeared successively in new localities and its range started to expand northward. Currently, *T. natans* is observed along the entire Odra River, the upper Vistula River, and the San River in southeastern Poland (Fig. 1d).

In the periods studied, the sites inhabited by *T. natans* were divided

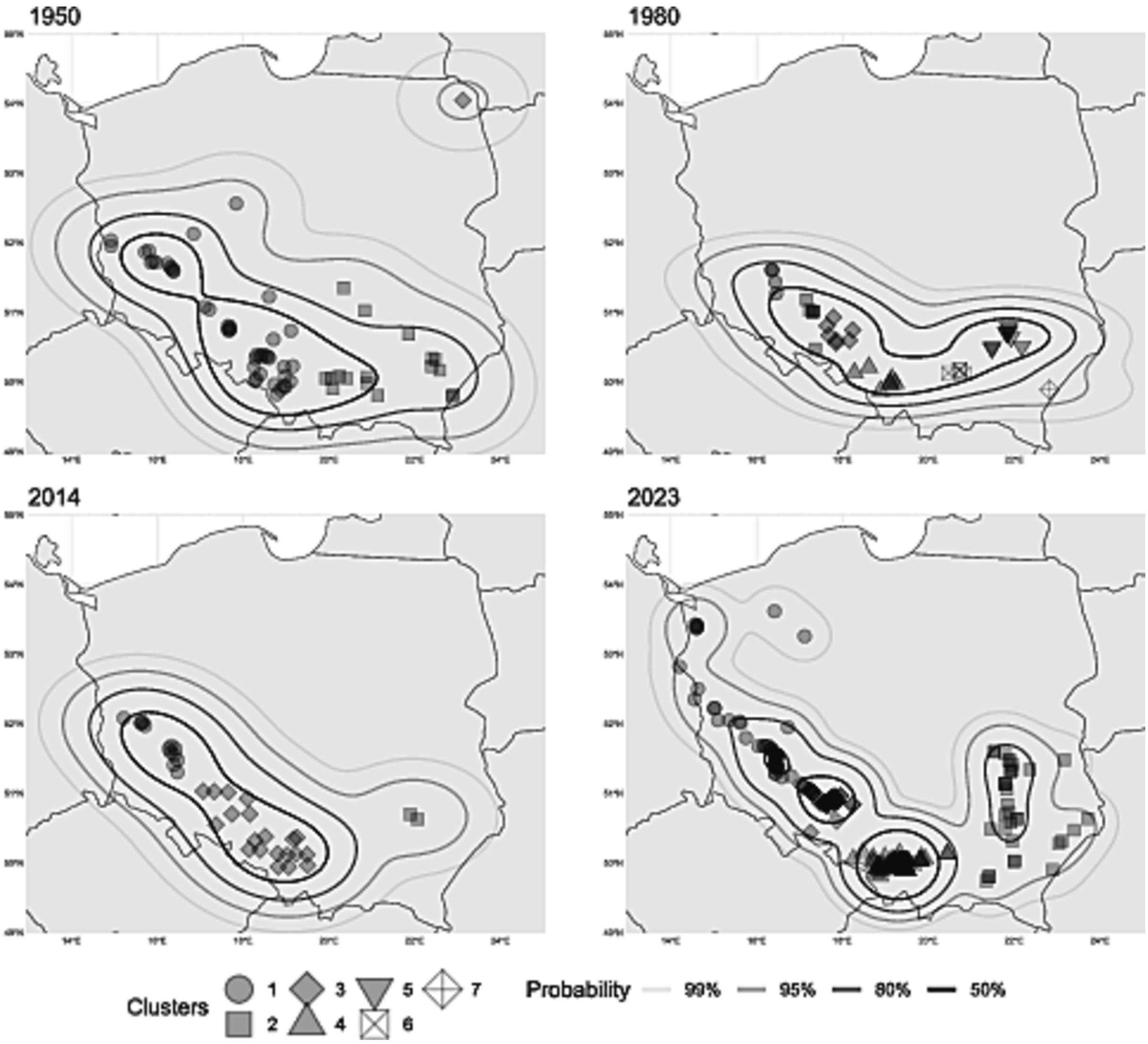

**Fig. 1.** Historical and current distribution *T. natans* with clusters showing population density in the following time periods: 1a) before 1950; 1b) 1950–1980; 1c) 1980–2010; 1d) 2010–2023; Figure guide: probs – probability level for data points to be bounded in specific Highest Density Regions (HDRs).

