



Multi-method distribution modelling of an invasive crayfish (*Pontastacus leptodactylus*) at Eurasian scale

J. Hodson · J. South · T. Cancellario ·
S. Guareschi

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Abstract Globally, human activities profoundly influence biodiversity, frequently favouring biological invasions. Crayfish, prominent invaders on multiple continents, pose significant varied threats. Using species distribution models (SDMs), this study explores the current and future potential distribution of *Pontastacus leptodactylus*, a widely introduced but understudied crayfish, at Eurasian scale. Climate is crucial for most species' distributions and historically SDMs focused primarily on these variables, while overlooking other environmental factors influencing species occurrence. This research employed 2 approaches: one climatic and one broader environmental model

encompassing soil pH and elevation data. Both methods revealed high suitability for the species, particularly currently in Central-Europe. Future climate scenarios for 2050 do not seem to favour the species in terms of intermediate-high suitability regions, with contractions also in the native regions with both approaches. However, remarkable discrepancies were observed in some North-European regions; with the climatic approach predicting high suitability where the environmental approach did not. This study identifies *P. leptodactylus* as a widespread successful species outside its native range with potential for expansion under current conditions. The synthesised continental overview and projected distribution maps aid in prioritising monitoring and prevention efforts while underlining the importance for using environmental as well as climatic variables in SDMs.

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J. Hodson · J. South
Water@Leeds, Faculty of Biological Science, University of Leeds, Leeds, UK

T. Cancellario
Department of Biology, Balearic Biodiversity Centre, University of the Balearic Islands, Palma, Spain

S. Guareschi (✉)
Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy
e-mail: simone.guareschi@unito.it

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Introduction

Globally, biological invasions are one of the most evident symptoms of human activities on biodiversity distribution (IPBES, 2023). The rate of invasions is not predicted to saturate in the future and will likely increase with climate change precipitating higher rates of successful establishment (Rahel & Olden,

2008; Pecl et al., 2017; Seebens et al., 2020). Inland waters are particularly vulnerable to biological invasion due to high connectivity between systems and a pervasive lag in detection time which makes early management particularly challenging (Strayer et al., 2006; Simberloff, 2021; Guareschi et al., 2021). Thus, to reduce future negative outcomes, an emphasis should be on preventing successful establishment of invasive species (Strayer, 2010), meaningful biosecurity legislation needs to be pre-emptive rather than reactive. By predicting which areas are threatened by invasion and how this may adjust with future scenarios, policy can be implemented proactively to prevent invasion and manage potential high impact invasive species (Bradley et al., 2023).

Freshwater crayfish are extremely successful global invasive species which have multiple and varied ecological and economic impacts (Twardochleb et al., 2013; Kouba et al., 2022). Crayfish are large-bodied polytrophic omnivores which consume resources across the food web and alter nutrient cycling through shredding behaviour (Dunoyer et al., 2014; Doherty-Bone et al., 2018; South et al., 2019; Madzivanzira et al., 2022). Predation and ecological engineering, through burrowing behaviours, have caused decline in native species and long-term change to macro-invertebrate and fish communities (Mathers et al., 2020; Galib et al., 2021; Sanders et al. 2021).

Pontastacus leptodactylus (Eschscholtz, 1823) (Crustacea: Decapoda, common name: narrow-clawed crayfish), despite uncertainty regarding the validity of the species complex (Bláha et al., 2023), is considered as native to the Ponto-Caspian region (e.g., drainage areas of the Azov, Black, and Caspian Seas, but also the lower Danube catchment area: Kouba et al., 2014; Bláha et al., 2023). It is one of the largest freshwater crayfish species, with a maximum body length of *ca.* 200 mm and mass of up to 178 g (Bök et al., 2013) and can be found in freshwater and brackish environments (Holdich et al., 1997) inhabiting both lotic (e.g., rivers) and lentic ecosystems (e.g., coastal areas of lakes and reservoirs). Due to these traits, the species has been widely introduced in Central and Northern Europe through the aquaculture pathway and in some instances to support fisheries (Alvanou et al., 2022; Bláha et al., 2023). Recent range expansions into northern Europe have been attributed to climate change reducing the thermal

invasion barrier to establishment (invasive status *sensu* Blackburn et al., 2011) and thermal plasticity in the species (e.g., Berezina et al., 2021). Some flagship invasive crayfish species have been studied intensively (e.g. *Pacifastacus leniusculus* (Dana, 1852) and *Procambarus clarkii* (Girard, 1852)), to predict and understand their invasive ranges and trajectories (e.g., Zhang et al., 2020; Guareschi et al., 2024). However, other potentially damaging non-native crayfish, such as *P. leptodactylus*, remain considerably under-studied to date, with records being rather old and scattered for various reasons (e.g., complex phylogeographic patterns, morphological diversity, and nomenclatural status, Bláha et al., 2023).

Robustly determining species future invasive range is a key step in creating preventative policy for biodiversity conservation. Species Distribution Models (SDMs) can be useful tools to predict potential suitable habitat for invasive species by incorporating bioclimatic and environmental variables with species occurrence data (Jeschke & Strayer, 2008; Guareschi et al., 2024). This can identify bridgehead regions through which invasion is likely, and areas of high invasion risk by single or multiple species as well as areas to be prioritised for protection (e.g., Guareschi et al., 2013; Gallardo & Aldridge, 2020; Ricciardi et al., 2020).

The distribution of a wide range of invaders is primarily limited by climate (Gallardo et al., 2015). Historically, many SDMs have mostly focused on climatic variables due to their wide availability at different scales, with little or limited consideration of other environmental variables (Gallardo & Aldridge, 2013; Zhang et al., 2020). However, species occurrence is not determined solely by climate (e.g., Heikkinen et al., 2006; Cosentino et al., 2023). Environmental characteristics such as elevation, soil characteristics, water parameters, and flow are also important (Pârvolescu & Zaharia, 2013; Beaune et al., 2018; Dornik et al., 2021; Satmary et al. 2023), but they can be difficult to obtain or integrate at large spatial scale. For instance, elevation is considered as a key, yet challenging, variable in SDMs as it is related to multiple features like topography, vegetation, and land uses. In some cases, its inclusion when modelling showed an increasing predictive accuracy compared to climate-only models (e.g., butterflies: Luoto & Heikkinen, 2007) and it has also been stressed as a relevant environmental predictor affecting crayfish (Mozsár et al.,

2021) and other freshwater taxa distributions (amphipods: Cancellario et al., 2023; fish: Markovic et al., 2012). Other factors, such as soil pH, can influence the availability of nutrients to plants and may consequently affect land cover in terms of vegetation, as well as have implications on the mobility of organic matter and nutrients in the recipient freshwaters (Osafu et al., 2023). Moreover, low value of water pH can be a limiting factor for calcifying organisms (like crayfish) as low pH directly affects calcification, moulting, growth and reproduction (e.g., Beaune et al., 2018). Thus, incorporating multiple variables into SDMs can enhance outputs and better inform future best practices.

Therefore, in this paper, we aim to compile and update the current known distribution of *P. leptodactylus* at global scale. Using this information, we will project *P. leptodactylus* current and future potential distributions at Eurasian scale under different climate change scenarios. This will provide a detailed spread risk assessment for *P. leptodactylus* in current and future conditions supporting proactive policy making for this potentially damaging non-native species. To explore the relevance of different variables, we focussed on two different approaches: i) a strictly climatic model, and ii) one using both climatic and environmental variables. This allows for further direct comparison of distributional patterns (e.g., overlap) obtained with different approaches.

Methods

Biological data

Distribution of *P. leptodactylus* was retrieved from occurrences on the Global Biodiversity Information Facility database (GBIF, 19 December 2023, <https://doi.org/10.15468/dl.gumenv>) and through additional literature searches for *P. leptodactylus* and its basionym *Astacus leptodactylus* (reference list and details available in S1) which compiled information from scientific and grey literature as well as technical reports.

Location data gathered covered both native and invaded ranges, as recommended to accurately model the invasive species' potential ranges (Sánchez-Fernández et al., 2011; Jiménez-Valverde et al., 2011; Santamarina et al., 2023). For numerous invasive

species it is quite common that most of the research focuses on the species' invasive ranges with the peculiar pattern of displaying more records in their invaded regions compared to the presumed native range (e.g., invasive amphipods: Cancellario et al., 2023). To minimise the risk of spatial biases during distribution modelling, duplicates were removed and a spatial thinning approach applied. Occurrences were thinned to a minimum of 20 km between records using the spThin R package (v 0.2.0; Aiello-Lammens, 2015). This was due to the unbalanced high number of records in areas particularly well studied and historically sampled (e.g. western Europe). In scientific bibliography, different values (e.g., 18 km in Guareschi et al., 2024, > 50 km distance in Jarnevich et al., 2018) have been used in multi continental contexts. In our specific case, a value of 20 km represented the best compromise between predictors' data and the need to ensure a large dataset (e.g., > 500 occurrences) for modelling. It produced 649 data points from the original 2,244 that representatively cover the current known distribution of the species at global scale, avoiding redundant/spatial biased information (Fig. 1).

