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Impacts of climate change on the global potential distribution of two notorious invasive crayfishes

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Abstract

1. Invasive alien species and climate change are two of the most serious global environmental threats. In particular, it is of great interest to understand how changing climates could impact the distribution of invaders that pose serious threats to ecosystems and human activities.
2. In this study, we developed ensemble species distribution models for predicting the current and future global distribution of the signal crayfish *Pacifastacus leniusculus* and the red swamp crayfish *Procambarus clarkii*, two of the most highly problematic invaders of freshwater ecosystems worldwide. We collected occurrence records of the species, from native and alien established ranges worldwide. These records in combination with averaged observations of current climatic conditions were used to calibrate a set of 10 distinct correlative models for estimating the climatic niche of each species. We next projected the estimated niches into the geographical space for the current climate conditions and for the 2050s and 2070s under representative concentration pathway 2.6 and 8.5 scenarios.
3. Our species distribution models had high predictive abilities and suggest that annual mean temperature is the main driver of the distribution of both species. Model predictions indicated that the two crayfish species have not fully occupied their suitable climates and will respond differently to future climate scenarios in different geographic regions. Suitable climate for *P. leniusculus* was predicted to shift poleward and to increase in extent in North America and Europe but decrease in Asia. Regions with suitable climate for *P. clarkii* are predicted to widen in Europe but contract in North America and Asia.
4. This study highlights that invasive species with different thermal preference are likely to respond differently to future climate changes. Our results provide important information for policy makers to design and implement anticipated measures for the prevention and control of these two problematic species.

KEYWORDS

climate change, habitat suitability, *Pacifastacus leniusculus*, *Procambarus clarkii*, species distribution modelling

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Zhixin Zhang, César Capinha, and Nisikawa Usio contributed equally to this work.

1 | INTRODUCTION

Climate change and invasive alien species are two of the most serious threats to biological diversity worldwide (Chown et al., 2015; Hulme, 2017; Rahel & Olden, 2008; Ward & Masters, 2007). Climate change can greatly alter the distribution of suitable habitats to species including invasive species (Faleiro, Nemésio, & Loyola, 2018; Guisan, Thuiller, & Zimmermann, 2017), which may ultimately define the regions that will be susceptible to their negative impacts, including habitat competition, predation, hybridisation, and pathogen transmission (Huxel, 1999; Muhlfeld et al., 2014; Rosewarne et al., 2016; Schrimpf, Schmidt, & Schulz, 2014; Zhang, Yokota, & Strüssmann, 2019). Therefore, it is crucial to understand how future climates could alter the distribution of suitable habitats for invasive alien species, in order to effectively protect native biodiversity and ecosystem functioning. Species distribution models (SDMs), which aim at predicting habitat suitability by linking species distribution data with environmental data, have been extensively used to investigate the impacts of climate change on the potential distribution of a number of species including invasive alien species (Elith & Leathwick, 2009; Guisan et al., 2017; Guisan & Thuiller, 2005; Peterson, 2003; Thuiller, Guéguen, Renaud, Karger, & Zimmermann, 2019).

