scientific reports

OPEN

Present and future distribution of the European pond turtle versus seven exotic freshwater turtles, with a focus on Eastern Europe

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Freshwater turtles are often used as terrarium pets, especially juveniles of exotic species. At the adult stage they are often released by their owners into the wild despite their high invasion potential. In Europe these thermophilic potentially invasive alien species occupy the habitats of the native European pond turtle *Emys orbicularis* (Linnaeus, 1758), with new records from the wild being made specifically in Eastern Europe (Latvia and Ukraine) during recent decades. Assessing the potential of alien freshwater turtles to establish in new territories is of great concern for preventing invasion risks while preserving native biodiversity in the present context of climate change. We explored this issue by identifying the present and future (by 2050) suitable habitats of the European pond turtle and several potentially invasive alien species of freshwater turtle already settled in Europe, using a geographic information system (GIS) modelling approach based on datasets from CliMond for climate, Near-global environmental information (NGEI) for freshwater ecosystems (EarthEnv) and Maxent modelling using open-access databases, data from the literature and original field data. Modelling was performed for seven species of alien freshwater turtles occurring from the extreme northern to southern borders of the European range of *E. orbicularis*: the pond slider *Trachemys scripta* (Thunberg and Schoepff, 1792), the river cooter *Pseudemys concinna* (Le Conte, 1830), the Florida red-bellied cooter *Pseudemys nelsoni* (Carr, 1938), the false map turtle *Graptemys pseudogeographica* (Gray, 1831), the Chinese softshell turtle *Pelodiscus sinensis* (Wiegmann, 1835), the Caspian turtle *Mauremys caspica* (Gmelin, 1774) and the Balkan terrapin *Mauremys rivulata* (Valenciennes, 1833). In Ukraine, the most Eastern limit of *E. orbicularis* distribution, were previously reported northern American originated *T. scripta*, *M. rivulata*, *M. caspica*, whereas in Latvia, *Emys'* most northern limit, were additionally reported *P. concinna*, *P. nelsoni*, *G. pseudogeographica* and Asia originated *P. sinensis*. The resulting Species Distribution Models (SDM) were of excellent performance (AUC > 0.8). Of these alien species, the most potentially successful in terms of range expansion throughout Europe were *T. scripta* (34.3% of potential range expansion), *G. pseudogeographica* (24.1%), and *M. caspica* (8.9%) and *M. rivulata* (4.3%) mainly in Eastern Europe, especially in the south of Ukraine (Odesa, Kherson, Zaporizhzhia regions, and Crimean Peninsula). Correlation between the built SDMs for the native *E. orbicularis* and the invasive alien *T. scripta* was reliably high, confirming the highly likely competition between these two species in places they cooccur. Moreover, a Multiple Regression Analysis revealed that by 2050, in most of Europe (from the western countries to Ukraine), the territory overlap between

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***E. orbicularis* and potentially invasive alien species of freshwater turtles will increase by 1.2 times, confirming higher competition in the future. Importantly, by 2050, Eastern Europe and Ukraine are predicted to be the areas with most suitable habitats for the European pond turtle yet with most limited overlap with the invasive alien species. We conclude that Eastern Europe and Ukraine are the most relevant priority conservation areas for the European pond turtle where it is now necessary to take protective measures to ensure safe habitat for this native species on the long-term.**

Keywords Freshwater turtles, Habitat, Competition, Latvia, Ukraine, Climate change, Stacked species distribution models, Priority conservation areas

In their recent report, IPBES reported that biological invasions are responsible of major native species extinction (IPBES, 2023). Being accidently or intentionally released into the wild, sometimes due to illegal trade[1], alien species may become invasive and affect native ecosystem functioning through interspecific interactions. Indeed, alien invasive species may compete with native species for space (e.g. resting, nesting and wintering places)[2,3], for food resources as additional consumers leading to significant decrease in local prey availability[4,5], while they also may convey new pathogens and parasites in the native ecosystems[6], but also participate in hybridization[7]. Consequently, considerable efforts, time and money are spent worldwide for controlling and mitigating the impacts due to invasive alien species, yet with limited success[8,9].

Exotic freshwater turtle (terrapins) species are a case study of biological invasions. They form the taxon with the globally highest number of introduction events among reptiles. Since the second world war, and still in recent years, international market of freshwater and terrestrial (tortoises) turtles as pets has grown significantly[10], leading to mass introduction of many exotic species throughout Europe[11,12]. Some of these species have already established self-sustaining populations in southern Europe[11,13,14]. One of them, namely the Balkan terrapin *Mauremys rivulata* (Valenciennes, 1833) has its natural range covering the Balkan peninsula, but for northern regions of Europe this species also can be treated as the invasive one on the local scale. Further, exotic freshwater turtles have been reported to threaten newly occupied territories[7,15–18], including the native European pond turtle *Emys orbicularis* (Linnaeus, 1758) reported as the reptile that suffered the most dramatic decline in Europe[19,20]. However, it should be noted that there are regional variations in the impact of the invasive alien species with no clear evidence of harmful consequences for native *E. orbicularis* at least under current climatic situation. Additionally, turtles are ectotherm species whose biology is directly driven by temperature: climate change can affect not only their physiology, their behaviour and their distribution, but also the structure of their population due to temperature dependent sex determination[21]. Consequently, the climate, as a determining set of factors, is of particular relevance for studying potential forthcoming distribution of exotic freshwater turtle species. Yet the prospects for these species' distribution in Europe are not fully described in the literature.

Former attempts to model the potential distribution of 15 species of exotic freshwater turtles throughout their European range were made[20]. This former study was based on small numbers of initial registrations, by selecting species according to their contribution in pet markets. Among these species can be mentioned those originated from North America (11 species including the pond slider *Trachemys scripta* (Thunberg and Schoepff, 1792) (here also all subspecies are included, namely: *Trachemys scripta elegans* (Wied, 1838), *Trachemys scripta scripta* (Schoepff, 1792), and *Trachemys scripta troostii* (Holbrook, 1836)), Asia (one species, the Chinese softshell turtle *Pelodiscus sinensis* (Wiegmann, 1835) and from Africa (one species, *Pelomedusa subrufa* (Lacépède, 1788)). For the pond slider, Masin et al. [21] concluded that its invasion success did not significantly exceed that calculated for the other exotic species. Such result is quite arguable considering the pond slider is listed as one of the 100 worst invasive alien species in the world[22]. As a result, Masin et al. [21] turned out that species such as the Asian *P. sinensis* and the African *P. subrufa* have a wider potential range, especially in Europe[21]. Yet, opposite situations are currently reported throughout Europe, with the overall dominance of *T. scripta* among other exotic turtles' species, as listed by Lowe et al.[22].

We applied GIS-modelling approaches to assess the potential for naturalization of the seven target alien freshwater turtle species and their potential competition with the native European pond turtle. This was done by investigating the following key directions: the possibility of naturalization of the seven alien species, chosen as those registered in the first two decades of XXI century in North-Eastern Europe, both in the present and in the future; the influence of various factors on the distribution patterns[23] of these seven alien and one native freshwater turtles; an assessment of the competitive (invasive) ability of the alien species, especially *T. scripta* as the most frequently reported invasive species in Europe, using correlation, multi-regression and cluster analyses. Based on the literature, representatives of *Trachemys* are mentioned more often both when creating a model of the entire range and in local modelling[24–27]. In the present study, we propose to update assessment of prospect of the alien species of freshwater turtles in Europe in the context of current climatic change by implementing GIS-modelling taking into consideration the increased number of records from Eastern Europe[5,18,28] that were not used by Masin et al. [22]. We also examined the potential for the spread of invasive alien species in potentially suitable areas, since there is a possibility of accidental introduction of turtles into natural environments (which was not assessed by other authors[22]). It is also of great importance to study the potential threats of the spread of alien turtles on the native European pond turtle to identify the key territories where appropriate conservation, control and mitigation measures have to be implemented in order to limit invasive risks while preserving native species[10,29]. By establishing the major climatic factors that drive the establishment of breeding populations of the mentioned species, we aim at adequately and timely provide scientific based knowledge for appropriate decision making in terms of biological invasion mitigation and native biodiversity conservation in present and future times.