Climatic and environmental approaches

To investigate the Eurasian suitability of *P. leptodactylus* we used two different approaches that differ by the nature and pool of predictors considered: i) climatic and ii) environmental (see Table 1). The first approach is a strictly climatic model that relies on the starting pool of predictors composed of the 19 climatic variables obtained from WorldClim V2.1 (Fick & Hijmans, 2017). To go beyond a climatic focus, the second approach expanded the climatic set of variables by also including environmental predictors that can affect the distribution of the species, like elevation and soil pH (e.g., Hof et al., 2012; Osafu et al., 2023). Elevation data (altitude above sea level) was obtained from WorldClim V2.1 while soil pH (0–5 cm) from the worldwide dataset SoilGrids2.0 (Poggio et al., 2020). In the latter, an Inverse Distance Weighted (IDW) interpolation has been used in cases of areas with no data due to reasons such as artificial or urban surfaces. IDW calculates values for locations based on nearby known values, assigning greater influence on closer known values. It has been extensively used in spatial interpolation for environmental

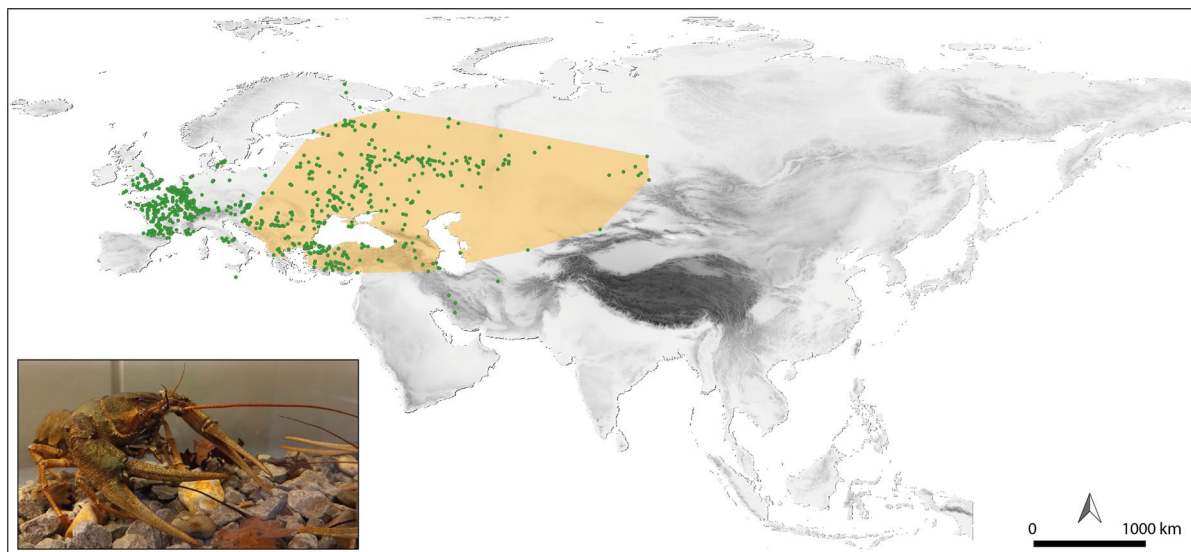


Fig. 1 Occurrences used in SDM analysis after spatial thinning procedure (649 occurrences). More details are provided in the Methods section. Grey colour represents elevation layer (higher values with darker colour). The presumed native area

is delineated with a Minimum Convex Polygon (highlighted in yellow), based on information from Kouba et al. (2014) and Bláha et al. (2023)

Table 1 List of climatic and environmental variables considered in the research. Complete details about variables selection are available in S3. A quarter is a period of three months (1/4 of the year). In bold the variables used when modelling

	Definition	Source
<i>Climatic variables</i>		
BIO1	Annual Mean Temperature (°C)	WorldClim V2.1
BIO2	Mean Diurnal Range (Mean of monthly (max temp—min temp)) (°C)	WorldClim V2.1
BIO3	Isothermality (BIO2/BIO7) (× 100)	WorldClim V2.1
BIO4	Temperature Seasonality (standard deviation × 100)	WorldClim V2.1
BIO5	Max Temperature of Warmest Month (°C)	WorldClim V2.1
BIO6	Min Temperature of Coldest Month (°C)	WorldClim V2.1
BIO7	Temperature Annual Range (BIO5-BIO6) (°C)	WorldClim V2.1
BIO8	Mean Temperature of Wettest Quarter (°C)	WorldClim V2.1
BIO9	Mean Temperature of Driest Quarter (°C)	WorldClim V2.1
BIO10	Mean Temperature of Warmest Quarter (°C)	WorldClim V2.1
BIO11	Mean Temperature of Coldest Quarter (°C)	WorldClim V2.1
BIO12	Annual Precipitation (mm)	WorldClim V2.1
BIO13	Precipitation of Wettest Month (mm)	WorldClim V2.1
BIO14	Precipitation of Driest Month (mm)	WorldClim V2.1
BIO15	Precipitation Seasonality (Coefficient of Variation)	WorldClim V2.1
BIO16	Precipitation of Wettest Quarter (mm)	WorldClim V2.1
BIO17	Precipitation of Driest Quarter (mm)	WorldClim V2.1
BIO18	Precipitation of Warmest Quarter (mm)	WorldClim V2.1
BIO19	Precipitation of Coldest Quarter (mm)	WorldClim V2.1
<i>Env. variables</i>		
Elevation	Altitude above sea level (mean value at cell scale) (m)	WorldClim V2.1
Soil pH	Soil pH (0–5 cm) calculated in water	SoilGrids2.0

modelling due to its computational efficiency (e.g., Mitas & Mitasova, 1999; Susanto et al., 2016). Finally, both approaches have been performed at 2.5 min resolution (4.5 km × 4.5 km at equator).

To avoid collinearity issues, in both approaches we first performed a hierarchical cluster analysis, resulting in a dendrogram indicating the similarity among all variables (Dormann et al., 2013). The chosen distance-threshold to select variables in the cluster was set at 0.3 (i.e., less than 70% correlation), following Rodrigo-Gómez et al. (2021). Variance Inflation Factor (VIF) was then applied to exclude variables with the highest multicollinearity (VIF > 3) on an individual basis using a stepwise procedure (Heiberger & Holland, 2015). The selection process steps are further outlined in S3. Overall, here we refer to “climatic suitability” as synonyms of the geographical representation suitable for the species when strictly climatic predictors are taken into account and use “environmental suitability” when an expanded set of variables is considered (climate, elevation, soil pH). Given the presumed native range of the species (e.g., Ponto-Caspian region, Anatolian Plateau, Fig. 1) and its current invasion into areas such as central-north Europe, focusing on a Eurasian scale emerges as particularly significant.

Estimation of species potential distributions: modelling procedure

To perform species distribution modelling, we used the R package biomod2 (v. 4.2–4; Biodiversity MODelling, Thuiller et al., 2009, 2023). Four widely applied algorithms (from different family of modelling algorithms, see details in S2) were used to model the potential distributions of the species: Generalized Linear Models (GLM), Generalized Boosted Models (GBM), Random Forest (RF) and Maximum Entropy Modelling (Maxent). Absence information is rarely available in record-based compilations and often scarcely reliable in the case of non-native and invasive species. For this reason, we randomly selected 10,000 background absence points from the studied area, a common practice in these cases (e.g., Gallardo & Aldridge, 2020; Santamarina et al., 2023). The absence randomization process was repeated three times to avoid results being affected by any specific set of background absences. The predictive performance of the models was evaluated by randomly

splitting the presence into two subsets: 70% of the original data was used for training the models, and the remaining 30% for evaluation (Araújo & New, 2007). This procedure was repeated with randomly mixed presences for each of the three replicates. Three cross-validations were run to account for the uncertainty associated with dataset partitioning. Thus, for each projection 36 model replicates (4 algorithms × 3 background absence sets up × 3 validations) were run.

Model performance was assessed using the true skill statistics (TSS) and the receiver operating characteristic curve (ROC). In both the closer the value to 1 (perfect discrimination), the better the model performance. Single model projections and TSS performance were used to create a weighted mean ensemble model (EMwmeanByTSS following Sherpa et al., 2022) in which only model replicates over a TSS threshold of 0.7 were used to reduce uncertainties associated with individual species distribution models (e.g., Araújo and New, 2007; Guareschi et al., 2024). Within the ensemble model variable importance was assessed using the “get_variables_importance” function of biomod2 with higher values indicating greater importance (Thuiller et al., 2023). All analyses were performed in R (v. 4.2.1; R Core Team, 2022) and data were visualised in QGIS (v. 3.28; QGIS.org, 2023).

Future potential distributions

The future potential distributions of *P. leptodactylus* were modelled using the CMCC-ESM2 global climate model for 2041–2060 (here coded 2050) obtaining future climatic scenarios from WorldClim v. 2.1 (Fick & Hijmans, 2017). We created the same type of climatic and environmental layers as described above for the current scenario. Shared socioeconomic pathways (ssp) 2–4.5 and 3–7.0 were explored, reflecting an intermediate and intermediate-high CO₂ emissions climate scenario. In ssp 2–4.5 mean warming is limited to around 3°C while in ssp 3–7.0 CO₂ levels continue to rise until 2100 but remain lower than ssp 5–8.5 (Hausfather, 2019). The latter, more extreme scenario, was avoided as recently recommended by Hausfather and Peters (2020). Geographic contractions and expansions are then explored examining both modelling approaches through time.