Crayfishes are a taxonomic group with a disproportionally high ratio of invasive alien species, causing detrimental impacts on native biodiversity and ecosystem services (Gherardi & Holdich, 1999; Lodge et al., 2012). The signal crayfish *Pacifastacus leniusculus* (Dana, 1852), which is native to western North America, has been introduced into Europe and Japan (Azuma, Usio, Korenaga, Koizumi, & Takamura, 2011; Bubb, Thom, & Lucas, 2004; Kawai, Mitamura, & Ohtaka, 2004; Kouba, Petrusek, & Kozák, 2014; Usio et al., 2016). The red swamp crayfish *Procambarus clarkii* (Girard, 1852) is native to north-eastern Mexico and southern USA and has successfully spread to North and Central America, Europe, Asia, Africa, and South America (Gherardi, 2006; Kouba et al., 2014; Loureiro, Anastácio, Araujo, Souty-Grosset, & Almerão, 2015; Oficialdegui et al., 2019). Invasion of the two crayfishes has resulted in a large number of negative ecological and economic impacts. For instance, in Japan the invasive *P. leniusculus* is competitively superior to the native *Cambaroides japonicus* (De Haan, 1841), which may partially explain the displacement of this species (Nakata & Goshima, 2003; Usio, Konishi, & Nakano, 2001). Previous studies have shown that *P. leniusculus* and *P. clarkii* prey on various native species; for example, *P. leniusculus* can consume Atlantic salmon eggs under laboratory conditions and *P. clarkii* was found preying on *Rhinella ornate*, a frog species in Brazil (Banci, Viera, Marinho, Calixto, & Marques, 2013; Findlay, Riley, & Lucas, 2015; Loureiro et al., 2015; Rosewarne et al., 2016). In addition, burrowing behaviours of *P. clarkii* and *P. leniusculus* can lead to river bank erosion which increases the water turbidity (Correia & Ferreira, 1995; Faller et al., 2016; Holdich, James, Jackson, & Peay, 2014; Loureiro et al., 2015). Besides, *P. clarkii* and *P. leniusculus* have been identified as vectors of crayfish plague pathogen *Aphanomyces astaci* Schikora, 1906, leading to many local extirpations of populations of native European crayfish species (Diéguez-Uribeondo & Söderhäll, 1993; Filipova, Petrusek, Matasova, Delaunay, & Grandjean, 2013; Gherardi, 2006).

For the purpose of effectively preventing new invasions and mitigating adverse effects of the two invasive crayfish species on native species, several SDMs have been developed for predicting their current potential distribution (Capinha & Anastácio, 2011; Capinha, Leung, & Anastácio, 2011; Chucholl, 2016; Larson & Olden, 2012; Zeng, Low, & Yeo, 2016). For instance, Capinha & Anastácio (2011) estimated habitat suitability of four invasive decapods including *P. clarkii* and *P. leniusculus* for the Iberian Peninsula, and Capinha et al. (2011) modelled global distributions of four decapod crustaceans including *P. clarkii* and *P. leniusculus*; these studies only focused on predicting habitat suitability under current climate conditions and did not consider climate change scenarios. Thus far, the impact of climate change on the potential distribution of the two targeted species was estimated by a single modelling algorithm (Capinha, Larson, Tricarico, Olden, & Gherardi, 2013; Liu, Guo, Ke, Wang, & Li, 2011) or considered limited geographical extents (Capinha et al., 2013; Gallardo & Aldridge, 2013). For example, Capinha et al. (2013) dealt with the distribution of the two invaders under climate change scenarios by single algorithm (i.e. Mahalanobis distance) at the European extent only and was mainly concerned with impacts over native European crayfishes. Previous studies have demonstrated the uncertainties in single modelling algorithms (Elith & Graham, 2009; Pearson et al., 2006; Qiao, Soberón, & Peterson, 2015). Considering the highly invasive nature of the two crayfishes and their negative impacts on native ecosystems, it is of great importance to project their potential distribution under climate change scenarios at a global scale while accounting for variability in predictions from distinct modelling algorithms.

To reduce uncertainties in single SDM algorithms, the ensemble modelling approach has been proposed as a more reliable alternative given that it explicitly accounts for the variability of distinct single predictions (Araújo & New, 2007; Guisan et al., 2017; Thuiller, Georges, & Engler, 2014). The ensemble modelling approach can integrate predictions from different single SDMs thus can reduce prediction uncertainties and provide more accurate predictions than those from single SDMs (Araújo & New, 2007). Thuiller et al. (2019) have addressed the high levels of uncertainties in SDM studies associated with choices of SDM algorithms, general circulation models (GCMs), and representative concentration pathways (RCPs). Therefore, it is highly recommended to consider multiple SDM algorithms, GCMs, and RCPs in SDM studies (Thuiller et al., 2019). To examine the impacts of climate change on the global potential distribution of the two crayfishes, we (1) developed ensemble SDMs for the two invaders to (2) predict their current habitat suitability and (3) forecast their future potential distribution under future climate change scenarios derived from six GCMs under two RCPs. We hypothesise that the two crayfishes with different environmental tolerances may respond differently to future climate change.

