

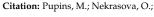
# Potential Threat of an Invasive Fish Species for Two Native Newts Inhabiting Wetlands of Europe Vulnerable to Climate Change

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Abstract: In the modern world, when the problems of the environment are most acutely associated with climate change, amphibians are considered to be the most vulnerable group of anamniotes as an indicator of the state of wetlands. Along with a decrease of numbers among amphibians in Europe, nowadays newts especially suffer from the impact of invasive species, in particular predators such as the Chinese sleeper, Perccottus glenii. This predatory fish species has recently spread to areas of primary relevance for newt reproduction. This fish consumes eggs, larvae, and even adult newt individuals. Using an ecological niche approach and climate based species distribution models (SDM), we applied the coefficient of determination  $(R^2)$  for comparing the level of similarity of the built SDM for the newts Triturus cristatus and Lissotriton vulgaris, and the Chinese sleeper. We show that by 2050, the level of climatic niche similarity for these native and invasive species will increase from 12% to 22% throughout Europe, and from 44% to 66% in Eastern Europe. This study highlights the expansion of the Chinese sleeper as a real threat to European biodiversity of wetlands in the near future, especially in their most northeastern distribution range.

Keywords: climate change; GIS-analysis; modelling; alien species; amphibians; wetlands; Europe



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## 1. Introduction

Amphibians have recently been reported to have dramatically decreased in numbers throughout Europe, especially in Eastern countries [1-3]. Wetlands as habitats, important for amphibians at certain stages of their life, are shrinking and degrading due to climate change [4,5], anthropogenic effects, pollution, and impacts of alien invasive species [6]. Occurrence of invasive or so-called alien species in the ecosystem is one of the results of its unfavorable state. Such species appear in the ecosystems disturbed, transformed or affected in other ways by human, along with decrease of biodiversity of native species. Alien invasive species often appear and adapt in new places far from their natural range, for example, as a result of uncontrolled release into the wild from captivity or other anthropogenic activities [6–9]. Among these species, such predators as redbreast sunfish Lepomis auritus (Linnaeus, 1758), pumpkinseed Lepomis gibbosus (Linnaeus, 1758), and Chinese sleeper Perccottus glenii (Dybowski, 1877) recently introduced in Europe along with northern pike Esox lucius (Linnaeus, 1758) and pikeperch Sander lucioperca (Linnaeus, 1758) that for a long time have been spreading in terms of developing aquaculture, pose the greatest threat to newts at all stages of their ontogenesis [10,11]. Mass appearance of the Chinese sleeper P. glenii in water bodies of European cities may result from deliberate releases by amateur aquarists and fishermen in the early 20th century. Until recently *P. glenii* has been considered ornamental. Yet due to its eurybiontic nature, aggressiveness, flexible

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and wide range of suitable food items (both invertebrates and small vertebrates on different stages of ontogenesis) and ecological plasticity, this species has spread extensively both in Northern and Southern Europe with the most western records known from Germany, Czech Republic, Poland, Hungary, and Serbia [11–18]. Since 2016, the Chinese sleeper *P. glenii* is included in the special list of Invasive Alien Species of Union concern in Europe (the Union list) [4].

According to the literature, *P. glenii* is a serious threat for local biota [15–27]. It was reported that its diet consists of macro- and micro crustaceans (Ostracoda, Copepoda, Cladocera, Isopoda, Amphipoda, Gastropoda), highly mobile invertebrates such as Coleoptera and Heteroptera [16], eggs and larvae of other fish and amphibians, including both anurans and urodeles [15,17–21]. Additionally, this species also affects the food base for local inhabitants acting as a trophic competitor for human resources. Habitats heavily invaded by *P. glenii* are usually associated with lower fish species richness and diversity [22,23]. Moreover, *P. glenii* can be a vector for several species of parasites, which can lead to significant damage to local ecosystems and aquaculture [24–27]. In addition, by feeding on macro- and micro-invertebrates, *P. glenii* noticeably reduces the transport of nitrogen from aquatic to terrestrial environments [27]. What is more, it was shown that *P. glenii* along with eggs of other fish species (e.g., roach *Rutilus rutilus* (Linnaeus, 1758), bream *Abramis brama* (Linnaeus, 1758), and perch *Perca fluviatilis* (Linnaeus, 1758) [27] consumes spawn (including that laid by newts) when it was mobile, either under the effect of flow or at the stage of the movable embryo [27].