Results

To determine the potential habitat (species distribution modelling (SDM)) of native and exotic turtle species (Fig. S1) in Europe and their potential expansion under climate change using Maxent models, we used various sets of factors from general (temperature-precipitation-solar radiation) to hydrological (including relief) variables. Models provided good fits with average AUCs > 0.87 (Table 1, Table S2).

For most species of the studied freshwater turtles (terrapins), including the European pond turtle and America originated species, the most important parameter driving habitat suitability was Annual mean temperature (bio1), whereas for the Middle East species (*M. rivulata*, *M. caspica*), it was Solar radiation (bio25).Please note that tables were not sequentially cited in the text, and have been renumbered in the text. Please check, and correct if necessary.The order of the tables and their number, taking into account the structure of the manuscript, are correct.

European pond turtle *E. orbicularis* was more tolerant to the temperature regime, which confirms the potential of this species to have a wide range throughout Europe (+ 3 to + 18 °C, Fig. 1a,b, Table 1). The most important factors of *E. orbicularis* present distribution were Annual mean temperature (bio1) and Isothermality (bio3) that accounted for 34.5% and 19.4% of the model, respectively, and temperature-dependent hydrological factors such as Annual mean upstream temperature (hydro1), Upstream temperature seasonality (hydro4) and Upstream temperature annual range (hydro7) (Figs. S4–S6, Table S2).

The America originated *T. scripta* presented the largest temperature range (+ 4.5 to + 25 °C), the most important factors in terms of contribution to the present distribution model being associated to temperature, with Mean temperature of coldest quarter (bio11), Annual mean temperature (bio1) and Isothermality (bio3) accounting for 33.1%, 19.4% and 15.6% of the model, respectively (Figs. 1c,d, 3, Table 1). In addition, hydrological factors such as Annual mean upstream temperature (hydro1) and Upstream temperature annual range (hydro7) contributed significantly to the model, which is similar to the performance of the European pond turtle (Figs. S4–S6, Table S2). According to the forecast projections, by 2050, the range of *T. scripta* is likely to expand to the northeast and occupy most of the territory of Ukraine and Belarus up to the Baltic countries and Sweden, posing a threat to the native European pond turtle.

Similarly for *G. pseudogeographica* (+ 5.5 to + 25 °C, Figs. 1e,f, 3, Table 1), the major factors of present distribution were Annual mean temperature (bio1) and Isothermality (bio3) that accounted to 31.2% and 24%, respectively, and temperature-dependent hydrological factors such as Upstream temperature seasonality (hydro4), Upstream isothermality (hydro3) and Upstream temperature annual range (hydro7), which is also similar to the previous two species (Figs. S4–S6, Table S2). According to the forecast projections, by 2050, the most promising territories for *G. pseudogeographica* are predicted to be Western-Central Europe and the Caucasus, with a shift in the range to the northeast up to the Baltic Sea and Western Ukraine and Belarus. This also predicts potential overlap with the native European pond turtle, whose population is particularly vulnerable at the edge of its range (Fig. 1f).

For other American originated turtles *P. concinna* and *Pseudemys nelsoni* (+ 8 to + 25 °C, Figs. 1g,h, 2i,j, 3), the variable Precipitation of driest week (bio14) was of greatest importance for shaping their present distribution (45.9% and 18.5%, respectively, Fig. S5) and Isothermality (bio3) (15.3% and 12.5%, Table 1) while the most important hydrological factors were Upstream isothermality (hydro3) for *P. concinna*, and Minimum upstream

Variable	Eo	Ts	Gp	Pc	Pn	Ps	Mc	Mr
Annual mean temperature	**34.5**	**19.4**	**31.2**	**14.8**	10.2	10.9	3	0.7
Mean diurnal temperature range	12.8	0.4	0.1	0.5	0.9	**15.8**	4.9	7.7
Isothermality	**19.4**	**15.6**	**24**	**15.3**	**12.5**	**11.6**	**15.3**	7.3
Min temperature of coldest week	1.1	1.8	0.1	0.8	3.9	0.4	7.3	4
Temperature annual range	1.4	0.5	1.6	1	6.9	1.1	4.2	**11.1**
Mean temperature of wettest quarter	0	0.4	0.7	0.4	**12.5**	0.5	**11.5**	7.1
Mean temperature of warmest quarter	6.9	2.4	4.9	3.3	1	10.6	6.5	1.1
Mean temperature of coldest quarter	0.4	**33.1**	3.3	10.2	6.2	1.5	4.8	1.3
Annual precipitation	0.6	8.5	9.9	3.1	2.4	5.4	**8.4**	**8.9**
Precipitation of driest week	1.6	14	**15.3**	**45.9**	**18.5**	1.2	0.3	0.4
Precipitation seasonality	**15.3**	1.6	5.1	0.3	1.5	0.8	2.1	0.5
Precipitation of warmest quarter	5.1	0.4	0.6	0.2	10	**25.8**	1.2	4.7
Radiation of driest quarter	0	0.4	0.2	0.2	4.4	10.6	**22.1**	**39.1**
Annual mean moisture index	0.7	0.4	2	3.5	8.1	0.6	0.4	0.7
Moisture index seasonality	0.2	0.7	0.3	0.3	0.3	1	0.7	3
Mean moisture index of warmest quarter	0.1	0.4	0.6	0.3	0.4	2.2	7.4	2.5
AUC	0.91	0.88	0.93	0.94	0.98	0.98	0.99	0.99

Table 1. Contribution to the major factors of potential (probabilistic) models of distribution of eight freshwater turtles in the world (CliMond). Values are indicated as % of contribution (permutation importance), with most significant contribution in bold, and AUC value of global model; Eo—*E. orbicularis*, Ts—*T. scripta*, Gp—*G. pseudogeographica*, Pc—*P. concinna*, Pn—*P. nelsoni*, Ps—*P. sinensis*, Mc—*M. capsica*, Mr—*M. rivulata*.