2 | METHODS

2.1 | Species distribution data

Occurrence records of *P. leniusculus* since 2000 were collected from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org), the Nonindigenous Aquatic Species database of the US Geological Survey (NAS, https://nas.er.usgs.gov), and published literature (Azuma et al., 2011; Kawai et al., 2004; Nakata, Tanaka, & Goshima, 2004; Usio et al., 2006, 2016). Distribution data of *P. clarkii* since 2000 were obtained from GBIF, NAS, Taiwan Biodiversity Information Facility (http://taibif.tw), previous studies (Banci et al., 2013; Foster & Harper, 2007; Liu et al., 2011; Loureiro et al., 2015; Magalhães et al., 2005; Nunes, Hoffman, Zengeya, Measey, & Weyl, 2017; Saad, Mehanna, Khalil, & Said, 2015; Smart et al., 2002; Wizen, Galil, Shlagman, & Gasith, 2008), and unpublished records from our own surveys from 2005 to 2018. After removing duplicated records, one occurrence record was randomly selected per each 5-min grid cell in order to reduce sampling bias effect (Boria, Olson, Goodman, & Anderson, 2014). After this data cleaning procedure, 2,307 records for *P. leniusculus* and 1,659 records for *P. clarkii* were retained.

2.2 | Predictor variables

The average values of 19 environmental predictor variables from 1979 to 2013 were downloaded from CHELSA version 1.2 (http://chelsa-climate.org) at a resolution of 30 arc-seconds (Karger et al., 2017). Gallardo et al. (2015) addressed the importance of human footprint on species distribution. Therefore, the global human influence index (HII, from Socioeconomic Data and Applications Center, http://sedac.ciesin.columbia.edu) at a resolution of 30 arc-seconds was also included into the models. The HII and 19 environmental predictor variables were resampled to 5 arc-minutes by bilinear interpolation. A multicollinearity analysis was performed for the 20 predictor variables, and only the ecologically most meaningful and non-correlated variables (Pearson's correlation coefficient $|r| < 0.7$) were used for further analysis (Dormann et al., 2013).

Projections of climate conditions for two future time periods, 2041–2060 (2050s) and 2061–2080 (2070s), were obtained from WorldClim 1.4 (http://www.worldclim.org) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). To reduce uncertainties among different GCMs, future climate projections were derived from six GCMs: BCC-CSM1-1, HadGEM2-ES, IPSL-CM5A-LR, MRI-CGCM3, MIROC-ESM-CHEM, and NorESM1-M. For each GCM, two RCP scenarios (RCP 2.6 and RCP 8.5) were considered. There is no available dataset about future HII; therefore, as with previous studies (Kelly, Leach, Cameron, Maggs, & Reid, 2014; Luo, Jiang, & Tang, 2015), we assume HII remain constant in the future. To reduce the uncertainty among different GCMs, mean values of selected predictor variables were calculated and used to predict future distributions (Yan et al., 2017).

2.3 | Modelling procedure

We used 10 modelling algorithms (artificial neural network, classification tree analysis, flexible discriminant analysis, generalised additive model, generalised boosting model, generalised linear model, multiple adaptive regression splines, maximum entropy, random forest, and surface range envelop) with their default settings in the biomod2 package (version 3.3.7) (Thuiller et al., 2014) in R (R Development Core Team, 2014). A total of 10,000 global pseudo-absence records were randomly generated, and a five-fold cross-validation approach with 10 repetitions was adopted to evaluate predictive performance of 10 algorithms. Model performance was assessed by two metrics: the true skill statistics (TSS) and the area under the receiver operating characteristic curve (AUC). Algorithms with TSS over 0.85 and AUC over 0.90 for both species were selected to develop committee averaging ensemble models (Costa, Muelbert, Vieira, & Castello, 2015; Thuiller et al., 2014). Committee averaging is simply the average of binary predictions from the distinct algorithms; this procedure has the advantage of indicating both the suitability of conditions and the level of agreement among predictions of distinct algorithms. Relative contribution of each predictor variable and response curves of important variables were determined (Guisan et al., 2017; Thuiller et al., 2014). All data were used to predict habitat suitability for the two species under current climate conditions. Potential distributions of the two crayfish under different GCMs climate change scenarios were predicted and future range size changes under different GCMs were calculated.