Of all amphibian species, newts are, due to their comparably low dispersal capability, especially vulnerable to climate change, anthropogenic influence and, as a result, from the emergence of new invasive predator species [28]. The two most widely distributed species of newts, yet preserved in the European Union, are the crested newt *Triturus cristatus* (Laurenti, 1768) and the smooth newt *Lissotriton vulgaris* (Linnaeus, 1758) [29,30]. Recently, it has been suggested that the expansion of *P. glenii* to new areas may have contributed to population decreases in these two newt species [31].

All the studied species are strictly bounded to different types of wetlands as sources for living space, water, spawning, and foraging areas. Such territories as wetlands are extremely important for conservation of biodiversity providing refugia for amphibians, reptiles, mammals, insects, rare plants, and other groups of living organisms that are strictly connected to the specific wetland habitats. At the same time, they provide valuable services to humans, protecting the land from flood, erosion, and soil degradation, being a source of water, accumulating carbon ad providing other ecological services [32]. Nowadays wetlands suffer from many threats both due to human activities, for example uncontrolled mining, irrigation, pollution on a local level and climate changes globally [33,34]. Therefore, restoration of wetlands becomes more and more popular and effective way to prevent their degradation and save their unique biological complexes. If organized properly, such restoration projects are quite efficient. There are more and more reports stating that local fauna and flora of restored wetlands do not differ much from those of the natural ones [33-36]. Taking into account the possible interactions of native species and the potential emergency of the invasive ones is important in such projects and the topic discussed in this work is dedicated just to this matter on the example of two native newt species and invasive predatory fish.

In this study, we aimed at modelling the present and near future distributions of *T. cristatus* and *L. vulgaris* in relation to that of *P. glenii* in Europe. In order to obtain a more complete forecast about the vulnerability of these native newts throughout their entire European range, we expanded the scope of our research to identify the most potentially suitable habitats for these species, as well as to make a forecast about the prospects in the face of the expansion of *P. glenii* as an aggressive predator of native newts in Europe.

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#### 2. Materials and Methods

#### 2.1. Occurrence Data Collection

Occurrence data on the studied species referred to the entire territory of Europe in order to increase the accuracy of the built models, despite the fact that the main focus of our investigation was to evaluate the potential future overlap of the considered species in Eastern Europe. The occurrence data for T. cristatus, L. vulgaris, and P. glenii was collected from the literature resources [12-24,37-40] and online Global Biodiversity Information Facility databases [41-43]. Data were supplemented by original datasets [11,28,31,37,40] and collection materials (I. I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kyiv; Department of Ecology, Institute of Life Sciences and Technologies, Daugavpils University, Daugavpils, Latvia; all non-duplicate data), thus covering the most eastern range where P. glenii was first reported. To account for potential sampling bias, we used the nearest neighbor distance ('ntbox' package in R [44]) method to thin the data: to avoid spatial autocorrelation, occurrence points  $\leq 0.1$  units (meaning approximately the spatial resolution of the climate factors' database (.tiff map file, 2,5' spatial resolution) used for the research) away from each other were removed. As a result, the numbers of points used for modelling were 2096 for L. vulgaris, 2277 for T. cristatus, and 944 for P. glenii.

Meanwhile, monitoring studies were carried out in the south of Latvia (near the town of Silene in 2018 and 2022) and in areas of north-western Ukraine (Volyn, Rivne, Zhytomyr, and Kyiv regions in 2017–2021). In order to find the evidence of co-habitation of the newts and fish, they were captured by a hoop-net alongside the water edge in spring months (April–May).