Finally, once we obtained the projection for the ensemble models, we converted the continuous

suitability maps into presence/absence (binary) layers using the threshold of suitability > 500 (biomod2 produces ensemble models with suitability value ranging from 0 to 1,000). This has been done for all scenarios (present and future) to assess spatial overlap between the two approaches (climatic vs environmental) and through time (see similar procedures in Cuyckens et al., 2016; Fournier et al., 2017; Cancellario et al., 2023). The robustness of the value 500 was confirmed by using the “bm_FindOptimStat” function (data not shown). This function suggests the threshold for converting continuous values to binary ones, optimizing the evaluation metric (in this case, true skill statistics—TSS). The areas with suitability > 500 are then considered zones of intermediate-high suitability (IHS) for the species and have been further explored at both Eurasian scale and native areas. The latter has been defined as just “presumed” in the review of crayfish distributions by Kouba et al. (2014). Taking this into account, we defined a tentative native range for the species following both Kouba et al. (2014) and the recent Bláha et al. (2023) using a conservative approach via minimum convex polygon (Fig. 1).

Results

To the best of our knowledge the occurrence dataset collated represents the most comprehensive geographical information available about the species and updates its distribution at a multicontinental scale (details in S1). Occurrences ranged from 1875 to 2023, although the majority fell within the period 1970–2023. After exploring for collinearity, 7 out of 21 variables (19 bioclimatic plus 2 environmental) were retained and used during modelling: Mean Diurnal Range (BIO2), Isothermality (BIO3), Mean

Temperature of Wettest Quarter (BIO8), Precipitation Seasonality (BIO15) and Precipitation of Coldest Quarter (BIO19), Elevation and soil pH (see Table 1 and values in S4). The climatic approach focussed just on the 5 climatic variables while the environmental perspective also included Elevation and soil pH. Regarding ensemble models, the most important variable for determining climatic suitability was BIO19 (0.27 ± 0.002 , mean \pm SD), followed by BIO15 (0.21 ± 0.002) and BIO3 (0.19 ± 0.001) while for determining environmental suitability (which uses both climatic and environmental predictors) it was BIO19 (0.29 ± 0.003), followed by BIO15 (0.17 ± 0.003) and pH (0.15 ± 0.002) (see S5 for variable importance results for each algorithm).

Ensemble models performed remarkably with TSS and ROC values of 0.76 and 0.94 for the climatic approach and 0.78 and 0.95 for the environmental approach. Within each approach, RF showed the highest TSS and ROC values (single evaluation plots available in S6).

Climatic potential distributions

Under a purely climatic approach, 13.6% of Eurasia may currently provide an intermediate-high level of suitability for *P. leptodactylus*. This slightly decreases when projected into 2050 under both climate scenarios: to 11.7% (ssp 2–4.5), and 11.4% (ssp 3–7.0, see Table 2). Ensemble model results indicated that much of western to eastern central Europe (e.g., Britain, Ireland, Denmark, Germany, France, Italy, the Balkan Peninsula, southern Sweden, central-northern Iberia, as well as some areas of eastern Europe and south-eastern Russia) currently provide suitable climatic conditions for the species (Fig. 2a and zooms in S7). Sections of Iceland were also identified as

Table 2 Percentage of Intermediate-High suitability (IH) in different temporal scenarios and approaches. Values for the tentative native areas are also displayed

Approach	Scenarios	% of IH suitability (Eurasian scale)	% of IH suitability (native area)
Climatic	Current	13.6	37.7
	ssp 2.45 at 2050	11.7	26.1
	ssp 3.70 at 2050	11.4	24.4
Environmental	Current	11.2	34.2
	ssp 2.45 at 2050	6.8	13.7
	ssp 3.70 at 2050	7.2	15.3

being suitable. Currently the majority of Asia was not identified as being particularly favourable for the species, except for native range areas around the Black Sea and Caspian Sea, and restricted areas in northern India, south-eastern China, Japan and Russia's Kamchatka peninsula (Fig. 2a). Considering future climate scenarios, the results remain broadly similar in both 2050 projections (Fig. 2b,c). Intermediate-high suitable areas remain consistent in central-western Europe, but reduce in eastern Europe, Ukraine and Russia. Their percentage values were higher when just focusing on the native region, ranging from 37.7% (current scenarios) to 24.4% (future scenarios, Table 2).

Environmental potential distributions

Under the environmental approach 11.2% of Eurasia may currently provide an intermediate-high level of suitability for *P. leptodactylus*. This decreases when projected into 2050 under both climate scenarios to 6.8% (ssp 2–4.5), and 7.2% (ssp 3–7.0, Table 2). Ensemble model results indicated that much of western to eastern-central Europe (except for mountain systems like the Alps and Pyrenees) currently provide highly suitable climatic conditions for *P. leptodactylus* (Fig. 3a and zooms in S7). This included areas of France, Germany, Italy, England, Ireland, Denmark, the Balkan Peninsula, the central Iberian Peninsula, the Baltic countries as well as some south areas of Russia. Sections of Iceland were still identified as being suitable, while, mirroring the climatic scenario, the majority of Asia was not identified as being particularly favourable for the species, except for native range areas around the Black Sea and Caspian Sea and a few restricted areas (Fig. 3a). Overall, considering future climate scenarios (Fig. 3b,c), the amount of area suitable for *P. leptodactylus* remained constant in western and central Europe, while strongly reducing in eastern Europe and south-western Russia, being similar considering both ssp 2–4.5 and 3–7.0 projections. When considering intermediate-high suitable areas, percentage values were higher when just focusing on the tentative native area, ranging from 34.2% (current scenario) to 13.7% (future scenarios, Table 2).

Modelling approach comparisons: Climatic vs Environmental

Both approaches exhibited similar patterns for future projections of areas reducing in suitability (red areas in Fig. 4), but they diverged in their outputs when examining areas increasing in suitability, which were primarily appreciable through the climatic approach (blue areas in Fig. 4a and 4c). Considerable areas that appear to be undergoing potential contraction belong to regions labelled as native (Fig. 1 and 4).

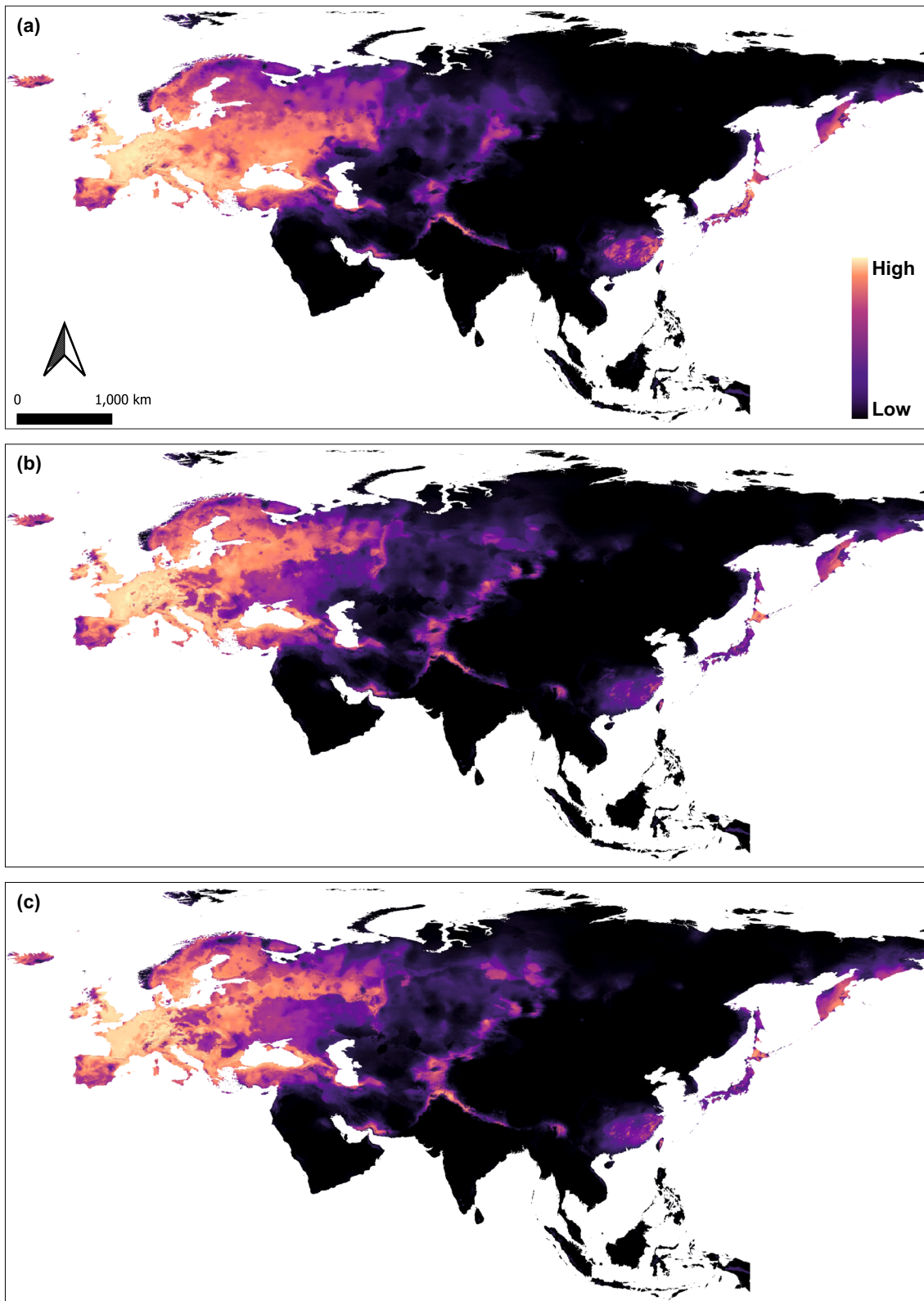
Currently, there is a 72.3% overlap in the areas detected with intermediate-high level of suitability (>500) predicted by both approaches (Fig. 5, Table 3). The overlap mainly occurred in a band across western-eastern Europe, south-western Russia, southern Europe, and native ranges around the Black Sea and Caspian Sea. Differences lie mainly in the climatic prediction of suitability in Scandinavian Peninsula (N Europe), and the environmental prediction of increased suitability in Latvia, Estonia and central Russia (Fig. 5a).