3 | RESULTS

3.1 | Model accuracy and contributions of predictor variables

Based on multicollinearity analysis results, 10 predictor variables were selected: annual mean temperature, mean diurnal range, temperature seasonality, maximum temperature of warmest month, annual precipitation, precipitation of driest month, precipitation seasonality, precipitation of warmest quarter, precipitation of coldest quarter, and HII (Table 1, Figure S1). AUC and TSS results suggested that in both species, the random forest algorithm performed best and surface range envelop performed worst (Table 2). For *P. leniusculus*, all algorithms except the surface range envelop showed high predictive performance; while for *P. clarkii*, only four algorithms, namely generalised additive model, generalised boosting model, generalised linear model, and random forest had high predictive performance (Table 2). Therefore, these four models were used to develop ensemble SDMs for both crayfishes. The ensemble SDMs for both species showed high predictive accuracy (Table 2).

TABLE 1 Predictor variables used in this study and their contribution to the ensemble species distribution models for the signal crayfish *Pacifastacus leniusculus* and the red swamp crayfish *Procambarus clarkii*

	Pacifastacus leniusculus	*Procambarus clarkii*
Annual mean temperature	0.620 (±0.049)	0.374 (±0.032)
Mean diurnal range	0.236 (±0.028)	0.028 (±0.004)
Temperature seasonality	0.497 (±0.038)	0.192 (±0.011)
Max temperature of warmest month	0.248 (±0.034)	0.116 (±0.018)
Annual precipitation	0.055 (±0.010)	0.075 (±0.012)
Precipitation of driest month	0.020 (±0.004)	0.131 (±0.020)
Precipitation seasonality	0.099 (±0.007)	0.056 (±0.007)
Precipitation of warmest quarter	0.045 (±0.006)	0.008 (±0.001)
Precipitation of coldest quarter	0.133 (±0.017)	0.036 (±0.003)
Human influence index	0.021 (±0.001)	0.235 (±0.011)

Note: Data were expressed as mean ± standard error.

TABLE 2 True skill statistics (TSS) and area under the receiver operating characteristic curve (AUC) values of the 10 modelling algorithms used to predict the potential distribution of the signal crayfish *Pacifastacus leniusculus* and the red swamp crayfish *Procambarus clarkii*

	Pacifastacus leniusculus		*Procambarus clarkii*	
	TSS	AUC	TSS	AUC
ANN	0.915 (±0.004)	0.970 (±0.004)	0.815 (±0.007)	0.935 (±0.007)
CTA	0.930 (±0.003)	0.979 (±0.000)	0.839 (±0.005)	0.938 (±0.003)
FDA	0.916 (±0.002)	0.989 (±0.000)	0.824 (±0.006)	0.964 (±0.001)
GAM*	0.952 (±0.001)	0.992 (±0.000)	0.856 (±0.004)	0.973 (±0.001)
GBM*	0.937 (±0.001)	0.991 (±0.000)	0.854 (±0.004)	0.975 (±0.001)
GLM*	0.942 (±0.001)	0.991 (±0.000)	0.851 (±0.005)	0.970 (±0.001)
MARS	0.943 (±0.001)	0.991 (±0.000)	0.843 (±0.005)	0.970 (±0.001)
Maxent	0.910 (±0.003)	0.966 (±0.002)	0.841 (±0.005)	0.968 (±0.002)
RF*	0.953 (±0.002)	0.995 (±0.000)	0.903 (±0.003)	0.986 (±0.000)
SRE	0.729 (±0.006)	0.865 (±0.003)	0.672 (±0.008)	0.836 (±0.004)
Ensemble model	0.962 (±0.001)	0.992 (±0.000)	0.901 (±0.004)	0.980 (±0.000)

Note: For the two species, each algorithm was run 10 times and data are expressed as mean ± *SE*. The asterisks (*) represent algorithms selected to develop ensemble species distribution models for the two species.