### 2.2. Environmental Data

We used 35 bioclimatic variables from the CliMond dataset ([45–47], Table S1), following A1B climate change prediction scenario of MIROC H global climate model. Out of 35 bioclimatic variables, highly correlated (>0.7) predictors were removed using the 'virtualspecies' package in R, resulting in a selection of 16 variables: annual mean temperature (°C) (Bio01), mean diurnal temperature range (mean (period max-min)) (°C) (Bio02), isothermality (Bio02/Bio07) (Bio03), temperature seasonality (Bio04), min temperature of coldest week (°C) (Bio06), temperature annual range (Bio05-Bio06) (°C) (Bio07), mean temperature of wettest quarter (°C) (Bio08), mean temperature of warmest quarter (°C) (Bio10), mean temperature of coldest quarter (°C) (Bio11), annual precipitation (mm) (Bio12), precipitation of driest week (mm) (Bio14), precipitation seasonality (Bio15), precipitation of driest quarter (mm) (Bio17), radiation of driest quarter (W m-2) (Bio25), lowest weekly moisture index (Bio30), and mean moisture index of warmest quarter (Bio34). Models were run with climate data for 1970–2000 and for 2041–2060 (hereafter referred as 1975 and 2050 periods). These intervals were provided by CliMond for modelling the current distribution (most of the records of the studied species dated from 1975 to around 2000) and for building probabilistic models for 2050 [9].

We also used 19 long-term climatic variables from the Near-global environmental information for freshwater ecosystems (river ecosystems, long-term hydroclimatic variables following the "bioclim" framework, EarthEnv NGEI, HydroSHEDS, https://www.earthenv.org/streams (6 February 2022), [48], Table S1). The dataset consists of near-global, spatially continuous, and freshwater-specific environmental variables in a standardized 1 km grid. This new set of variables provides a basis for spatial ecological and biodiversity analyses in freshwater ecosystems at near global extent.

## 2.3. Model Building

Ecological niche modeling and species distribution modelling (SDM) methods were used to determine the potential home range of invasive species in new environments (Maxent with 25 replicates, DivaGis (Bioclim) [49,50]). We used two evaluation metrics for SDMs performance, namely binomial tests and the area under the receiver operating characteristic (ROC) curve (AUC) for assessing the discriminatory capacity of the models. ROC is a

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visual graphical representation of comparison of the amount of true positive versus false positive pixels through an incremental binary classification of the factors used in building distribution maps [44,51,52]. AUC > 0.85 is considered excellent [53,54]. We carried out separate modelling for each set of factors and for each species. Logistic output format was used to describe the relative probability of presence, which is a continuous habitat suitability (HS, %) range between 0 (unsuitable) and 1 (the most suitable). Prospective habitat suitability (HS > 0.5) was used to express the amount of potentially suitable areas for each species according to the built SDMs. Binomial tests were used to highlight SDM areas where the target species has actually been registered. We used the coefficient of determination to assess similarity (p < 0.05) between the predicted HS maps (pairwise) obtained through Maxent for each species across the study area [8]. GIS-modelling was accomplished using SAGA GIS, DivaGis, and QGis [49]. Linear regression analysis of SDM grid of *P. glenii* as dependent and multiple grids (SDM *T. cristatus* and/or *L. vulgaris*) as independent (predictor) variables was carried out using the program SAGA GIS. Details of the regression/correlation analysis are provided in the supplement. Optionally the regression model is used to create a new grid (SDM P. glenii and T. cristatus and/or L. vulgaris) with regression-based values [55]. Statistical processing of the obtained data was carried out using Statistica for Windows v.10.