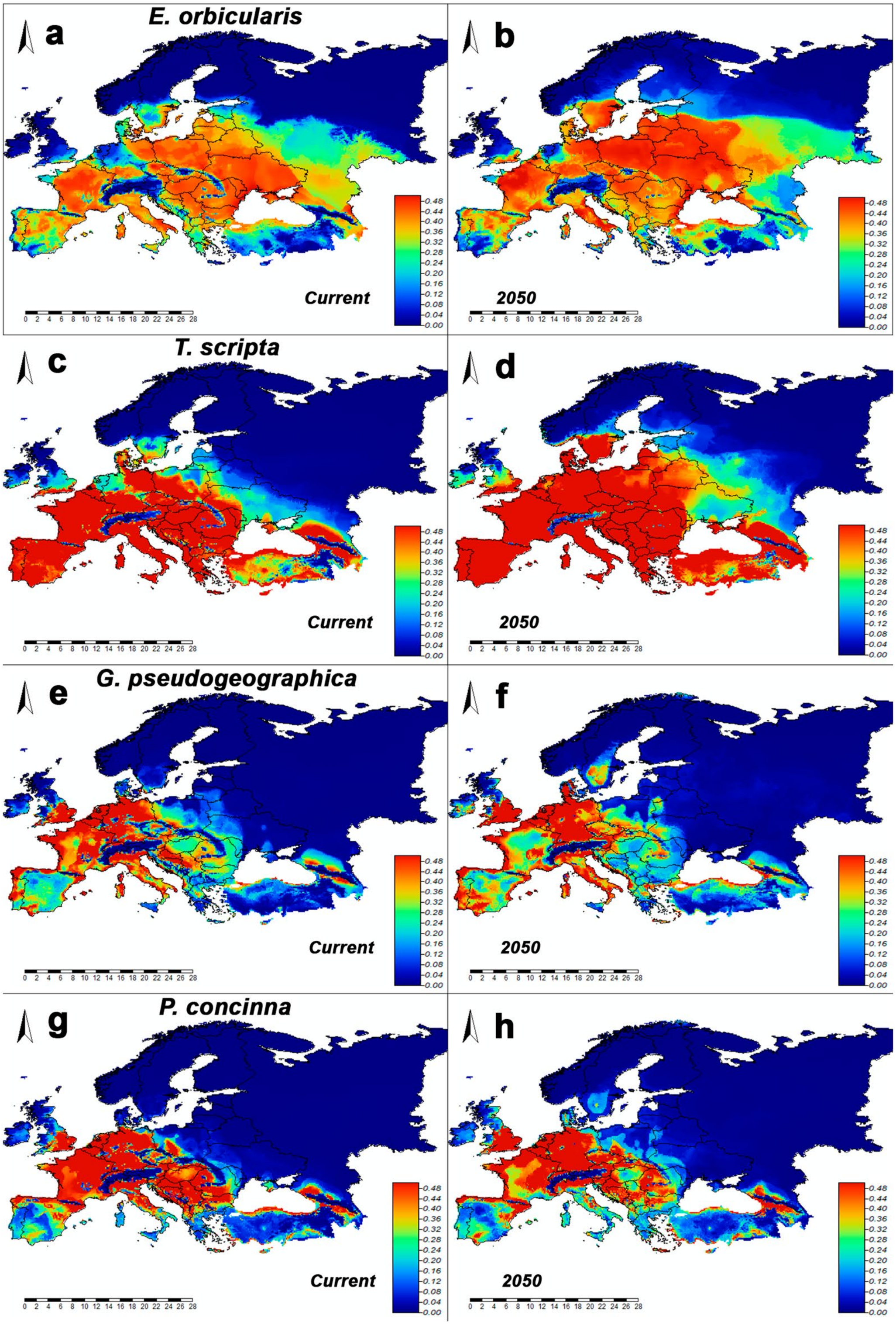

Fig. 1. Potential (probabilistic) distribution model of: *E. orbicularis* (**a**—current; **b**—2050); *T. scripta* (**c**—current; **d**—2050); *Graptemys pseudogeographica* (Gray, 1831) (**e**—current; **f**—2050); *Pseudemys concinna* (Le Conte, 1830) (**g**—current; **h**—2050); the map was created in SAGA GIS software using the open-source "World Administrative Boundaries—Countries and Territories" map under Open Government Licence v3.0 (WorldClim, Fig. S2—with "relief").

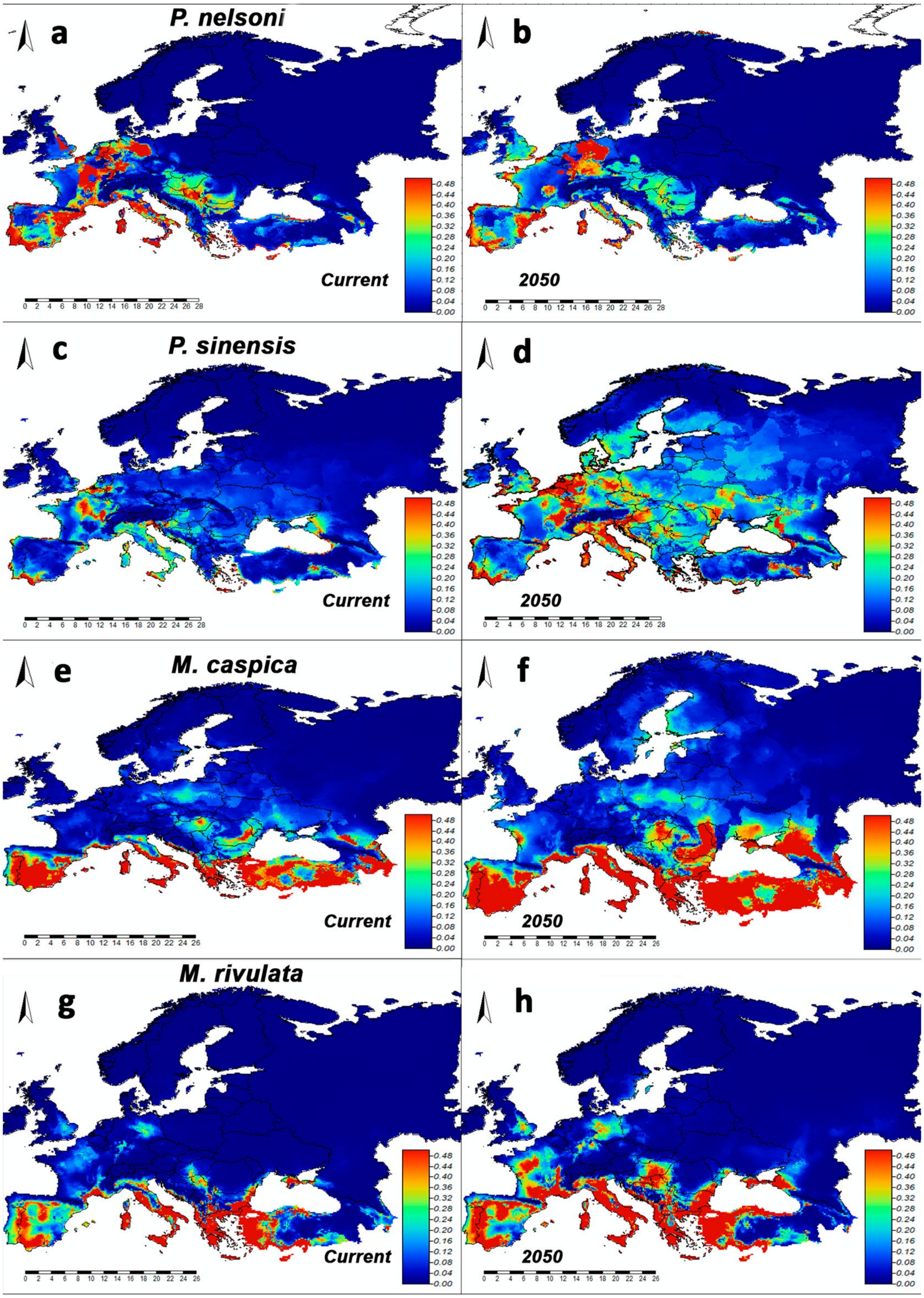

Fig. 2. Potential (probabilistic) distribution model of: *P. nelsoni* (**a**—current; **b**—2050); *P. sinensis* (**c**—current; **d**—2050); *Mauremys caspica* (Gmelin, 1774) (**e**—current; **f**—2050); *Mauremys rivulata* (Valenciennes, 1833) (**g**—current; **h**—2050); the map was created in SAGA GIS software using the open-source "World Administrative Boundaries—Countries and Territories" map under Open Government Licence v3.0 (WorldClim, Fig. S3—with "relief").