Abbreviations: ANN, artificial neural network; CTA, classification tree analysis; FDA, flexible discriminant analysis; GAM, generalised additive model; GBM, generalised boosting model; GLM, generalised linear model; MARS, multiple adaptive regression splines; Maxent, maximum entropy; RF, random forest; SRE, surface range envelop.

Results of relative contribution of each predictor variable suggest that the two species have different environmental requirements. Annual mean temperature, temperature seasonality, and maximum temperature of warmest month are the three most important predictor variables determining the distribution of *P. leniusculus*, while annual mean temperature, HII, and temperature seasonality contribute most to the potential distribution of *P. clarkii* (Table 1). Although different predictor variables contributed differently to the distribution of the two crayfish species, annual mean temperature is consistently most important. The response curves of the occurrence probability of the two species against annual mean temperature were presented in Figure 1, which clearly showed that the two crayfishes have different thermal preferences: the optimal annual mean temperature is about 5–12°C for *P. leniusculus* and 12–23°C for *P. clarkii*.

3.2 | Potential distribution under current and future climate conditions

The predicted potential global distribution of *P. leniusculus* under current climate conditions is presented in Figure 2. Occurrence records of *P. leniusculus* are mainly distributed in the west coast of North America, Europe, and the north part of Japan. The ensemble model also predicted these areas to be suitable for this species (Figure 2). In addition, the ensemble model predictions showed that the potential suitable habitat for *P. leniusculus* in Europe is much larger than its current known range (Figure 2) (Kouba et al., 2014). In addition to these known distribution areas, other areas including the east coast of North America, South America, Australia, and New Zealand were also predicted to be suitable for *P. leniusculus* (Figure 2). The ensemble

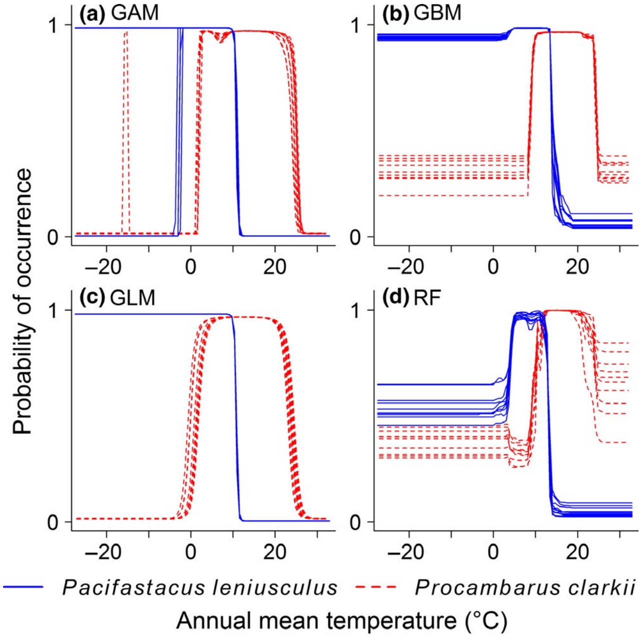

FIGURE 1 Response curves of occurrence probability of the signal crayfish *Pacifastacus leniusculus* and the red swamp crayfish *Procambarus clarkii* against annual mean temperature. GAM: generalised additive model; GBM: generalised boosting model; GLM: generalised linear model; RF: random forest [Colour figure can be viewed at wileyonlinelibrary.com]

SDM for *P. clarkii* predicted the occurrence records of this species in a wide range of areas around the world such as part of North America, Europe, China, Japan, South America, and Africa (Figure 3). Although *P. clarkii* has neither been reported in Australia nor in New Zealand, our ensemble model suggests that these areas are also suitable for this species (Figure 3).