#### 3. Results

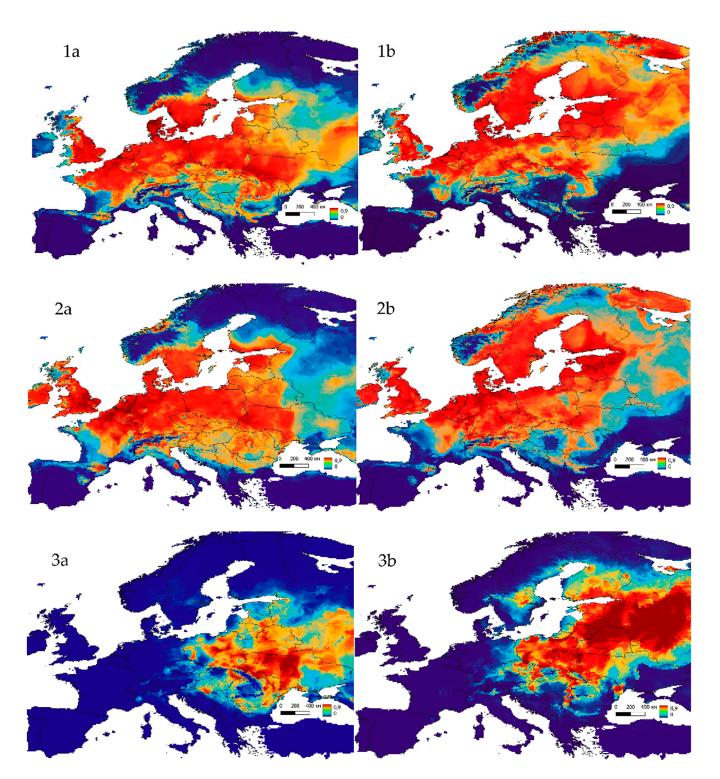
The Maxent distribution models for the three considered species using 16 CliMond variables showed that their average AUCs after 10 repetitions were 0.85, 0.85, and 0.93, respectively (Figure 1).

As a first result of our study, it was found that before 2000, prospective habitat suitability (HS > 0.5) areas in Europe made up 30.3% for *T. cristatus* (binomial test—25.4%), 28% for *L. vulgaris* (binomial test—25.4%), and 12.3% for *P. glenii*—12.3% (binomial test—11.6%) ([44], Figure S1). The modeling results allowed to conclude that these species occupy similar habitats and the range partially overlaps (Figures S2–S4). However, our models indicate that by 2050, the invasive *P. glenii* will double its range compared to the considered newts, leading to a significant spatial overlap of the species' distributions in the near future. Native newt species of Eastern Europe (including the Baltic countries; Figure S1) will especially suffer from the influence of *P. glenii* due to such overlap of future distributions amongst species.

Secondly, the climatically suitable range for the Chinese sleeper is predicted to increase significantly by 2050. In addition, the coefficient of determination as a measure for comparing the distribution models of P. glenii with those for T. cristatus and L. vulgaris at once, will significantly increase (p < 0.05) from 12% to 22% throughout Europe, and more importantly from 44% to 66% in Eastern Europe.

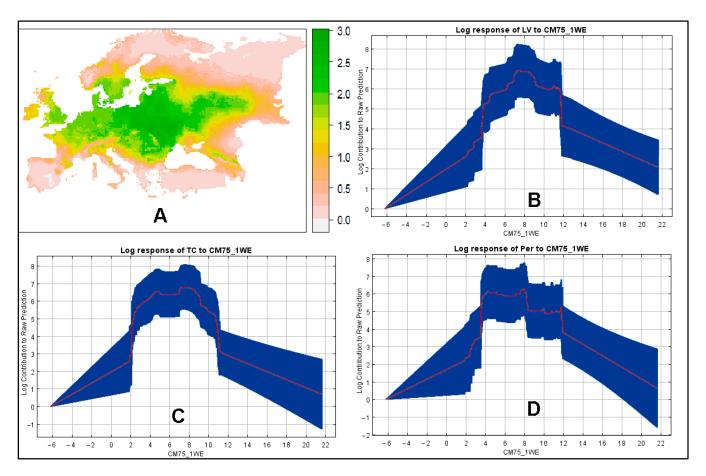
Finally, our results show that a combination of factors (namely, annual mean temperature, mean temperature of wettest quarter, precipitation of warmest quarter, mean moisture index of warmest quarter), associated with average temperature amplitudes for different periods, and humidity has the greatest influence on the spatial distribution of all considered species (both the fish and the newts). In addition, the factor radiation of coldest quarter complements this combination of factors since it affects humidity within habitats [31]. Importantly, *P. glenii* appeared to be the most tolerant and resistant species to the temperature regime with annual mean temperature having its optimal values between +2 and +12 °C (Figure 2). Since *P. glenii* prefers shallow reservoirs that can dry up in the summer-autumn period, the Bio08 Mean temperature of wettest quarter is an especially important factor for the species.