When projected to 2050, the percentage of overlapping suitable areas decreased in similar way (52.2% in ssp 2–4.5 and 54.8% in ssp 3–7.0). In 2050 the overlap is mainly in central-western Europe, and along the upper regions of the Mediterranean basin, as well as around the Black Sea (Fig. 5b-c). The main difference in 2050 between both modelling approaches is swathe of highly climatically suitable area predicted in northern Europe (e.g., Scandinavian region) and central-western Russian, with which there is no overlap. Again, overlap is broadly similar between both 2050 climate scenarios, however in ssp 2–4.5 there is slightly greater overlap detectable in Baltic areas.

Overlap values between approaches were higher when focusing just on the native area in the current scenario (80.1%) and decreased similarly, to between 48.5 and 55.9%, when considering the 2050 scenarios (Table 3).

Discussion

Determining future potential species distributions is critical for effective biosecurity policy. *Pontastacus leptodactylus* records are spread across multiple European and Asian countries, some (e.g., France,



◀**Fig. 2** Strictly climatic approach: **a** current potential distribution of *P. leptodactylus* in Eurasia; **b** future potential distribution of *P. leptodactylus* for 2050 considering ssp 2–4.5 scenario; **c** future potential distribution of *P. leptodactylus* for 2050 considering ssp 3–7.0 scenario. Suitability ranges from 0 (black—low) to 1000 (light yellow—high)

the UK) clearly outside its native range. Despite this, distribution data at a broader scale was highly scattered across a variety of sources, and there was no research on potential distributions under future climate change scenarios. Therefore, we synthesised a continental overview of *P. leptodactylus*' known distribution and proposed maps of current and future potential distribution based on two complementary modelling approaches. Ensemble species distribution models confirmed highly suitable conditions exist across numerous geographic areas of Europe that have already been colonised by the species. This conclusion was supported through both the climatic and environmental models. The results also allowed detection of potential contact zones among currently colonised regions and potential areas with remarkable suitability (e.g., large regions of Iberian Peninsula and Italy, but also areas of northern Europe) and can be used to prioritise locations for monitoring across Eurasian water bodies.

There is still high potential for *P. leptodactylus* range to expand based on currently invaded locations, despite ultimate contractions in intermediate-high suitable areas forecasted by both approaches and climate scenarios. Moreover, rapid adaptation and potential shifts in ecological niche may also facilitate *P. leptodactylus* in overcoming thermal stresses, as observed in other expanding species (e.g., Liu et al., 2020; Chown & McGeoch, 2023; Viana et al., 2023). However, similar to the predicted reduction in range with climate change for signal crayfish, *Pacifastacus leniusculus* (Gallardo & Aldridge, 2013; Zhang et al., 2020), SDMs indicated that changing climate considered will not further benefit the invasion range of *P. leptodactylus* and will likely cause contractions in the native area. Invasive species often show niche conservatism and environmental matching where they are pre-adapted to an optimal range of climatic conditions, although aquatic species have higher potential for niche expansion (Liu et al., 2020; Nikkel et al., 2023). Therefore, rather than a blanket assertion that climate change will favour most invasive species, it

should be considered that there will instead be a constant shift in gamma diversity and community composition reorganisation (Haubrock & Soto, 2023; Briski et al., 2023).

In SDMs, bioclimatic data have been shown to be useful in predicting species distributions, including invasive crayfish (e.g., Guareschi et al., 2024). Nevertheless, complementary environmental approaches, developed in parallel, can be used to further refine and better anticipate possible trajectories of invasions. In this study, despite both approaches showing similarly high TSS and ROC indicator values, their geographical representations varied considerably. The climatic model identified a northerly shift in European distribution which matched future predictions for other invasive crayfish (Gallardo & Aldridge, 2013; Zhang et al., 2020), that was not identified in the environmental model. This indicates potential mismatches when aiming to disentangle or anticipate invasion patterns.

Precipitation data (e.g., patterns and quantity of rainfall) were important variables in both the climatic and environmental models. Precipitation significantly influences crayfish distribution and richness via habitat availability and quality, fostering habitat connectivity and temporary establishment in intermittent waterbodies (Díaz-Paniagua et al., 2014), while potentially enhancing resource availability, substrate characteristics and reducing competition (e.g., Walker & Entekin, 2023; Wood et al., 2024). When included, soil pH was particularly relevant for determining environmental suitability, and should be incorporated in future studies relating to *P. leptodactylus*. Indeed, soil-related predictors have been associated with crayfish distribution in numerous European species, including *P. leptodactylus* which was also associated with high clay content and deep sediment cover (Dornik et al., 2021). Thus, we recommend that both modelling approaches are considered to obtain the most robust predictions, and that the incorporation of environmental variables will assist management decisions, especially in the early detection phase (Funk et al., 2020). To support this integration, we also emphasise the value of broad scale environmental datasets (such as soil pH) and other aspects that could be made available through remote sensing applications (e.g., Randin et al., 2020).

Furthermore, organisation of biological communities is not only driven by abiotic factors; biotic