Results of the range size change of both *P. leniusculus* and *P. clarkii* varied among different GCMs, and habitat of *P. leniusculus* is consistently predicted to contract in future (Table 3). For instance, under RCP2.6 scenario in 2050s, the range size change of *P. leniusculus* varied from −45.3% (HadGEM2-ES) to −11.5% (BCC-CSM1-1), whereas in *P. clarkii* the range size change was from −17.5% (MRI-CGCM3) to 8.0% (IPSL-CM5A-LR) (Table 3). Predictions based on mean values of the six GCMs suggested that *P. leniusculus* will lose suitable habitat in future while *P. clarkii* will expand its ranges (Table 3); besides, the two species respond differently to future climate change depending on the region (Figures 4 and 5, Table 4). Generally, under future climate conditions, the distributions of both species are predicted to decrease in North America and Asia (Table 4). In South America, habitat of *P. leniusculus* is predicted to decrease by >15% under future climates while habitat of *P. clarkii* is likely to increase by at least 12% (Table 4). In Europe, *P. clarkii* is predicted to increase >22% of suitable habitat while habitat of *P. leniusculus* will be reduced by at least 23% under future climate scenarios (Table 4). In Australia and New Zealand, suitable habitat for *P. clarkii* will expand by >22% while it will decrease by at least 87% for *P. leniusculus* under future climate conditions (Table 4). In the future, Africa will still be unsuitable for *P. leniusculus* and the potential distribution of *P. clarkii* is predicted to increase with the exception of RCP8.5 scenario during the 2070s (Table 4). In addition, the potential distribution of *P. leniusculus* shows a northward shift in the future: Southern Europe, including the North Iberian Peninsula, South France, Italy, and Greece, will become less

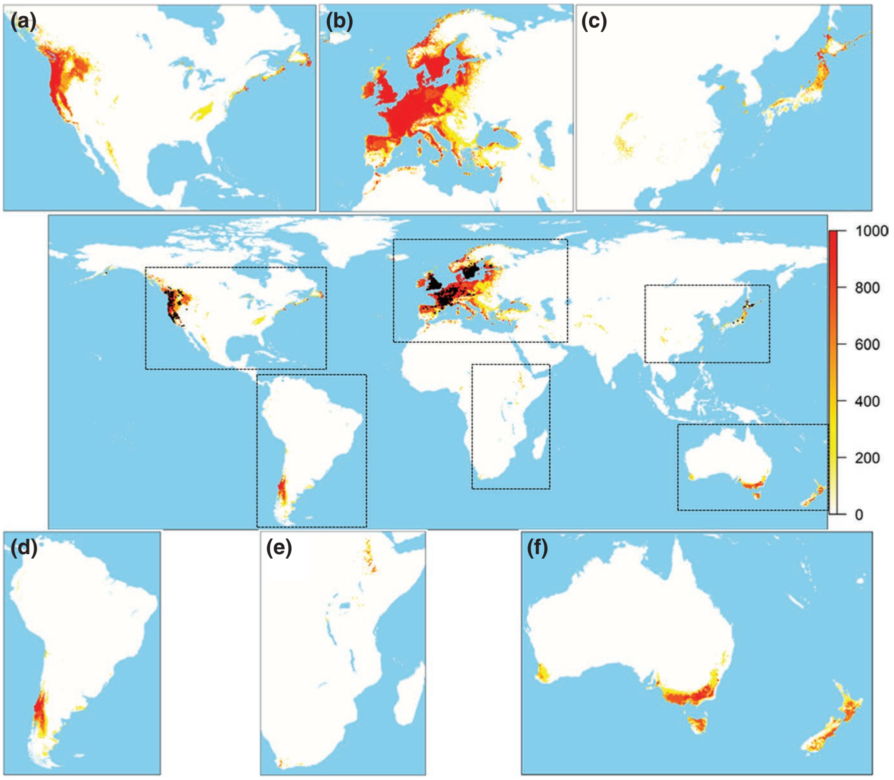

FIGURE 2 The potential distribution of the signal crayfish *Pacifastacus leniusculus* under current climate conditions in (a) North America, (b) Europe and Mediterranean Basin, (c) East Asia, (d) South America, (e) Africa, and (f) Australia and New Zealand. Black points represent occurrence records used to develop the species distribution model. Habitat suitability ranges from 0 to 1,000 [Colour figure can be viewed at wileyonlinelibrary.com]