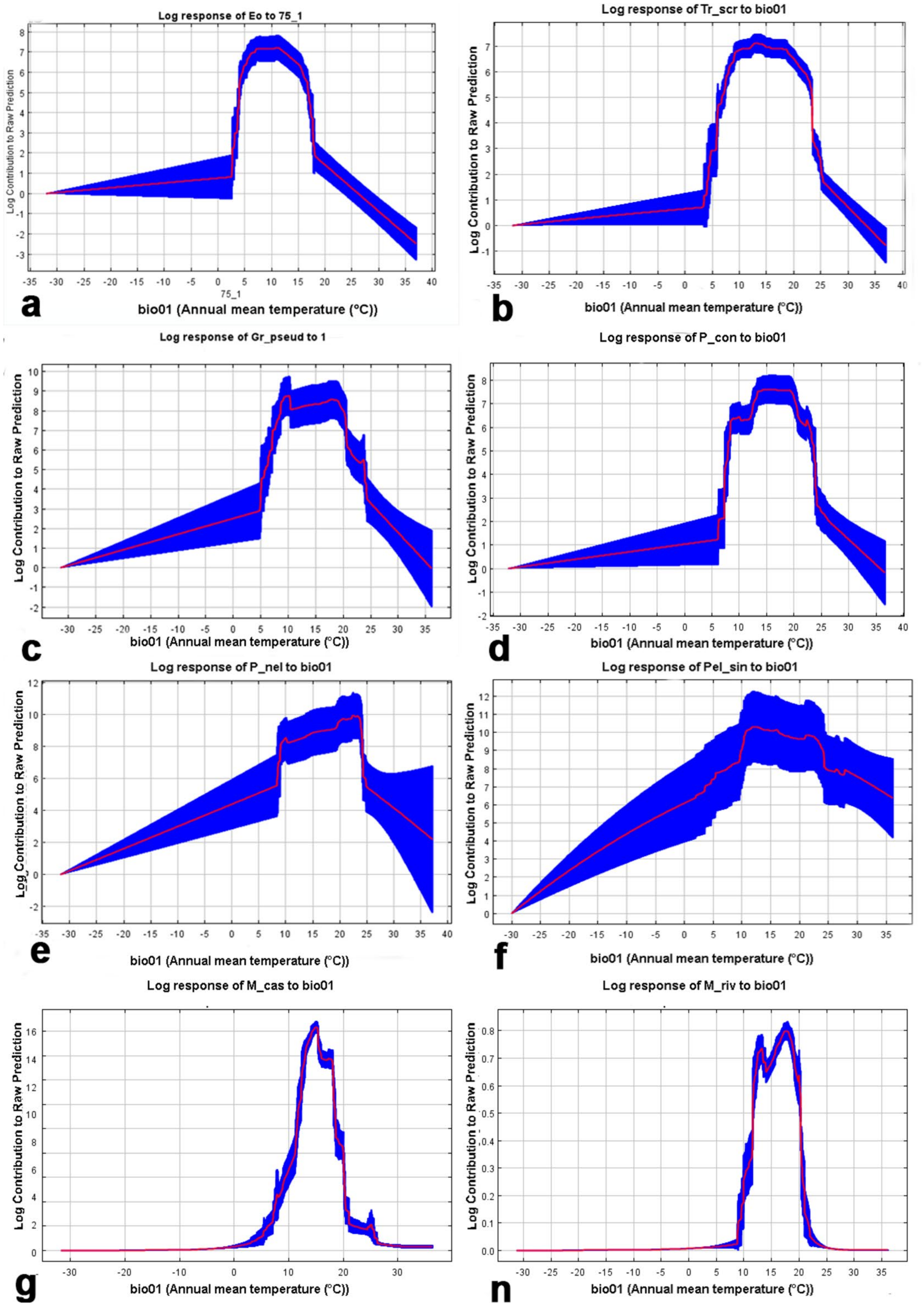

Fig. 3. Response curves generated by Maxent – bio01 (Annual mean temperature (°C)): (**a**) *E. orbicularis*, (**b**) *T. scripta,* (**c**) *G. pseudogeographica*, (**d**) *P. concinna,* (**e**) *P. nelsoni*, (**f**) *P. sinensis,* (**g**) *M. capsica,* (**n**) *M. rivulata*.

temperature of the coldest month (hydro6) for *P. nelsoni* (Figs. S4–S6, Table S2). According to the forecast projections, by 2050, Western Europe (Spain, France, Germany, Italy) is confirmed as the most promising territories for *P. concinna* but this species distribution may also move east to the Baltic countries and Western Ukraine. While *P. nelsoni* is less common, its range is predicted to expand by 1.8 times by 2050 mainly toward Western and Southern European countries (Fig. 2a,b).

For the most thermophilic species, namely the Asia originated *P. sinensis* (+ 10 to + 26 °C, Fig. S7), the most important indicator of present occurrence was Precipitation of warmest quarter (bio18) that contributed to

25.8% of the model (Fig. 2c,d, Table 1), and Upstream temperature annual range (hydro7) (Figs. S4–S6, Table S2). Consistently, the most favourable climate conditions for *P. sinensis* are in coastal countries, especially in Western Europe (Spain, France, Italy), but forecast projections predict that global warming will lead to a more diffuse distribution of this species in more eastern countries (Fig. 2d).

For *M. caspica* (+7 to +23 °C) and *M. rivulata* (+8 to +22 °C, Fig. 2e–h), the models were mainly associated to radiation of driest quarter (bio25) that contributed to 22.1% and 39.1%, respectively (Fig. 2e,f, Table 1), while the major hydrological factor was Upstream precipitation seasonality (hydro15) (Figs. S4–S6, Table S2). Based on our GIS-modelling results, the range of this species is predicted to spread to the north whereas suitable habitats in the south of the present range may significantly decrease by 2050. The most promising northern habitats will be the territories of the Mediterranean countries, as well as Bulgaria, Romania, the south-eastern part of Ukraine (Odesa, Kherson, Zaporizhzhia, Donetsk regions and Crimea) and the Caucasus (Fig. 2f). In the future, by 2050, the range of *M. rivulata* is predicted to expand more than for *M. caspica*, by almost 3 times compared to present distribution area, with particularly promising habitats in the Mediterranean countries, as well as Bulgaria, Romania, southern Ukraine (Odesa, Kherson regions and Crimea) and the Caucasus (Fig. 2h).

Consistent with these results, a cluster analysis with the use of distribution data shows two major groups, with the European *E. orbicularis* and the America originated *T. scripta* and *G. pseudogeograpica* being clearly distinguisable from the five other species (Fig. 4).

Discussion

In our study, the SDMs built using the wide range of bioclimatic variables represent combinations of these factors that are or will (to some extent, depending on the calculated habitat suitability) be favorable for the native European pond turtle and/or for at least one of the seven target exotic freshwater turtles. Because of the ectothermic and thermophilic biology of the species that make them primary subject to temperature regimes, we focused mainly on climatic factors rather than other geographical ones. Nevertheless, since the distribution of these species is majorly, yet not only, determined by climate (e.g., some species of turtles do not inhabit elevations higher than 1000 m a.s.l.[30]), the geological peculiarities of the pan-European territory, such as elevation of the relief and river systems, were also taken into account (Figs. S2, S3) and appeared to be factors that narrow the area of climatically suitable territories (higher HS level) according our bioclimatic modelling, made using only bioclimatic variables.