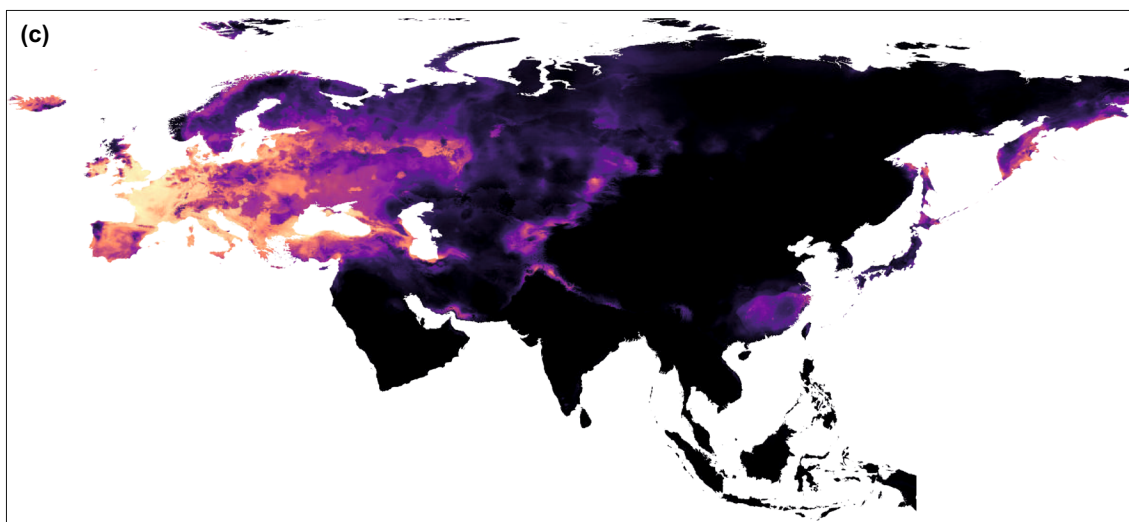
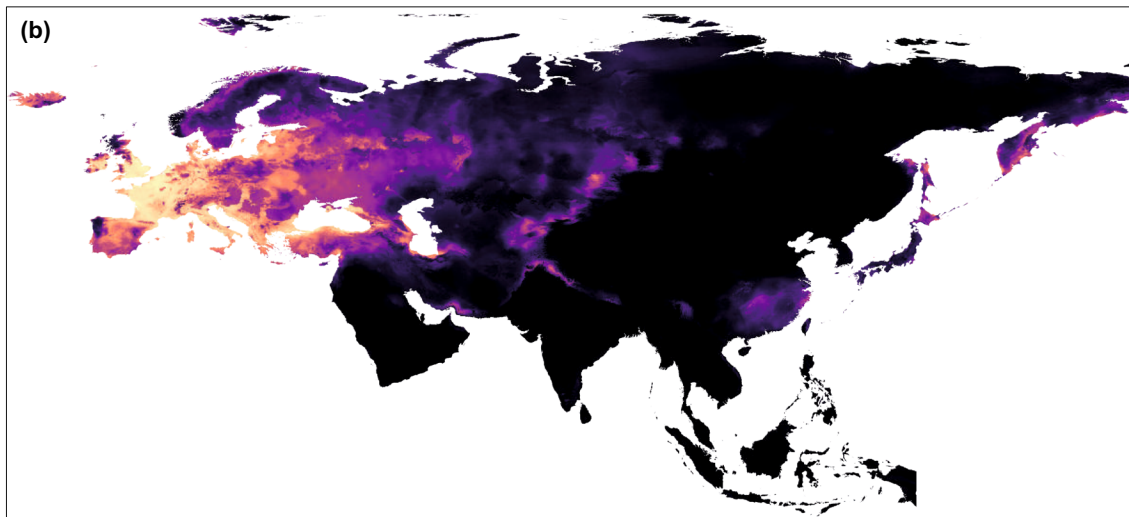
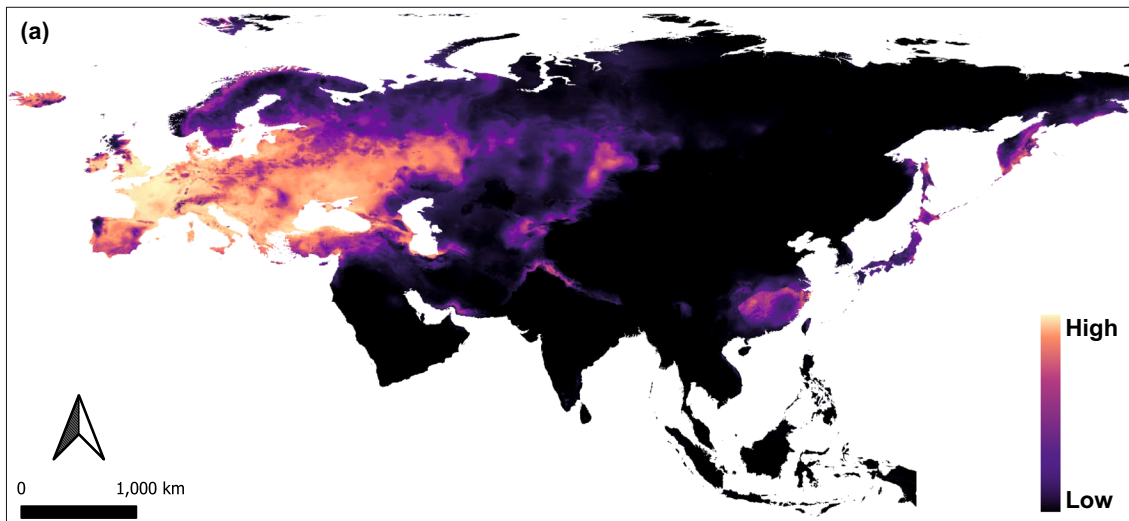


Fig. 3 Environmental approach: **a** current potential distribution of *P. leptodactylus* in Eurasia; **b** future potential distribution of *P. leptodactylus* for 2050 considering ssp 2–4.5 scenario; **c** future potential distribution of *P. leptodactylus* for 2050 considering ssp 3–7.0 scenario. Suitability ranges from 0 (black–low) to 1000 (light yellow–high)

interactions are also critical in determining species presence and shaping diversity trends across environmental gradients (Blois et al., 2013; Cosentino et al., 2023; Paradinas et al., 2023). In ecologically degraded regions, there is often a decrease in biotic resistance which can facilitate tolerant non-native species establishment and potential invasion meltdown (Tilman, 1999; Simberloff & Von Holle, 1999; Alofs & Jackson, 2014). Alternately, over-invasion scenarios by functionally similar species, such as *P. leniusculus*, can also cause new competition and co-introduce pathogens such as the causative agent of

crayfish plague *Aphanomyces astaci* Schikora, 1906 which may displace species (Russell et al., 2014; James et al., 2015; South et al., 2020). Interestingly, while *A. astaci* can have devastating impacts on *P. leptodactylus*, some populations have shown resilience to the pathogen depending on the haplotype of *A. astaci* (Svoboda et al., 2017; Kokko et al., 2018). Therefore, the incorporation of joint species distribution models and biotic interactions may help in refining and improving potential distributions (e.g., Cosentino et al., 2023; da Silva et al., 2023; Paradinas et al., 2023). Equally, this can be challenging to smoothly integrate when working at continental or global scale.

Similarly, attempts to integrate physiological limits, like the reproductive thermal tolerance, into species distribution models should be explored. Males may become sterile, or sperm may become less potent at sub-lethal temperatures, which ultimately drives

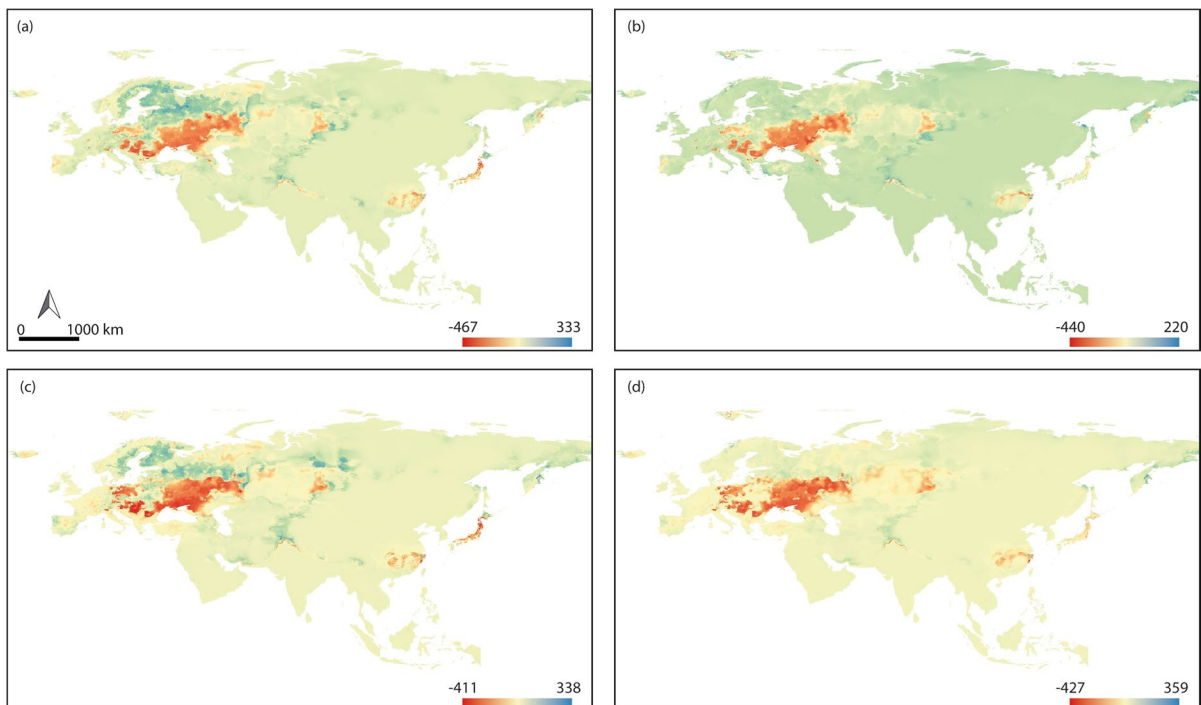
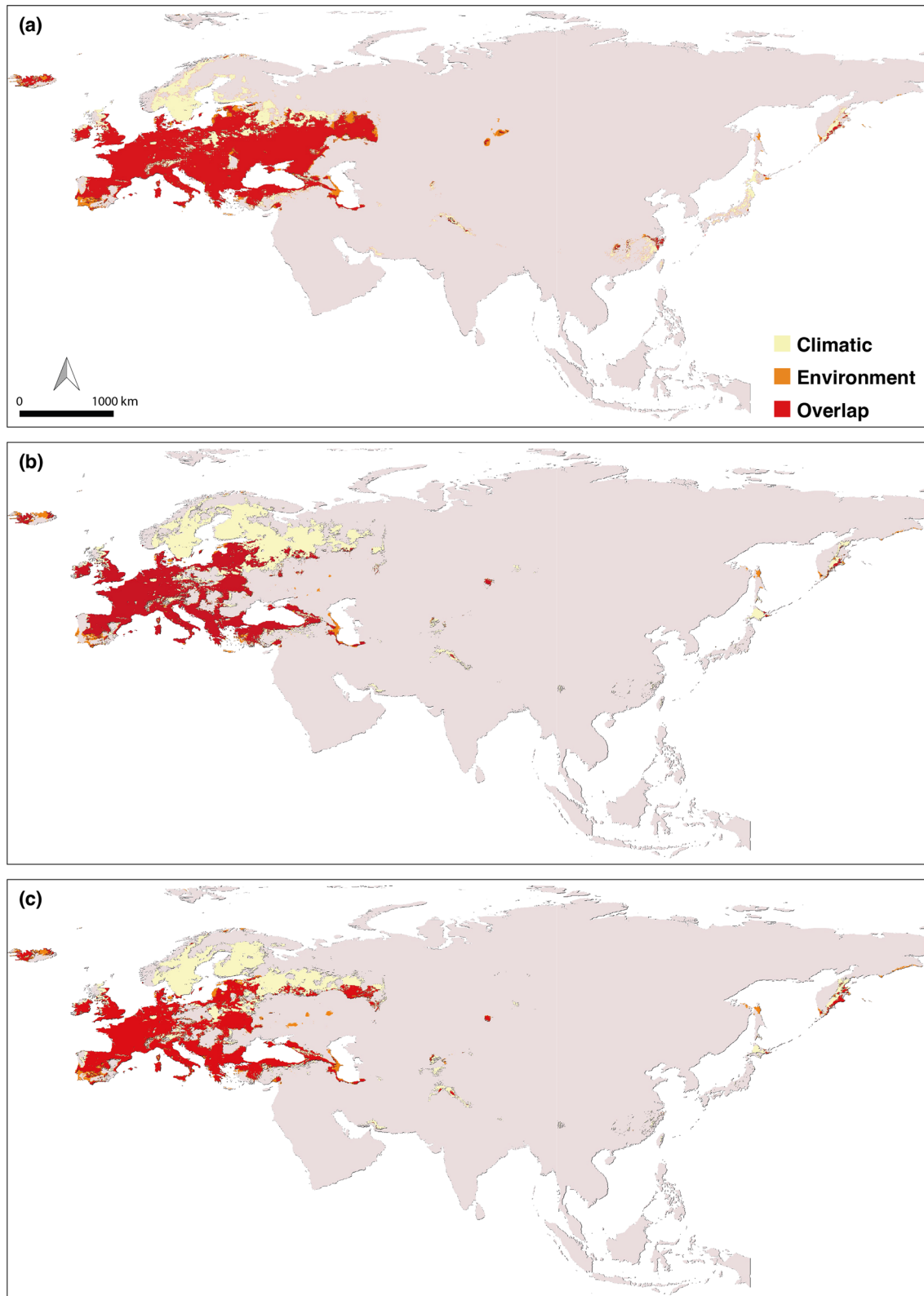