into a different number of clusters, which were distinguished on the basis of measuring population connectivity. Before 1950, only 3 clusters were distinguished: 1) valleys of the Odra and Warta rivers (southwestern and western Poland); 2) valleys of the Vistula and San rivers (southern and southeastern Poland); 3) isolated habitats in the northeastern part of Poland (Suwałki region). The analysis showed that in this period the mean Euclidean distance to the nearest neighbour was 0.212 units. In the period between 1950 and 1980, seven clusters were identified in the valleys of the Odra, Vistula and San rivers - all in southern Poland - and the analysis of the nearest neighbour distance showed that the mean Euclidean distance decreased to 0.128 units. However, in the period from 1980 to the turn of the 20th-21st century, only 3 clusters were found: 1) the middle Odra River; 2) the upper Vistula River; 3) a single, isolated site in the San River valley, and the mean distance between nearest neighbours increased slightly to 0.169 units. Currently, 5 clusters were found: 1) Odra (middle and lower river); 2) upper Odra river; 3) upper Vistula river; 4) middle Vistula river; 5) San river (Fig. 2), and the mean Euclidean distance between nearest neighbours decreased significantly to 0.048 units. Statistical analyses showed that mean temperature of the warmest quarter (BIO10) and precipitation of the driest month (BIO14) were the most important climatic variables determining habitat suitability of *T. natans* (Supplement 2). Inflection of the response curve for BIO10 showed that a mean temperature of 15 – 20°C in the warmest quarter represents a critical threshold for the occurrence of *T. natans*. In the case of BIO14, precipitation values of more than about 25 mm in the driest quarter determine the suitability of the habitat for this species. Less important variables were: the seasonality of precipitation (BIO15) and the mean annual temperature (BIO1), and the least important were: annual precipitation (BIO12), annual temperature range (BIO7), and precipitation in the wettest quarter (BIO16, Supplement 3).

Habitat suitability for *T. natans* in Europe, modelled based on WorldClim data, showed that the likelihood of the species occurring by 2020 was greatest in France, northern and central Italy, the Adriatic