Our GIS-modelling shows that the distribution of virtually all (native and alien) species of freshwater turtles is greatly influenced by Isothermality (bio3) (determines the reaction of species to temperature changes), and Annual mean temperature (bio1) (Fig. 3), except for the Middle Eastern species of turtles for which the most important factors are related to solar radiation and humidity. Importantly, the native European pond turtle showed the lowest isothermal performance of all 8 studied freshwater turtles. This can be explained by the fact that the native European species can tolerate wide temperature changes between seasons, making it better adapted to temperature fluctuations throughout the year compared to alien species. As a consequence, the highly suitable habitats for *E. orbicularis* cover 37.0% of the European total surface area. Besides, according to hydrological indicators, new promising regions for future breeding for the European pond turtle were located in Eastern Europe (Fig. 1b), with the number of potentially suitable territories increasing by 1.2 times by 2050,

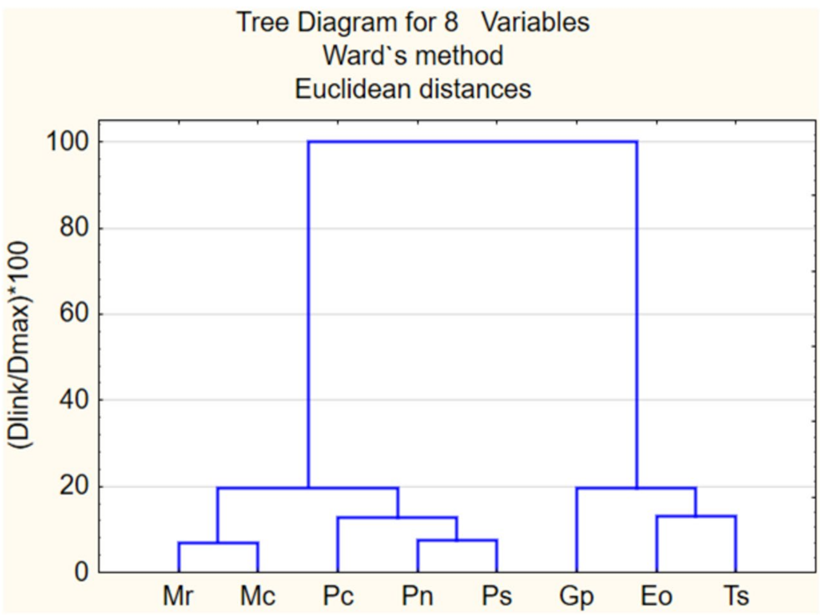

Fig. 4. Results of cluster analysis with the use of distributional data: Mc—*M. capsica*, Mr—*M. rivulata*, Pc—*P. concinna,* Pn—*P. nelsonii*, Ps—*P. sinensis*, Gp—*G. pseudogeographica,* Eo—*E. orbicularis*, Ts—*T. scripta*.

especially in the northeast of its range. Interestingly, the areas around the Baltic Sea and even the territory of southern Sweden may also become suitable habitats for the European pond turtle.

Species distribution models (SDMs) created for the seven alien species of freshwater turtles showed that the America originated *T. scripta* tends to have the widest area of potential habitat and has the highest chance to be adapted to Europe conditions under climate change by 2050. Based on field records, this species is also the most common of all alien species of freshwater turtles in Europe. Highly suitable habitats for *T. scripta* cover one third of Europe and range from about 30% (result of the Binomial test) to 56% (result of Continuous map test) of the Europe total surface area (Fig. S10, Table 2). The value of highly suitable habitat counted for *T. scripta* (34.3% of Europe territory) is very similar to *E. orbicularis* (37.0%, see above), which supports the idea of present and forthcoming competition between these two species[2,3,18]. Further, correlation level between the built SDMs for *E. orbicularis* and *T. scripta* was reliably high (Table 2, Fig. S7). Consistently, *T. scripta,* the most common species of turtle among alien species, is found in large numbers in water bodies of European cities and urban parks[12]. Also, former studies support this result by demonstrating greater activity of pond slider during the winter periods compared to the European pond turtle. This confirms a higher tolerance to winter temperatures and a later entry into hibernation for *T. scripta* compared to *E. orbicularis*[31]. In the southern part of Ukraine in the urban parks of Odesa, the alien species dominates over the native *E. orbicularis* and accounts for 94% of recorded turtles, representing strong potential competition[18]. However, it should be emphasised that despite the two species may compete for space and resources, well-established experimental studies should be conducted for confirming it.

The second place in the potential for wide distribution is occupied by another America originated species, *G. pseudogeographica* that covers 24.1% of Europe and ranges from 10.3% (result of the Binomial test) to 52.9% (result of Continuous map test) of the area (Fig. S10, Table 2). This American species is less competitive for the native species *E. orbicularis*[11,22], reaching 23.1% in terms of the coefficient of determination (value that expresses the degree of similarity or overlapping of the most climatically suitable areas within the built SDMs). But most of all it competes with the American turtle *P. concinna*—79.2%, and with *P. nelsoni*—44.5% in terms of coefficient of determination. The habitats of widespread American turtles are much less similar to those from middle East southern European species—about 6% similarity (*Mauremys*) (Fig. S9, Table S3).

The species scoring the third highest value of highly suitable habitat is *M. caspica*, with 8.9% of Europe being favourable in terms of introduction and acclimatization (according to the Binomial test—8.8%), while the Continuous map test provided a higher value of 14.8% (Figs. S6, S7). Moreover, competition of *M. caspica* with *E. orbicularis* is still small, with a coefficient of determination of about 6%, while with the close species *M. rivulata* this coefficient reaches 51.1% (Fig. S8, Table S3). Recently, the authors have also observed an increase in the number of *M. caspica* in Turkey, in the Caucasus and in the Crimea (pers. obs. from 2010 to 2021). The number of *M. rivulata* has also recently increased significantly in freshwater bodies of Turkey (especially in the Antalya region), and this species also thrives in Ukraine (Crimea and Odesa).

It is only recently that the authors have observed We have observed an increase in the numbers and locations of invasive species of turtles in Eastern Europe, which is confirmed by our findings in Eastern countries (pers. obs., Table S4). Having a larger number of finds of exotic turtles in Europe (open databases—GBIF, iNaturalist, our data), we check not only predictions about turtle distribution trends[22,27,32], but also obtain alternative models that provide more detailed results better models than those of earlier authors[22,27,31] due to more numerous and diverse bioclimatic and landscape variables used in the simultaneous modelling. In addition, we also carried out ground-based verification and confirmation of these finds in different countries.

Over the last three decades we have witnessed the expansion of the European pond turtle's range to the northeast parts of Europe[5]. For example, the number of *E. orbicularis* in the north-east of Ukraine has increased significantly, and the number of breeding cases in the very northern edge of natural range (i.e. in Latvia) has raised as well (10 verified cases of turtle reproduction in the wild, made by field surveys, route counts, fishing traps and citizen science reports)[5,20,33–35].