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**Figure 1.** Potential (probabilistic) model: 1—*T. cristatus* (AUC = 0.85; Bio01 Annual mean temperature: Percent contribution—41.3%, Permutation importance—30.1%); 2—*L. vulgaris* (AUC = 0.85; Bio01 Annual mean temperature: Percent contribution—30.7%, Permutation importance—12.2%); 3—*P. glenii* (AUC = 0.93; Bio08 Mean temperature of wettest quarter: Percent contribution—42.8%, Permutation importance—5.9%); world expansion built in the Maxent program based on the CliMond (a—1975; b—2050) climatic data, GBIF data (2022) and original data. Areas of the highest habitat suitability (>0.5) are colored in red and areas of the lowest (<0.1)—in blue.

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**Figure 2.** Map of the Maxent model: **(A)**—Map of the cohabitation of 3 species (SDM) in Europe; and the plots of response curves of the Maxent model using only the Bio01 variable—Annual mean temperature (°C, CliMond) from: **(B)**—*L. vulgaris*; **(C)**—*T. cristatus*; **(D)**—*P. glenii*.

#### 4. Discussion

Our models show that the greatest similarity of species distribution models and habitat suitability is found for both newt species. This is well illustrated by the high value of the coefficient of determination of 67.8% used to compare the models for *L. vulgaris* and *T. cristatus*. Such modeled overlap in distribution is consistent with the fact that these two newt species do coexist in their native biotopes. Yet, biotopic specialization and shifts in phenology have been reported in these amphibians since the end of the 20th century as a result of climate change [56–58]. For instance, suitable water bodies for amphibian reproduction have recently been reported to become less abundant and smaller, with reproduce in the same water body, but at different times of the year, the number of cases of simultaneous breeding increases with more frequent overlapping of breeding seasons of different species. Yet, not all species of amphibians, being forced to share the same spawning sites by various environmental changes, can effectively and successfully breed in such conditions [56–58].

Newts are found mainly in small water bodies, streams and ditches, where they spawn in spring and in the first half of summer and then winter on land [27,28,31]. Yet, since the expansion of the invasive predatory fish *P. glenii* throughout Europe, field observations report negative impacts on native newt species. For example, in the Volyn, Rivne, Zhytomyr, and Kyiv regions of Ukraine monitored in 2017–2021 newts were found only in water bodies where *P. glenii* was not recorded (Figure 3, personal observations).

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**Figure 3.** Field observations of spawning of native newts *T. cristatus* (**lower right corner**) and *L. vulgaris* (**lower left corner**) in the same temporary seasonal pond without any presence of *P. glenii*, 29.04.2021, Rivne region, Ukraine; upper part of the picture illustrates the typical spawning water body, shared by both species of newts.

During the net capturing, very few cases of syntopic occurrence of the fish and the newt(s) were recorded. The water body types did not differ from each other, so their type did not affect the presence or absence of the animals. For example, among 31 water bodies in the Shatsk district of the Volyn region examined in May 2021 (3 lakes, 18 channels, 8 seasonal shallow ponds, 2 small rivers on the territory of approximately 5000 ha) 11 water bodies were invaded by *P. glenii*, 2 were inhabited together by *L. vulgaris* and *T. cristatus*, 10 were inhabited by one of the newt species in addition to other amphibian species, 8 water bodies did not have any of the considered species expected to be caught by a net.

However, several cases of presence of *P. glenii* and *T. cristatus* and/or *L. vulgaris* were recorded during the spawning period and the development of larvae, with the number of newts being reduced to several individuals only: (1) Rivne oblast', Sarny district, Starosil'ske forestry, an old amber-mining service channel (51.693331 N 27.089842 E); (2) Volyn oblast', Kivertsi district, and old swampy lake near the village of Berestiane (50.963063 N 25.914284 E); and (3) Zhytomyr oblast', Malyn district, an oxbow lake of Irsha river (50.761216 N 29.251534 E). In addition, field observations in Latvia reported that newt larvae found in the water bodies invaded by *P. glenii* showed more physical damages than in waters where *P. glenii* was absent [40]. Moreover, similar observations were made for another European newt species closely related to *T. cristatus*, the Danube crested newt (*Triturus dobrogicus*), where newts had not been recorded anymore in previously occupied spawning water bodies after *P. glenii* invasion [59].