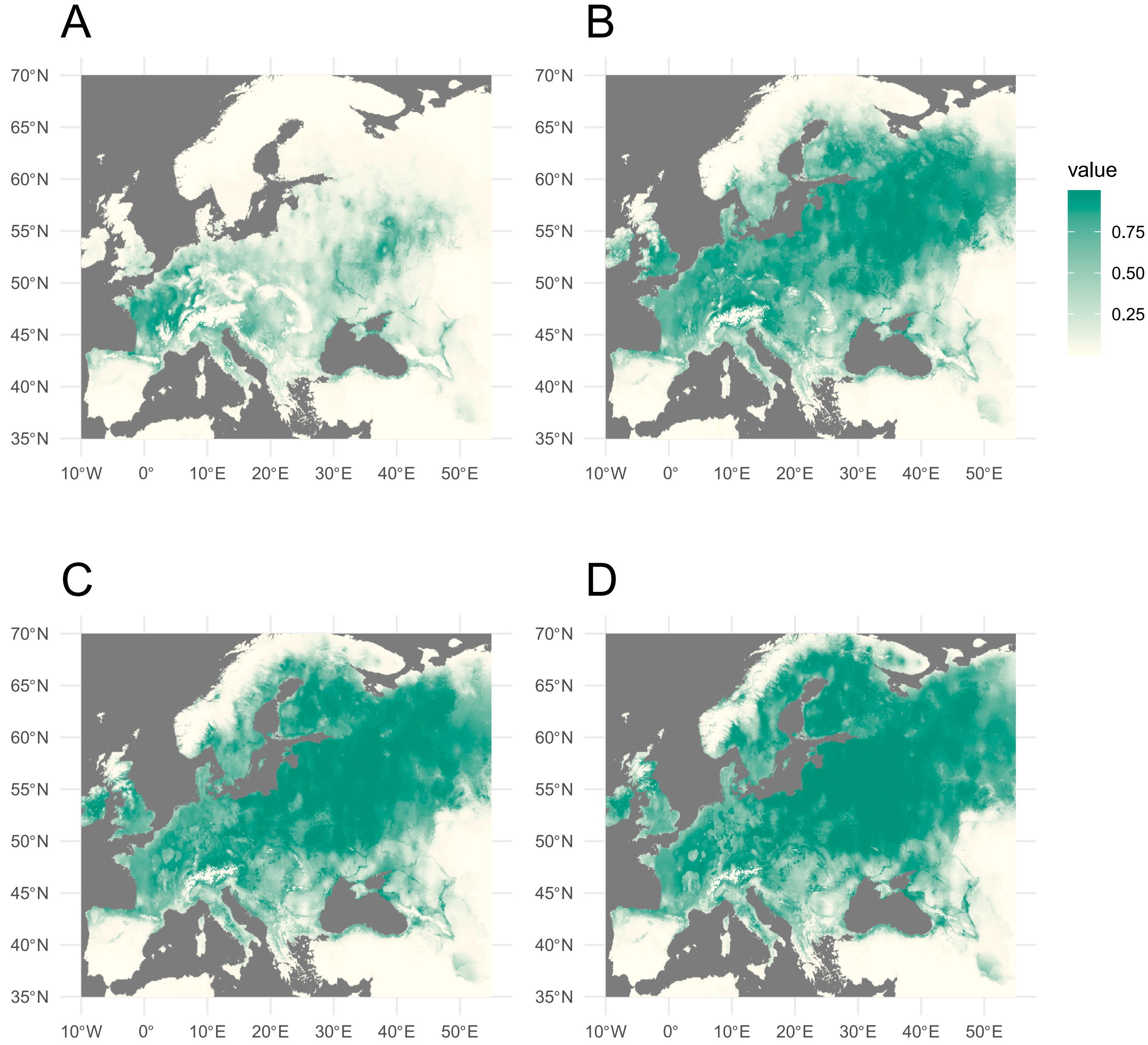

**Fig. 2.** Model of the most suitable habitats for. *T. natans* in Europe: 2a) pre-2020 period; 2b) 2020–2040; 2c) 2041–2060; 2d) 2061–2080; Figure guide: value – predicted probability of habitat suitability for *T. natans*.

basin, and the Balkans (Fig. 2a).

Based on CMIP6 climate projections and habitat preferences of the species, we created models for suitable habitats of *T. natans* throughout Europe. The model for 2020–2040 shows an expansion of habitats suitable for the species to the north (UK and Ireland, Scandinavia), to the east (Germany and Central Europe), to the northeast (Eastern Europe, e.g., Lithuania, Latvia), and to the south (Italy and Southern Europe, Fig. 2b). In the next two time periods (2041——2060 and 2061——2080), the models show that all of Europe, with the exception of the high mountain regions and Spain, is suitable for colonization by the species (Fig. 2c and 2d).

## 4. Discussion

A major characteristic of most living organisms is the movement and colonization of new areas where they find conditions favorable for life. One of the most important effects of climate change on the functioning of living organisms is the shift in the boundaries of zones optimal for life (Lustenhouwer and Parker, 2022). For many species, especially those with low adaptive capacity, this means losing some of their habitat and reducing their geographic range. However, there are also species that take advantage of the changes and expand into new areas where favorable conditions have emerged.