However, it should be noted that in general, for all turtles, i.e. not only *E. orbicularis*, there is a range expansion trend observed along north-eastern vector[5,10,33–36] and confirmed by the latest records in the past decade (Table S4). Overall, this confirms our earlier assumption, based on our previous works[10,17,18,20,28,33], that for thermophilic aquatic animals there is a north-eastern shift and/or expansion of the range. However, such prospects for the appearance of alien species of turtles in the northeast of the range of the native *E. orbicularis* are

Species	Percent of European territory (%)		
	Highly suitable habitat	Binomial test	Continuous map
E. orbicularis	37.0	32.1	68.3
T. scripta	34.3	29.6	55.8
G. pseudogeographica	24.1	10.3	52.9
M. caspica	8.9	8.8	14.8
P. concinna	4.6	0.6	35.3
M. rivulata	4.3	4.2	9.5
P. sinensis	1.4	0.7	23.6
P. nelsoni	1.0	0.4	14.1

Table 2. Values of the home range analysis (%) of 8 species of freshwater turtles in Europe under climate change, derived from the analysis of SDMs (highest suitable habitat, Binomial test, Continuous map).

dangerous, since this native species is most vulnerable at the edge of its range and can be greatly affected by the appearance of competitors, especially in urban water bodies.

As a result of GIS-modelling and multiple regression analysis, it was revealed that the Europe territory is promising as suitable habitat for invasive alien species of freshwater turtles originated from America, Africa and Asia—this is most of Western Europe, in fact, up to Ukraine. At the same time, we showed future potential expands of the areas of overlap between the native and these invasive alien species of turtles, with an increase by 1.2 times of the possible areas of competition and other negative impacts[2–6]. Therefore, only part of Eastern Europe remains for the native *E. orbicularis* as relatively "safe from the invaders", right up to the Baltic Sea (Fig. 5). The results of the Binomial test indicate that the proportion of predicted presence is less than the proportion of actual presence data. This supports our assumption that people release exotic turtles into any water bodies and even into poorly suitable ones (actual data on presence), where they have no chance of long-term surviving (including the modelling results as well). Thus, as a result of the arealogical analysis, it was revealed

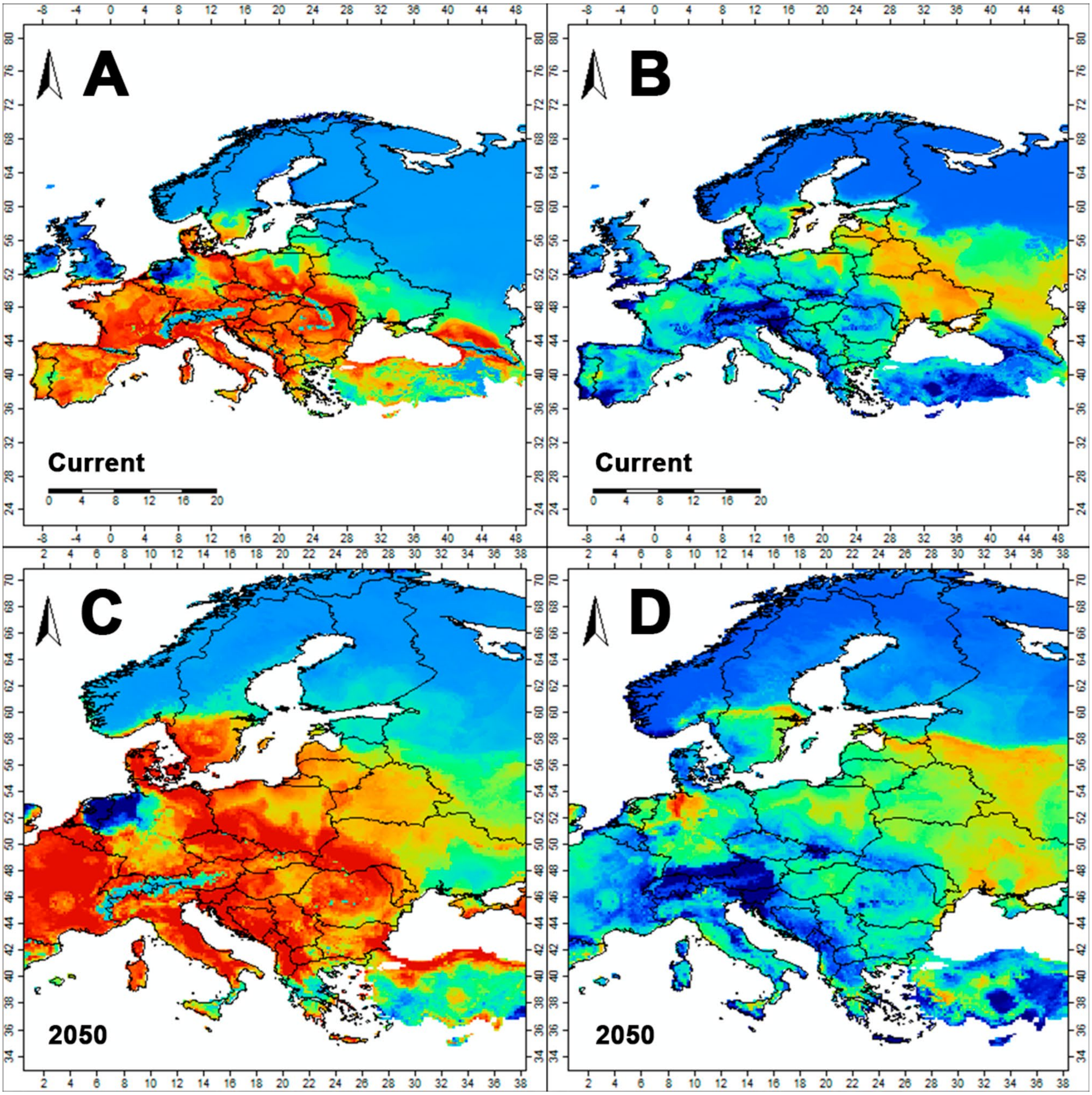

Fig. 5. As a result of Multiple Regression Analysis, models outcomes for: (**A**) area of intersection of current promising habitats for the native European pond turtle *E. orbicularis* and 7 exotic turtle species; (**B**) area of current promising habitat for *E. orbicularis*, without seven species of invasive aquatic turtles; (**C**) area of intersection of further promising habitats (to 2050) of all 8 species of turtles; (**D**) area of further promising habitats (to 2050) for *E. orbicularis*, without seven species of invasive aquatic turtles.

that alien turtle species from other continents and climatic zones cannot sufficiently occupy new perspective habitats in Europe. This may result from their limited dispersal capabilities independent from anthropogenic conditions[18,20,33]. However, the results of the cluster analysis supported the Gause's law (competitive exclusion principle) and the different directions of possible strategies for the development of new ecological niches within the genus (the group of the most vulnerable thermophilic turtles occupies a separate cluster) (Fig. 4). At the same time, species that can compete strongly enough with each other occupy a separate cluster, namely *T. scripta*, *G. pseudogeographica* and *E. orbicularis* (Fig. 4). In most cases, the spread of exotic turtles is also facilitated by popularity among terrariumists due to ease of husbandry. Therefore, *T. scripta,* as the most popular pet-turtle, can often be found in the fresh water bodies of Eastern European cities, where it is often discarded[18].

For the most invasive turtle species (*T. scripta* and *G. pseudogeographica*), the most promising territories are the countries of Western Europe, right up to Ukraine, and in the future the situation may worsen and such eurybiont species turtles may compete with native species *E. orbicularis*, expanding its range. Exotic turtles are increasingly becoming synanthropic, meaning they are adapting to human-modified environments and thriving in urban areas, particularly in artificially warmed urban water bodies. And even now, *T. scripta* as the most invasive alien freshwater turtle species in Europe, can compete with native *E. orbicularis*, through disrupting the ecological balance in the environment as a predator competing for food resources and a carrier of infections[37,38]. It should be noted, that most of our finds of exotic turtles within Northern Europe (Latvia) currently have no prospects for naturalization based on the results of modelling. However, there are such prospects for turtles in other places of Eastern Europe, especially in the south of Ukraine—Odesa, Kherson, Zaporizhzhia regions, and Crimean Peninsula (in the spring of 2023, in some water bodies of Ukraine, *T. scripta* numerically prevails over other species).