Fig. 4 Range size changes of the narrow-clawed crayfish *Pontastacus leptodactylus* under future climate scenarios. Climatic evolution is displayed on the first column (left): **a** current vs ssp 2–4.5 at 2050; **c** current vs ssp 3–7.0 at 2050. Environmental evolution is displayed on the second column (right): **b** cur-

rent vs ssp 2–4.5 at 2050; **d** current vs ssp 3–7.0 at 2050. Loss (in red) indicates areas which suggested contractions for the species in future; gain areas (in blue) represent areas that may expand in the future



◀**Fig. 5** Maps indicating geographical areas with intermediate-high level of suitability (IHS) for the species (i.e., values > 500) at Eurasian scale. **a** current conditions; **b** ssp 2–4.5 at 2050; **c** ssp 3–7.0 at 2050. Overlapping areas are labelled in red

realised environmental niche (Wang et al., 2009; Parratt et al., 2021; Harishchandra et al., 2022; Gong et al., 2023). It has been postulated that water temperatures of 19 °C reduce spermatozoal production in *P. leptodactylus* compared to their optimal reproductive temperature of 7–12 °C (Skurdal & Taugbø, 2002; Farhadi & Harlioglu, 2018). Therefore, similar water temperatures may slow the spread of the species without necessarily hindering establishment and thus these limits should be considered.

In conclusion, narrow-clawed crayfish have the potential to be a wide-spread invader, especially in Europe in which there are currently suitable, uninvaded areas which may be colonised. Our outcomes can guide and facilitate decision-making for the monitoring and control of *P. leptodactylus*. Looking forward, patterns of precipitation, and temperature associated with climate change will not particularly benefit narrow-clawed crayfish, with potential contractions also in the postulated native region (Blaħa et al., 2023). This finding hints towards the invasion paradox, wherein localities which the species has no eco-evolutionary context become more suitable than the native ranges (Marchetti & Engstrom, 2016). Better understanding of the biotic interactions which underpin the success of establishment and species biogeography are needed to make accurate assessments of conservation and invasion management, without these any assertion is speculative. In this context, we highly recommend that new confirmed records should be incorporated into the model and

Table 3 Summary of the overlap detected between methods (climatic vs environmental) in different temporal scenarios

Climatic	Environmental	Overlap Eurasian scale (%)	Overlap native range (%)
Current	Current	72.3	80.1
ssp 2.45 at 2050	ssp 2.45 at 2050	52.2	48.5
ssp 3.70 at 2050	ssp 3.70 at 2050	54.8	55.9

Values for the tentative native areas are also displayed

maps to refine estimates of potential distributions. While there was little difference in model performance, comparing climatic to environmental modelling approaches reveals some differences in output. Thus, we would suggest caution when relying solely on one type of approach when modelling spatial distribution and encourage further exploration of biologically relevant variables.

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Author contributions J. Hodson: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. J. South: Conceptualization; investigation; project administration; visualization; writing – original draft; writing – review and editing. T. Cancellario: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – review and editing. S. Guareschi: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – review and editing.

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Data availability The raw data that support the findings of this study are available in the supplementary materials. Scripts and raster layers in OSF here: https://osf.io/fz953/?view_only=85527dc4a24b443e869e74e54d8dc22d

Declarations

Conflict of interest The authors declare that they have no potential conflict of interest in relation to the study in this paper.

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References

- Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic & B. Vilela, 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545.
- Alofs, K. M. & D. A. Jackson, 2014. Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. *Ecology* 95: 3259–3270.
- Alvanou, M. V., D. K. Papadopoulos, A. Lattos, I. Georgoulis, K. Feidantsis, AP. Apostolidis, B. Michaelidis & I. A. Giantsis, 2022. Biology, distribution, conservation status and stocking perspective of freshwater crayfish in Greece: an updated review. *Aquaculture Research* 53: 5115–5128.
- Araújo, M. B. & M. New, 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22: 42–47.
- Beaune, D., Y. Sellier, G. Luquet & F. Grandjean, 2018. Freshwater acidification: an example of an endangered crayfish species sensitive to pH. *Hydrobiologia* 813: 41–50.
- Berezina, N., P. Terentjev, A. Sharov & A. Maximov, 2021. New records and disappearance from old sites of narrow-clawed crayfish *Pontastacus leptodactylus* in northwestern Russia. *BioInvasions Records* 10: 894–903.
- Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson & D. M. Richardson, 2011. A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339.
- Bláha, M., J. Patoka, T. Policar, K. Šliwińska, A. Alekhovich, N. Berezina, A. M. Petrescu, L. Mumladze, A. Weiperth, M. Jelic & P. Kozák, 2023. Phylogeographic patterns of genetic diversity in *Pontastacus leptodactylus* (Decapoda: Astacidae): is the hypothesis of the taxonomically rich genus *Pontastacus* true? *Zoological Journal of the Linnean Society* 199: 140–155.
- Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick & S. Finnegan, 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341: 499–504.
- Bök, T. D., H. Aydın & C. Ateş, 2013. A study on some morphological characteristics of *Astacus leptodactylus* (Eschscholtz 1823) in seven different inland waters in Turkey. *Journal of the Black Sea/Mediterranean Environment* 19: 190–205.
- Bradley, B. A., E. M. Beaury, E. J. Fusco & B. E. Lopez, 2023. Invasive species policy must embrace a changing climate. *BioScience* 73: 124–133.
- Briski, E., S. Kotronaki, R. Cuthbert, A. Bortolus, M. Campbell, J. Dick, P. Fofonoff, B. Galil, C. Hewitt, J. Lockwood, H. MacIsaac, A. Ricciardi, G. Ruiz, E. Schwindt, U. Sommer, A. Zhan & J. Carlton, 2023. Does non-native diversity mirror Earth's biodiversity? *Global Ecology and Biogeography* 33: 48–62.
- Cancellario, T., A. Laini, P. J. Wood & S. Guareschi, 2023. Among demons and killers: current and future potential distribution of two hyper successful invasive gammarids. *Biological Invasions* 25: 1627–1642.
- Chown, S. L. & M. A. McGeoch, 2023. Functional trait variation along animal invasion pathways. *Annual Review of Ecology, Evolution, and Systematics* 54: 151–170.
- Cosentino, F., E. Seamark, V. Van Cakenberghe & L. Maiorano, 2023. Not only climate: the importance of biotic interactions in shaping species distributions at macro scales. *Ecology and Evolution* 13: e9855.
- Cuyckens, G. A. E., J. A. Pereira, T. C. Trigo, M. Da Silva, L. Gonçalves, J. C. Huaranca, N. Bou Pérez, J. L. Cartes & E. Eizirik, 2016. Refined assessment of the geographic distribution of Geoffroy's cat (*Leopardus geoffroyi*) (Mammalia: Felidae) in the Neotropics. *Journal of Zoology* 298: 285–292.
- da Silva, J. P., D. V. Gonçalves, A. Garcia-Raventós, M. Lopes-Lima, S. Varandas, E. Froufe, A. Teixeira, F. K. C. Hui, A. F. Filipe & R. Sousa, 2023. Joint species distribution models unveil co-occurrences between freshwater mussels and their fish hosts. *Journal of Biogeography* 50: 730–742.
- Díaz-Paniagua, C., C. Keller, M. Florencio, A. C. Andreu, A. Portheault, C. Gómez-Rodríguez & I. Gomez-Mestre, 2014. Rainfall stochasticity controls the distribution of invasive crayfish and its impact on amphibian guilds in Mediterranean temporary waters. *Hydrobiologia* 728: 89–101.
- Doherty-Bone, T. M., A. M. Dunn, C. Liddell & L. E. Brown, 2018. Transformation of detritus by a European native and two invasive alien freshwater decapods. *Biological Invasions* 20: 1799–1808.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell & S. Lautenbach, 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46.
- Dornik, A., M. C. Ion, M. A. Chețan & L. Pârvulescu, 2021. Soil-related predictors for distribution modelling of four European crayfish species. *Water* 13: 2280.
- Dunoyer, L., L. Dijoux, L. Bollache & C. Lagrue, 2014. Effects of crayfish on leaf litter breakdown and shredder prey: are native and introduced species functionally redundant? *Biological Invasions* 16: 1545–1555.
- Farhadi, A. & M. M. Harhioğlu, 2018. Elevated water temperature impairs gamete production in male narrow-clawed crayfish *Pontastacus leptodactylus* (Eschscholtz, 1823). *Knowledge and Management of Aquatic Ecosystems* 419: 40.
- Fick, S. E. & R. J. Hijmans, 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Fournier, A., M. Barbet-Massin, Q. Rome & F. Courchamp, 2017. Predicting species distribution combining multi-scale drivers. *Global Ecology Conservation* 12: 215–226.
- Funk, J. L., I. M. Parker, V. Matzek, S. L. Flory, E. T. Aschehough, C. M. D'Antonio, W. Dawson, D. M. Thomson & J. Valliere, 2020. Keys to enhancing the value of invasion ecology research for management. *Biological Invasions* 22: 2431–2445.
- Galib, S., J. Findlay & M. Lucas, 2021. Strong impacts of signal crayfish invasion on upland stream fish and