Considering such dangerous invasive predatory fish species as *P. glenii*, *L. gibosus*, and others is extremely important during implementation of projects aimed on restoration of wetlands. Such projects usually include complicated counting of all factors, that play significant role for well-being of local amphibians. There are numerous examples when properly designed restored wetlands showed almost now significant differences in terms of impacts on amphibian communities. For example, during experimental

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designing of mitigation wetlands to replace wetland habitat that was lost during road construction authors have estimated occupancy of 4 amphibian species in 8 created mitigation wetlands, 7 impacted wetlands, and 7 reference wetlands in the Greater Yellowstone Ecosystem in Wyoming, USA [33]. As a result, occupancy did not differ between impacted and reference wetlands for any of the registered 4 amphibian species: western toads (*Anaxyrus boreas* Baird & Girard, 1852), Columbia spotted frogs (*Rana luteiventris* Thompson, 1913), western tiger salamanders (Ambystoma mavortium Baird, 1850), and boreal chorus frogs (Pseudacris maculata Agassiz, 1850) [33]. Another study highlighted the results of comparison of habitat suitability for smooth newt (L. vulgaris), that is the only native newt species in Ireland [36]. The study showed that even such factor as presence/absence of natural barriers (logs, stones, gulches, roads etc.) may affect the suitability of the habitat for the newt, which resulted in lower HS for L. vulgaris among constructed wetlands (2 of 8 suitable) comparing to higher HS (7 of 8 suitable) for natural wetlands [36]. However, it should be noted that presence of invasive species in this particular study was not used as a factor to be included in HS counting, as there are no knowns cases of *P. glenii* or other aggressive fish predator registered in the country. Based on our research we strongly recommend to add actual records of invasive fish presence/absence, number of registered individuals, density of populations, and other aspects to be included in the assessing of habitat suitability for native amphibian species when planning any mitigation measures towards saving of the biodiversity of wetlands.

In Latvia, when the authors created isolated wetlands within the frame of national conservation strategies (2018, 2022), the crested newt was also recorded only in geographically isolated wetlands (GIWs) located far from a large lake and where P. glenii and other fish species were not found—doctor fish Tinca tinca (Linnaeus, 1758), E. lucius and weatherfish Misgurnus fossilis (Linnaeus, 1758). In the course of this wetland creation in 2022, out of 14 ponds (7 of them are GIWs, and 7 are connected with larger water bodies), during monitoring (hoop-net mowing method), fish (*T. tinca*, *E. lucius*, *M. fossilis* and *P. glenii*) were found only in 6 non-isolated water bodies. T. cristatus (1 larvae per 10 mowings) was found in 1 GIW and in 4 GIWs L. vulgaris was registered (up to 5 larvae per 10 mowings). At the same time, in 2018, newts were found in almost all non-isolated ponds where P. glenii individuals were not found. The number of registered T. cristatus larvae was higher (up to 3 individuals per 10 mowings). Moreover, in isolated ponds, where no fish were found in 2022, 10 mowings captured up to 8 larvae of *T. cristatus* and up to 26 larvae of L. vulgaris. Thus, we conclude that only in GIWs the number of newts remain optimal, while in non-isolated wetlands for 4 years (until 2022) a negative trend in the number of recorded newts has been confirmed.

The reduction of the number and sometimes the disappearance of newt micro-populations in the south of their natural range have led to the fact that they were included in the Red Book in some countries. For example, *T. cristatus* is now included in the Red Book of Ukraine and *L. vulgaris* is now a candidate to be listed in the nearest future [28,31,60].

Consistently, our models of newt distribution in Eastern Europe show that the continental biogeographical zone has the highest priority in terms of potentially suitable territories for these native species. In the western part of this area, newts can move south into the steppe zone along the eco-corridors associated with large rivers, such as the Danube and the Dniester (Figures S2 and S3). The invasive predatory fish *P. glenii* has a similar, yet more fragmented, range (Figure S4). Our study shows that the distribution range of newts will be considerably reduced by 2050, whereas the range of their potential predator, the Chinese sleeper will on the contrary double its extend. This is consistent with field observation since 2010 when we have been reporting rapid spread of *P. glenii* in the continental zones of Ukraine and in eastern Latvia, that is also confirmed by our monitoring studies in recent years. In most cases, temporary water bodies of wetlands stay uninvaded, becoming key spawning areas for the native newts (Figure 3). Thus, alien fish-free wetlands, which many geographically isolated wetlands are often harbor more species of amphibian than typical pond or lake ecosystems. The main reason for this is that amphibians' larvae need less

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time to grow to the ontogenetic stages able to leave the water and lead a terrestrial lifestyle. Meanwhile *P. glenii* requires more time to breed and cannot escape the water. Therefore, it is impossible for the invasive fish to create a stable population in small temporary water bodies that usually dry out by the end of summer, giving enough time for the newts to complete metamorphosis and shift to terrestrial lifestyle.