It is important to note that this study was conducted using current climatic values. Climate change is expected to further exacerbate the threat of exotic turtle invasions, as it may create more suitable habitats for alien species and may serve as a trigger and thresholds for successful invasion. Further, former studies have reported that the presence of exotic turtles (*Trachemys*, *Pseudemys*, *Mauremys*, *Graptemys*) may lead to exchange of pathogens between native and exotic animals. For example, parasites of genus *Spirorchis* associated to exotic freshwater turtles can be fatal in native *E. orbicularis* with cases already been reported from Spain[39], Switzerland[40] and Poland[41]. These parasite-host interactions should be studied in the new latitudes where exotic turtles are found, since they may represent a threat to the conservation of the native turtle[42]. Further, *Trachemys* has also been described as a carrier of Ranavirus, a virus pathogenic for amphibians[43,44]. Although the latest analyses carried out on wild captured *Trachemys* are negative in Croatia[45] and in Spain[46], the risk in Europe is high and epidemiological surveillance must be maintained in the future.

According to climate data and our field observations, the most potentially promising areas for *E. orbicularis* spread where there are the fewest invasive turtle species («coldspot»)[47] in the present and future are the areas of Eastern Europe (starting from Ukraine). Further, from hydrological maps (Figs. S4, S5, Near-global environmental information EarthEnv NGEI, Tables S1, S2) and according to climatic parameters, our study highlights the North-Central and Eastern regions of Europe, and the countries of Eastern Europe (starting with Ukraine and the Baltic countries, where there will be less competition with invasive species) as the most promising areas for the native species and for future conservation—e.g. reintroduction—initiatives, in favor of the native European pond turtle.

To effectively mitigate the spread of exotic turtles, comprehensive adaptive management plans must be implemented. These plans should include measures to limit the introduction and release of non-native turtles, as well as strategies to control and eradicate established populations. Additionally, conservation efforts for native European pond turtle should incorporate the potential impacts of exotic species, ensuring the long-term survival of this unique reptile in Europe. Overall, this study highlights Eastern Europe and Ukraine as key priority conservation areas for the European pond turtle, and supports recent suggestions for smart conservation strategies for reptiles at range edges in Eastern Europe amidst climate change.

Methods

We performed species distribution models for Europe for 8 aquatic turtles, including the native European pond turtle E. orbicularis and seven of the most frequently recorded turtles (including subspecies) originated from North America (the pond slider T. scripta, the river cooter P. concinna, the Florida red-bellied cooter P. nelsoni and G. pseudogeographica, from Asia (the Chinese soft-shell turtle P. sinensis) and from middle East (the Caspian turtle M. caspica and the Balkan terrapin M. rivulata). These 7 exotic species were selected because they constitute a complete list of invasive species turtles found throughout the range of the European pond turtle, up to its northern and southern border areas in Eastern Europe, namely Latvia and Ukraine. Ground verification of the obtained results was conducted by the latest field studies and occasional finds made through "citizen science" resources (i.e. iNaturalist) (Table S4).

Databases were created based on the available points of registration of the target species using original records as well as data published in literature[16–18,29,34,48–57] UkrBin, GBIF.org, 2022. Records of these exotic turtle species in Europe are not numerous, uneven and do not reflect neither the ecological niche nor their natural habitat. Therefore, we used occurrence data reflecting the entire range of each species separately to create species specific standard distribution models (SDMs). From the initial number of registrations downloaded, those marked as "absence", lacking information on data, coordinates, associated with zoo or private collections (therefore with high chance of being supported by humans) and indicated as a result of machine observation, were removed in order to minimize the data of false presence in the introduced state. Duplications of coordinates were removed as well. To account for sampling bias, we used the nearest neighbor distance method ('ntbox' package in R[58]) for clearing the data in order to avoid autocorrelation. Occurrence points that were ≤ 0.1 units (10 arcminutes) away from each other were removed. Then the 'random selection' module in QGIS (QGIS Development Team 2020[28]) was applied allowing to avoid errors due to spatial autocorrelation. As a result, the number of points significantly decreased to 9438 (Table 3). In addition, we included recent original records[18] with 583 finds of E. orbicularis, 123 finds of T. scripta and 9 finds of M. rivulata, M. caspica, P. sinensis, P. nelsoni and P. concinna, and G. pseudogeographica (Table S4). To understand the role of environmental conditions, gradients and their significance in shaping the distribution of every species, we used a set of 35 bioclimatic variables (10 arcminutes resolution) exported from the CliMond database for the period 1970–2000 (https://climond.org/, accessed 27 December 2020, A1B)[59,60] (Table S1) as current and for 2050 as future. We used the global climate model MIROC-H (IPCC IV SRES Scenarios A1B). MIROC-H: Centre for Climate Research, Japan. MIROC climate data is based on the simulation of historically collected climate data (temperature, humidity, precipitation, solar radiation, wind and other atmospheric phenomena, etc.) and is a global climate model that can be extrapolated into the future under several scenarios, according to various forecasts from the development of our world[59]. This scenario represents the lower bound of the range of future climate development paths according to the IAM (integrated assessment models). This scenario is projected to produce a multi-model mean global warming of less than 2 °C by 2100. This model takes into account significant changes in natural resource use, incorporates changes in forest cover (including even potential increases in global forest cover), and is based on LUMIP (Land Use Model Intercomparison Project) to help solve scientific issues related to climate change in the context of agricultural transformation. This scenario is extremely relevant because it combines the low vulnerability of the model with low challenges for mitigation as well as for a low strength signal. That is, it is this scenario that concentrates the most on climate changes and their indirect management or changes under the influence of the transformation of the biosphere due to the intensification of agriculture[61]. We used the CliMond database for modeling at global scale, and from the resulting models we only selected the European part to study the possibilities of dispersal of exotic species living on other continents. In order to avoid autocorrelation between the variables, highly cross-correlated (> 0.7) ones were removed using the 'virtualspecies' package in R, resulting in a selection of only 16 variables: bio01 Annual mean temperature (°C)), bio02 (Mean diurnal temperature range (mean (period max–min)) (°C)), bio03 (Isothermality (Bio02/Bio07)), bio04 (Temperature seasonality), bio06 (Min temperature of coldest week (°C)), bio07 (Temperature annual range (Bio05-Bio06) (°C)), bio08 (Mean temperature of wettest quarter (°C)), bio10 (Mean temperature of warmest quarter (°C)), bio11 (Mean temperature of coldest quarter (°C)), bio12 (Annual precipitation (mm)), bio14 (Precipitation of driest week (mm)), bio15 (Precipitation seasonality), bio17 (Precipitation of driest quarter (mm)), bio25 (Radiation of driest quarter (W m-2)), bio30 (Lowest weekly moisture index), bio34 (Mean moisture index of warmest quarter).

For creating SDMs for the eight studied species we used highly non-correlated covariates obtained after principal components analysis (PCA). PCA allows significant reducing of the number of variables used for modelling by calculating hypothetical additional covariates. These covariates represent highly non-correlated data from the initial datasets in a form of much smaller set of variables that still contains most of the information in the large initial dataset. These covariates account for more than 90% of the variance of the initial 35 Bioclim variables and are proposed to be called: bio36 (first principal component of 35 Bioclim variables); bio37 (second principal component of 35 Bioclim variables); bio38 (third principal component of 35 Bioclim variables), bio39 (fourth principal component of 35 Bioclim variables), bio40 (fifth principal component of 35 Bioclim variables)[62] (Table S1).