- invertebrate communities. *Freshwater Biology* 66: 223–240.
- Gallardo, B. & D. C. Aldridge, 2013. Evaluating the combined threat of climate change and biological invasions on endangered species. *Biological Conservation* 160: 225–233.
- Gallardo, B. & D. C. Aldridge, 2020. Priority setting for invasive species management by the water industry. *Water Research* 178: 115771.
- Gallardo, B., A. Zieritz & D. C. Aldridge, 2015. The importance of the human footprint in shaping the global distribution of terrestrial, freshwater and marine invaders. *PLOS ONE* 10: e0125801.
- Gong, S., Y. Gao, H. Duan, Y. Ge & Y. Wei, 2023. Incorporating physiological data into species distribution models to predict the potential distribution range of the red-eared slider in China. *Ecological Indicators* 154: 110749.
- Guareschi, S., C. Coccia, D. Sánchez-Fernández, J. Carbonell, J. Velasco, L. Boyero, A. Green & A. Millán, 2013. How far could the Alien Boatman *Trichocorixa verticalis verticalis* spread? Worldwide estimation of its current and future potential distribution. *PLOS ONE* 8: e59757.
- Guareschi, S., A. Laini, J. England, J. Barrett & P. J. Wood, 2021. Multiple co-occurrent alien invaders constrain aquatic biodiversity in rivers. *Ecological Applications* 31: e02385.
- Guareschi, S., T. Cancellario, F. J. Oficialdegui & M. Clavero, 2024. Insights from the past: invasion trajectory and niche trends of a global freshwater invader. *Global Change Biology* 30: e17059.
- Harishchandra, A., H. Xue, S. Salinas & N. Jayasundara, 2022. Thermal physiology integrated species distribution model predicts profound habitat fragmentation for estuarine fish with ocean warming. *Scientific Reports* 12: 21781.
- Haubrock, P. J. & I. Soto, 2023. Valuing the information hidden in true long-term data for invasion science. *Biological Invasions* 25: 2385–2394.
- Hausfather, Z., 2019. CMIP6: the next generation of climate models explained. *Carbon Brief*. [Accessed 23 January 2023]. <https://www.carbonbrief.org/cmip6-the-next-generation-of-climate-models-explained/>.
- Hausfather, Z. & G. P. Peters, 2020. Emissions – the ‘business as usual’ story is misleading. *Nature*. 577: 618–620.
- Hof, A. R., R. Jansson & C. Nilsson, 2012. How biotic interactions may alter future predictions of species distributions: future threats to the persistence of the arctic fox in Fennoscandia. *Diversity and Distributions* 18: 554–562.
- Holdich, D. M., M. M. Harlioğlu & I. Firkins, 1997. Salinity adaptations of crayfish in British waters with particular reference to *Austroptamobius pallipes*, *Astacus leptodactylus* and *Pacifastacus leniusculus*. *Estuarine Coastal and Shelf Science* 44: 147–154.
- IPBES, 2023. Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Roy, H. E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B. S., Hulme, P. E., Ikeda, T., Sankaran, K. V., McGeoch, M. A., Meyerson, L. A., Nuñez, M. A., Ordóñez, A., Rahlao, S. J., Schwindt, E., Seebens, H., Sheppard, A. W., and Vandvik, V. (eds.). IPBES secretariat, 56 pp. Bonn, Germany. <https://doi.org/10.5281/zenodo.7430692>
- James, J., J. R. Thomas, A. Ellis, K. A. Young, J. England & J. Cable, 2015. Over-invasion in a freshwater ecosystem: newly introduced virile crayfish (*Orconectes virilis*) out-compete established invasive signal crayfish (*Pacifastacus leniusculus*). *Marine and Freshwater Behaviour and Physiology* 49: 9–18.
- Jarnevich, C. S., M. A. Hayes, L. A. Fitzgerald, A. A. Yackel Adams, B. G. Falk, M. A. Collier, L. R. Bonewell, P. E. Klug, S. Naretto & R. N. Reed, 2018. Modeling the distributions of tegu lizards in native and potential invasive ranges. *Scientific Reports* 8: 10193.
- Jeschke, J. M. & D. L. Strayer, 2008. Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences*. 1134: 1–24.
- Jiménez-Valverde, A., A. T. Peterson, J. Soberón, J. M. Overton, P. Aragón & J. M. Lobo, 2011. Use of niche models in invasive species risk assessments. *Biological Invasions* 13: 2785–2797.
- Kokko, H., M. M. Harlioglu, H. Aydin, J. Makkonen, G. Gökmen, Ö. Aksu & J. Jussila, 2018. Observations of crayfish plague infections in commercially important narrow-clawed crayfish populations in Turkey. *Knowledge and Management of Aquatic Ecosystems* 419: p10.
- Kouba, A., A. Petrusek & P. Kozák, 2014. Continental-wide distribution of crayfish species in Europe: update and maps. *Knowledge and Management of Aquatic Ecosystems* 413: 5.
- Kouba, A., F. J. Oficialdegui, R. N. Cuthbert, M. Kourantidou, J. South, E. Tricarico, R. E. Gozlan, F. Courchamp & P. J. Haubrock, 2022. Identifying economic costs and knowledge gaps of invasive aquatic crustaceans. *Science of the Total Environment*. 813: 152325.
- Liu, C., C. Wolter, W. Xian & J. M. Jeschke, 2020. Most invasive species largely conserve their climatic niche. *Proceedings of the National Academy of Sciences* 117: 23643–23651.
- Madzivanzira, T., O. Weyl & J. South, 2022. Ecological and potential socioeconomic impacts of two globally-invasive crayfish. *NeoBiota* 72: 25–43.
- Marchetti, M. P. & T. Engstrom, 2016. The conservation paradox of endangered and invasive species. *Conservation Biology* 30: 434–437.
- Markovic, D., J. Freyhof & C. Wolter, 2012. Where are all the fish: potential of biogeographical maps to project current and future distribution patterns of freshwater species. *PLOS ONE* 7: e40530.
- Mathers, K. L., J. C. White, S. Guareschi, M. J. Hill, J. Heino & R. Chadd, 2020. Invasive crayfish alter the long-term functional biodiversity of lotic macroinvertebrate communities. *Functional Ecology* 34: 2350–2361.
- Mitas, L., Mitasova, H., 1999. Spatial Interpolation. In: P. Longley, M.F. Goodchild, D.J. Maguire, D.W. Rhind (Eds.), *Geographical Information Systems: Principles, Techniques, Management and Applications* 1: 481–492.
- Mozsár, A., D. Árva, V. Józsa, K. Györe, B. Kajári, I. Czeglédi, T. Erős, A. Weiperth & A. Specziár, 2021. Only one can remain? Environmental and spatial factors influencing habitat partitioning among invasive and native crayfishes