According to our GIS modelling data, the range of newts and their abundance will be greatly reduced by 2050 compared to the area they used to occupy before 2000, especially in the south. *T. cristatus* will be especially affected.

Our results of the GIS-analysis are supported in recent years by numerous field investigations when wetlands, heavily invaded by *P. glenii* showed either no signs of *L. vulgaris* or *T. cristatus*, or only several individuals were found either during the peak of the breeding season or the development of larval stages [16–18,59].

#### 5. Conclusions

Two most widely distributed species of newts (*L. vulgaris* and *T. cristatus*) protected in the European Union will decrease in abundance and range, whereas the expansion of the invasive predatory fish Chinese sleeper (*P. glenii*) will intensify within the next decades. The expansion of this invasive predator, due to considerable overlap of suitable combination of bioclimatic factors, is an additional threat to native species of wetlands [61,62]. Therefore, it is necessary to establish management plans for the protection of native herpetofauna species taking adequately into account the heavy influence of invasive species and bringing their further expansion under strict control.

Suggested good practices for controlling *P. glenii* and protecting native newts include educational works with the general public and key stakeholders; control of stocking fry; banning any types of publications of alien invasive species at online marketplaces; increasing legal liability; running reintroduction programs for newts; regularly removing *P. glenii* from the ponds using fyke-nets; and GIS-modelling of the invasion and incorporation of associated results into conservation plans for newts. Of great importance in the protection of amphibians are geographically isolated wetlands (shallow and dry at the end of metamorphosis of newts) as habitats free from alien fish. Therefore, the creation of isolated water bodies should be included in active plans for the management and protection of amphibians.

Our research can serve for further plans for the restoration of the areas of wetlands that are suitable for the newts, as well as for help for their reintroduction. This study will help in future to implement practical plans for the conservation of amphibians in a global all-European scale, especially as an example of wetlands biodiversity conservation.

**Supplementary Materials:** The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/d15020201/s1, Figure S1: Result of the analysis of Binomial tests (5 bioclimatic CliMond covariates): 1—T. cristatus; 2—L. vulgaris; 3—P. glenii; a—2000, b—2050; Figure S2: GIS modeling results—Potential (probabilistic) model built with the consideration of river systems: A—T. cristatus; B—L. vulgaris; C—P. glenii; D—regression model (SAGA GIS) is used to create a new grid (SDM P. glenii and T. cristatus and/or L. vulgaris) world expansion built in the Maxent program based on the 19 environmental variables (EarthEnv NGEI, SAGA GIS, Table S1) and the most important factors. Areas of the highest habitat suitability (>0.5) are colored in red and areas of the lowest (<0.1)—in blue; Figure S3: The result of pairwise comparison of SDM grids (Potential (probabilistic) model, coefficient of determination (R2), SAGA GIS)—dependence graphs of 3 species: A—T. cristatus/P. glenii; B—L. vulgaris/P. glenii; C—T. cristatus/L. vulgaris; world expansion built in the Maxent program based on the 19 environmental variables (EarthEnv NGEI, Table S1); areas of the highest habitat suitability (>0.5) are colored in red and areas of the lowest (<0.1)—in blue; Figure S4: Maps of the joint habitation of the newts with P. glenii (red bold line shows the areas of cohabitation of the fish with the newts): A—with *T. cristatus*; B—with *L. vulgaris*; Table S1: Bioclimatic variables (35) from the CliMond dataset and 19 environmental variables (Long-term hydroclimatic variables) from the Near-global environmental information (EarthEnv NGEI) for freshwater ecosystems in 1 km resolution.

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