While predicting the spread and expansion of invasive alien species is a conservation challenge (Rodriguez-Merino et al., 2018), native species migration is not considered a potential problem. However, the range expansion of native species caused by climate change is not environmentally neutral, even if they are rare or protected species. Davis et al. (2011) noted that species and habitat management and conservation plans should focus on assessing species function, not just species origin. *T. natans* is a decent example. In North America, where the species is treated as the most undesirable invasive alien species, this aquatic plant causes enormous economic problems. Between 1982 and 2001, $4,597,351 was spent on water caltrop control on both sides of Lake Champlain (USA; Naylor, 2003). The lack of similar calculations in the native habitat of *T. natans* is a major omission in the field of aquatic habitat conservation, but this is due to inadequate knowledge of the distribution of this species. Adequate knowledge of the species' distribution is critical to properly determining its conservation status (Marcer et al., 2013).

In Europe, *T. natans* is a native species, and although it is classified as a rare, strictly protected plant species (Appendix I of the Bern Convention), our study shows its spread into new areas. Analyzing changes in the distribution of *T. natans* at the regional level (Poland), we found that the species spreads rapidly to new sites in the north.

Analysis of historical data showed that the distribution of water caltrop decreased in the years between 1950 and 1980, while at the same time the distance between the nearest neighbours decreased. In the period up to 1950, three population clusters were found, but in the following years (1950–1980) we found the presence of 7 smaller population clusters with increasing Euclidean distance between nearest neighbours, which may indicate a trend toward isolation of populations. Next, we recorded a significant increase in the number of new sites of *T. natans*, especially from the turn of the century XX and XXI, followed by a significant decrease in the mean Euclidean distance between nearest neighbours of the sites (clusters) of the species, indicating connectivity of the *Trapa* population. We relate this process to temperature changes over the past 70 years.

Statistical analysis of area-wide average air temperature series showed that the period between 1951 and 1985 was relatively constant (Twardosz et al., 2021), with temperature ranges between 7.3 and 7.5 °C (Institute of Meteorology and Water Resources https://danepubliczne.imgw.pl/). However, a linear increase with statistical significance was observed for the period between 1985 and 2020 (Twardosz et al., 2021), with the annual average temperature exceeding 9̊C (Żmudzka, 2009, Institute of Meteorology and Water Resources https://danepubliczne.imgw.pl/).

Detecting changes in habitats suitable for *T. natans* at regional scales is valuable for better understanding the impacts of climate change on thermophile native species at European scales (Marković et al., 2015). Currently, we are observing changes in the abundance and distribution of the water caltrop, resulting in a change in status from a rare, endangered species to a spreading species. Climate change, particularly temperature increases and changes in precipitation, have been shown to be the most important factors affecting species ecophysiology, distribution, and interactions with other organisms (Field and Barros, 2014), which is also recognized in our studies.

There is no doubt that air temperature in Europe has increased linearly over the 70-year period (1951–2020) since 1985. The largest increase over the 1985–2020 period was characteristic of spring and the smallest of autumn: 0.061 °C/year and 0.045 °C/year, respectively (Twardosz et al., 2021). The strongest warming (from autumn to spring) on the continent occurs in northeastern Europe (Twardosz et al., 2021). A strong gradient of change is observed mainly in winter and spring and is also pronounced in autumn (Twardosz et al., 2021), which could be helpful for the northward and east-northward dispersal of the species. In previous time it was found that seed germination of *T. natans* begins at the turn of April and May, when the water temperature reaches 10 °C (Piórecki, 1980; Zhigacheva, 2012). However, increasing the temperature from fall to spring can promote earlier germination and a prolonged growing season, providing an opportunity for the production of better quality nuts. The decisive influence of temperature on the germination process of nuts is evidenced by the differences in germination time within a population, which can be even up to one month (Janković, 1958). These dynamics are visible in the model for predicted occurrence of the *T. natans*, where the trend of increasing suitable climatic conditions to the north and east-north is estimated.