We also used 19 long-term climatic variables from the NGEI—Near-global environmental information for freshwater ecosystems (river ecosystems, long-term hydroclimatic variables following the "Bioclim" framework, EarthEnv, HydroSHEDS, https://www.earthenv.org/ (06 February 2022, Table S1, EarthEnv NGEI). The dataset consists of near-global, spatially continuous, and freshwater-specific environmental variables in a standardized 1 km grid within the geographic boundaries of Europe. All variables presented in this dataset are subsequently averaged across single water reservoirs of the Global lakes and Wetlands Database that are connected to the river network. We used the elevation data of the relief that was used to produce WorldClim 2.1 and were derived

Species	Origin	N of initial records worldwide	N of initial records from Europe	Final N of records used in the study	GBIF database
E. orbicularis	Europe	22,066	1763	1984	https://doi.org/10.15468/dl.pssnfg
T. scripta	America	97,730	10,421	3177	https://doi.org/10.15468/dl.kxgtfv
P. concinna	America	8776	130	1675	https://doi.org/10.15468/dl.r8v2vb
P. nelsoni	America	2477	55	537	https://doi.org/10.15468/dl.w9zkdk
G. pseudogeographica	America	3344	644	369	https://doi.org/10.15468/dl.78g9qs
P. sinensis	Asia	1460	16	290	https://doi.org/10.15468/dl.qd9wjz
M. caspica	Middle East	1096	70	450	https://doi.org/10.15468/dl.p3j7s6
M. rivulata	Middle East	1344	18	956	https://doi.org/10.15468/dl.tgcfqd
Total		138,293	13,117	9438	

Table 3. Records of native and invasive turtle species that were used in the study originating from GBIF databases and after adding records of the authors.

from the SRTM elevation data[63]. Values of bioclimatic variables here are summarized into 19 long-term climatic variables following the "bioclim" framework[55]. This dataset was used in order to make the modelling more "bounded" to the specific ecological niche occupied by the target turtle species—different water bodies. This new set of variables provides a basis for spatial ecological and biodiversity analyses in freshwater ecosystems at near global extent.

Thus, out of 59 variables (Table S1), we selected 40, which allowed us to analyze different models both in the CliMond climate cloud (using the influence of individual climate factors and their covariates) and using factors for freshwater ecosystems (EarthEnv NGEI), where turtles spend most of their time.

The area under the receiver-operator curve (AUC) was used for assessing the discriminatory capacity of the models: AUC > 0.8 is considered excellent. With a reference to the classification proposed by Yang et al.[64], several grades of potential habitats can be distinguished: from barely suitable habitat (threshold > 0.2 for Continuous map test) to highly suitable habitat (> 0.5). Then we tested the model and calculated the proportion of potentially suitable territory using Evaluation metrics for SDMs. These methods include binomial test and the confusion matrix[55]. Binomial test helps to make a significance estimation of a niche model by using the cumulative binomial probability of success of predicting an occurrence given the validation data and the proportional area predicted as present in the niche model[65,66]. GIS-modelling was used to explore the potential distribution of turtles worldwide and particularly in Europe. Modelling and calculations were carried out using Maxent v3.3.3 k software with 25 replicates (75% training, 25% testing)[67,68], according to the published methods[69]. At the same time, models were built both for the distribution of each species of turtles and for a complex of species for the current and future, using correlation, multi-regression and cluster analyzes (SAGA GIS v.2.14 (for visualizations of modelling results), QGIS v.2.18.2 (for mapping of existing records of turtles)). The world map "World Administrative Boundaries—Countries and Territories" in a format of shape file (.shp) was used under the Open Government Licence v3.0 (compatible with the Creative Commons Attribution License 4.0 and the Open Data Commons Attribution License) for creating of the maps presented in this work (https://public.opendatasoft.com/explore/dataset/world-administrative-boundaries/export/).

SAGA GIS is a specific software for GIS that can visualize various data, including the results of multi-regression and cluster analysis. The goal of multi-regression is to find the equation that best fits the data, allowing to predict the value of the dependent variable based on the values of the independent variables and also help to understand the relative importance of each independent variable in affecting the dependent variable. Cluster analysis is used to identify hidden patterns or groupings within our data. Segment the data into meaningful categories based on inherent similarities, and gain insights into the underlying structure of our data. For clustering the obtained data using modeling, we used the Ward method and Euclidean distance (Statistica). Thus, the combination of the Ward method and Euclidean distance allows for effective grouping of data into clusters, minimizing within-cluster variance and ensuring a high degree of homogeneity within each cluster. In SAGA GIS it is possible to create maps showing how predicted values from a multi-regression model vary across a geographic area. Visualize clusters identified through cluster analysis, with different colors representing different groups. By combining these techniques one can gain deeper insights from our spatial data. Statistical processing of the obtained data was carried out in Statistica v 10.0.

Multiple regression analysis was applied to assess the areas suitable for all 7 invasive species together with the native E. orbicularis according to the built standard distribution models. We used SDMs for each species, which we described in the methods section. Then we combined the models. Next, examined the model of the native turtle species and the influence of other turtle species on its distribution, thereby summing the ranges of all turtle species. The habitat suitability area for the native turtle species that is not affected by invasive turtle species remained in the residual.Since the references were not cited in numerical order, they have been renumbered in the order of appearance. Please check.Thank you. Everything is correct.

Data availability

The data presented in this study are openly available in [GBIF.org (28 April 2022) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.pssnfg] [70]; [GBIF Secretariat (2022). GBIF.org (18 April 2022) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.kxgtfv] [71]; [GBIF.org (06 April 2022) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.r8v2vb] [72]; [GBIF.org (06 April 2022) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.w9zkdk] [73]; [GBIF Secretariat (2023). GBIF.org (25 July 2023) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.78g9qs] [74]; [GBIF.org (06 April 2022) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.qd9wjz] [75]; [GBIF.org (18 April 2022) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.p3j7s6] [76]; [GBIF.org (18 April 2022) GBIF Occurrence Download https://doi.org/https://doi.org/10.15468/dl.tgcfqd] [77].

Received: 18 April 2024; Accepted: 2 September 2024
Published online: 10 September 2024

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Acknowledgements
We acknowledge the project Emys-R (https://emysr.cnrs.fr) under the joint Biodiversa + and Water JPI joint call for research projects, under the BiodivRestore ERA-NET Cofund (GA N°101,003,777), with the EU and the funding organisations Agence Nationale de la Recherche (ANR, France, grant ANR-21-BIRE-0005), Bundesministerium für Bildung und Forschung (BMBF, Germany, grant BMBF 16LW015), State Education Development Agency (VIAA, Latvia, grant ES RTD/2022/2), and National Science Center (NSC, Poland, grant grant 2021/03/Y/NZ8/00101). And also, thanks to support from the Collège de France and Agence Nationale de la Recherche ANR through the PAUSE ANR Ukraine programme (Nekrasova O., grant ANR-23-PAUK-0074), and the project "Ecological and socioeconomic thresholds as a basis for defining adaptive management triggers in Latvian pond aquaculture" (lzp-2021/1-0247), project 16-00-F02201-000,002 for the possibility of using the mobile complex of scientific laboratories for research purposes.

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Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-024-71911-4.

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