- in the Pannonian Ecoregion (Hungary). *Science of the Total Environment* 770: 145240.
- Nikkel, E., D. R. Clements, D. Anderson & J. L. Williams, 2023. Regional habitat suitability for aquatic and terrestrial invasive plant species may expand or contract with climate change. *Biological Invasions* 25: 3805–3822.
- Osafo, N. O. A., J. Jan, P. Porcal & J. Borovec, 2023. Contrasting catchment soil pH and Fe concentrations influence DOM distribution and nutrient dynamics in freshwater systems. *Science of the Total Environment* 858: 159988.
- Paradinas, I., J. Illian & S. Smout, 2023. Understanding spatial effects in species distribution models. *PLOS ONE* 18: e0285463.
- Parratt, S. R., B. S. Walsh, S. Metelmann, N. White, A. Manser, A. J. Bretman, A. A. Hoffmann, R. R. Snook & T. A. R. Price, 2021. Temperatures that sterilize males better match global species distributions than lethal temperatures. *Nature Climate Change* 11: 481–484.
- Parvulescu, L. & C. Zaharia, 2013. Current limitations of the stone crayfish distribution in Romania: Implications for its conservation status. *Limnologica* 43: 143–150.
- Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I.-C. Chen, T. D. Clark, R. K. Colwell, F. Daniels, B. Evengård, L. Falconi, S. Ferrier, S. Frusher, R. A. Garcia, R. B. Griffis, A. J. Hobday, C. Janion-Scheepers, M. A. Jarzyna, S. Jennings, J. Lenoir, H. I. Linnetved, V. Y. Martin, P. C. McCormack, J. McDonald, N. J. Mitchell, T. Mustonen, J. M. Pandolfi, N. Pettoelli, E. Popova, S. A. Robinson, B. R. Scheffers, J. D. Shaw, C. J. B. Sorte, J. M. Strugnell, J. M. Sunday, M.-N. Tuanmu, A. Vergés, C. Villanueva, T. Wernberg, E. Wapstra & S. E. Williams, 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355: 9214.
- Poggio, L., L. M. De Sousa, N. H. Batjes, G. Heuvelink, B. Kempen, E. Ribeiro & D. Rossiter, 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. *Soil* 7: 217–240.
- QGIS.org, 2023. QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>
- Randin, C. F., M. B. Ashcroft, J. Bolliger, J. Cavender-Bares, N. C. Coops, S. Dullinger, T. Dirnböck, S. Eckert, E. Ellis, N. Fernández, G. Giuliani, A. Guisan, W. Jetz, S. Joost, D. Karger, J. Lembrechts, J. Lenoir, M. Luoto, X. Morin, B. Price, D. Rocchini, M. Schaeppman, B. Schmid, P. Verburg, A. Wilson, P. Woodcock, N. Yoccoz, D. Payne & D. Payne, 2020. Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. *Remote Sensing of Environment* 239: 111626.
- R Core Team, 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rahel, F. J. & J. D. Olden, 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22: 521–533.
- Ricciardi, A., J. Iacarella, D. Aldridge, T. Blackburn, J. Carlton, J. Catford, J. Dick, P. Hulme, J. Jeschke, A. Liebhold, J. Lockwood, H. MacIsaac, L. Meyerson, P. Pyšek, D. Richardson, G. Ruiz, D. Simberloff, M. Vilà & D. Wardle, 2020. Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews* 29: 119–141.
- Rodrigo-Gómez, S., D. Gil-Tapetado, J. García-Gila, J. Blasco-Aróstegui & C. Polidori, 2021. The leaf beetle *Labiostomis lusitanica* (Coleoptera: Chrysomelidae) as an Iberian pistachio pest: projecting risky areas. *Pest Management Science* 78: 217–229.
- Russell, J. C., N. S. Sataruddin & A. D. Heard, 2014. Over-invasion by functionally equivalent invasive species. *Ecology* 95: 2268–2276.
- Sánchez-Fernández, D., J. M. Lobo & O. L. Hernández-Manrique, 2011. Species distribution models that do not incorporate global data misrepresent potential distributions: a case study using Iberian diving beetles. *Diversity and Distributions* 17: 163–171.
- Sanders, H., S. P. Rice & P. J. Wood, 2021. Signal crayfish burrowing, bank retreat and sediment supply to rivers: a biophysical sediment budget. *Earth Surface Processes and Landforms* 46: 837–852.
- Santamarina, S., R. G. Mateo, E. Alfaro-Saiz & C. Acedo, 2023. On the importance of invasive species niche dynamics in plant conservation management at large and local scale. *Frontiers in Ecology and Evolution* 10: 1049142.
- Satmari, A., K. Miok, M. C. Ion, C. Zaharia, A. Schrimpf & L. Pârvolescu, 2023. Headwater refuges: flow protects Austropotamobius crayfish from *Faxonius limosus* invasion. *NeoBiota* 89: 71–94.
- Seebens, H., S. Bacher, T. M. Blackburn, C. Capinha, W. Dawson, S. Dullinger, P. Genovesi, P. E. Hulme, M. van Kleunen, I. Kühn, J. M. Jeschke, B. Lenzner, A. M. Liebhold, Z. Pattison, J. Pergl, P. Pyšek, M. Winter & F. Essl, 2020. Projecting the continental accumulation of alien species through to 2050. *Global Change Biology* 27: 970–982.
- Sherpa, S., C. Kebaïli, D. Rioux, M. Guéguen, J. Renaud & L. Després, 2022. Population decline at distribution margins: assessing extinction risk in the last glacial relictual but still functional metapopulation of a European butterfly. *Diversity and Distributions* 28: 271–290.
- Simberloff, D., 2021. Maintenance management and eradication of established aquatic invaders. *Hydrobiologia* 848: 2399–2420.
- Simberloff, D. & B. Von Holle, 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32.
- Skurdal, J. & T. Taugbøl, 2002. *Astacus*, crayfish of commercial importance. In Holdich, D. (ed), *Biology of Freshwater Crayfish* Blackwell, Oxford: 467–503.
- South, J., T. C. Madzivanzira, N. Tshali, J. Measey & O. L. F. Weyl, 2020. In a pinch: mechanisms behind potential biotic resistance toward two invasive crayfish by native african freshwater crabs. *Frontiers in Ecology and Evolution* 8: 72.
- South, J., M. Mccard, D. Khosa, L. Mofu, T. Madzivanzira, J. Dick & O. Weyl, 2019. The effect of prey identity and substrate type on the functional response of a globally invasive crayfish. *NeoBiota* 52: 9–24.
- Strayer, D. L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55: 152–174.

- Strayer, D. L., V. T. Eviner, J. M. Jeschke & M. L. Pace, 2006. Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* 21: 645–651.
- Susanto, F., P. de Souza Jr & J. He, 2016. Spatiotemporal interpolation for environmental modelling. *Sensors* 16: 1245.
- Svoboda, J., A. Mrugała, E. Kozubíková-Balcarová & A. Petrusek, 2017. Hosts and transmission of the crayfish plague pathogen *Aphanomyces astaci*: a review. *Journal of Fish Diseases* 40: 127–140.
- Thuiller, W., Georges, D., Gueguen, M., Engler, R., Breiner, F., Lafourcade, B., Patin, R., 2023. biomod2: Ensemble Platform for Species Distribution Modeling. R package version 4.2–4. <https://CRAN.R-project.org/package=biomod2>
- Thuiller, W., B. Lafourcade, R. Engler & M. B. Araújo, 2009. BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* 32: 369–373.
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455–1474.
- Twardochleb, L., J. Olden & E. Larson, 2013. A global meta-analysis of the ecological impacts of nonnative crayfish. *Freshwater Science* 32: 1367–1382.
- Viana, D. S., F. J. Oficialdegui, M. del Soriano & C., Hermoso, V., and Clavero, M., 2023. Niche dynamics along two centuries of multiple crayfish invasions. *Journal of Animal Ecology* 92: 2138–2150.
- Walker, R. H. & S. A. Entrekin, 2023. All in moderation: crayfish populations are affected by precipitation-driven habitat availability and water quality in a non-perennial stream. *Aquatic Sciences* 85: 94.
- Wang, X.-G., M. W. Johnson, K. M. Daane & H. Nadel, 2009. High summer temperatures affect the survival and reproduction of olive fruit fly (Diptera: Tephritidae). *Environmental Entomology* 38: 1496–1504.
- Wood, T. C., P. C. Smiley, R. B. Gillespie & J. M. Gonzalez, 2024. Identifying the environmental variables that predict crayfish assemblage structure in agricultural headwater streams. *Freshwater Science* 43: 18–36.
- Zhang, Z., C. Capinha, N. Usio, R. Weterings, X. Liu, Y. Li, J. M. Landeria, Q. Zhou & M. Yokota, 2020. Impacts of climate change on the global potential distribution of two notorious invasive crayfishes. *Freshwater Biology* 65: 353–365.

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