An interesting result is the prediction that the range of *T. natans* will also expand to southern regions. Temperatures are also expected to rise in the south and southwest (Twardosz et al., 2021). In contrast, the greatest warming of about 0.060 °C/year was found to occur in summer in southern and central Europe. This could lead to an expansion of habitat suitability for *T. natans* in southern Europe as well, coinciding with the predicted increase in precipitation (including extreme precipitation events; Hosseinzadehtalaei et al., 2020), a phenomenon that also seems to be crucial for the spread of *T. natans* (Marković et al., 2015), as the heavy nuts of *Trapa* are more easily transported to new locations by floods. Rapid renewal of plant communities with *T. natans*, even after catastrophic floods, occurs in bays, meanders, and quiet drainages of hard-bottom water bodies.

Our results are consistent with reports that climate change may act as a catalyst for plant range expansion and subsequent climatic expansion at higher latitudes (Lustenhouwer and Parker, 2022). The currently observed increase in global average temperature and precipitation appears to favour some species associated with aquatic ecosystems. Seed dispersal occurs primarily through migration corridors such as river valleys and as a result of sudden floods. The extension of the growing season under optimal environmental conditions may have a positive effect on the dispersal rate, revealing their high expansion potential within a biotope.

In the face of rapid climate change and shifting species distributions, there is an urgent need to develop appropriate approaches to native species management. Many of them are transforming from rare, endangered species to expanding species that pose a threat to biodiversity and can cause economic losses. Given the dynamic spread of *T. natans*, we suggest that current changes in the species' ranges warrant an urgent review of the rare and endangered species list, which is important for conservation.

The results of our study highlight a neglected aspect of global warming and climate change, namely the spread of native species, which, like the spread of alien species, may pose a threat to the environment and economy. These findings are also relevant to the development of biodiversity conservation strategies. They illustrate that spreading species, both native and invasive alien species, are the architects of future biodiversity, and they enable the development of a new system for managing native species, both rare and common.

We should also be aware that the effects of expansion (native species) and invasion (invasive alien species) pose a similar threat and can lead to biodiversity decline and economic losses. The final, but no less important, conclusion is that changes in the range of rare species, such as *T. natans*, are a good indicator of global warming. The conclusion for conservationists is that the status of species classified as rare needs to be urgently reviewed.

Species management and conservation measures should aim to recognize changes in the decrease or increase of new habitats suitable for species. In addition, a new and "live" (on an ongoing basis) map of species presence should be created to perceive the actual distribution of species and their changes. The next action should be to identification of opportunities for the restoration of habitats suitable for the species. On the other hand, sites where the species is over-spreading and could pose a threat should be released to reduce individuals. Future studies will focus on assessing the ratio of overgrown habitats using UAV tools and on molecular studies. The genetic structure of *T. natans* s. l. will be examined to determine the extent of variability and diversity within its population.

Our studies are limited by impossibility of identification of every single site inhabited by *Trapa*, especially in regions with ongoing armed conflicts, e.g. in Africa and in the territory of Russia, Belarus and Ukraine. Historical data on the distribution of the species is also a limitation, as their occurrence and access to them is much more restricted than current data.

## CRediT authorship contribution statement

**Edward Walusiak:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Wojciech Krztoń:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing. **Elżbieta Cieślak:** Investigation, Writing – original draft, Writing – review & editing. **Magdalena Szczepaniak:** Investigation, Conceptualization, Writing – original draft, Writing – review & editing. **Elżbieta Wilk-Woźniak:** Investigation, Conceptualization, Writing – original draft, Writing – review & editing.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Edward Walusiak reports financial support was provided by National Science Centre Poland. Edward Walusiak reports financial support was provided by Institute of Nature Conservation Polish Academy of Sciences.

## Data availability

Data available in the Supplement 1.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.111349.

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