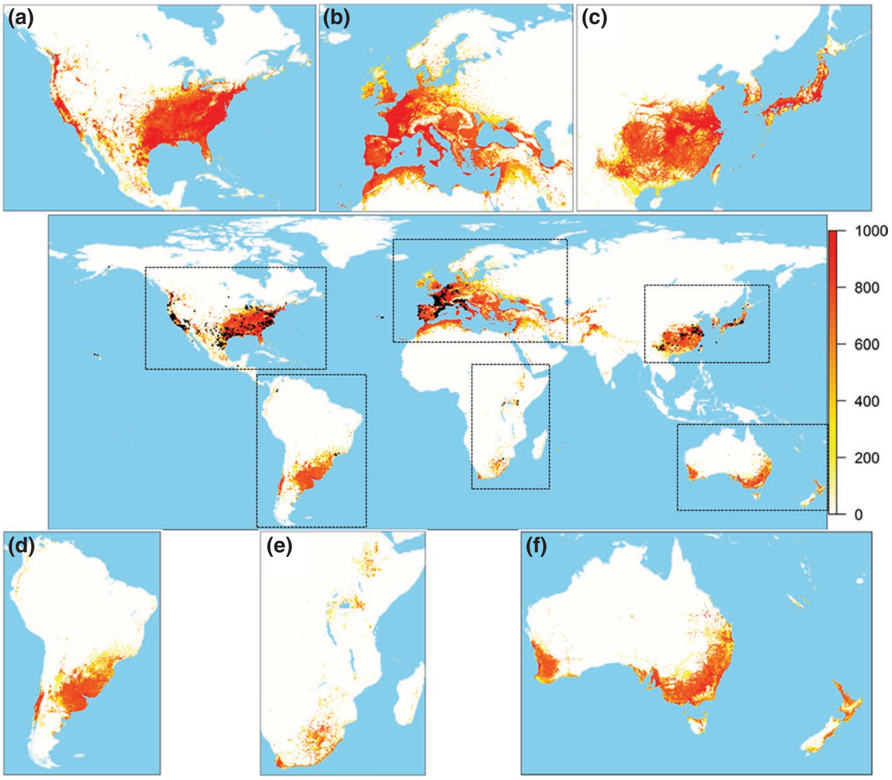

FIGURE 3 The potential suitable habitat for the red swamp crayfish *Procambarus clarkii* under current climate conditions in (a) North America, (b) Europe and Mediterranean Basin, (c) East Asia, (d) South America, (e) Africa, and (f) Australia and New Zealand. Black points represent occurrence records used to develop the species distribution model. Habitat suitability ranges from 0 to 1,000 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Range size change (%) of the signal crayfish *Pacifastacus leniusculus* and the red swamp crayfish *Procambarus clarkii* under future climate conditions in 2050s and 2070s for various global climate models

	Pacifastacus leniusculus				*Procambarus clarkii*			
	RCP2.6 2050	RCP2.6 2070	RCP8.5 2050	RCP8.5 2070	RCP2.6 2050	RCP2.6 2070	RCP8.5 2050	RCP8.5 2070
BCC-CSM1-1	−11.5	−21.1	−8.9	−1.5	−14.2	−9.0	−9.4	−12.8
HadGEM2-ES	−45.3	−43.3	−46.1	−60.8	−4.9	−1.3	−9.4	−24.4
IPSL-CM5A-LR	−30.4	−20.0	−33.9	−49.4	8.0	19.2	30.3	44.2
MRI-CGCM3	−30.8	−15.9	−26.9	−14.9	−17.5	−5.5	−7.5	3.1
MIROC-ESM-CHEM	−37.2	−43.6	−54.1	−63.9	4.9	3.5	2.7	22.1
NorESM1-M	−34.4	−36.9	−44.7	−42.2	−17.2	−7.5	−13.5	0.0
Mean layers	−27.2	−24.5	−29.3	−28.8	−6.6	1.7	0.0	8.7

Note: Positive values indicate habitat will expand in future while negative values suggest habitat will contract.
Abbreviation: RCP: representative concentration pathway.

suitable for *P. leniusculus*, whereas northern Europe such as Iceland, Norway, Sweden, and Finland, will receive wider areas with suitable conditions (Figure 4). Habitat of *P. clarkii* in Europe is predicted to expand further north and eastward under future climates (Figure 5).

4 | DISCUSSION

In this study, ensemble species distribution models were developed, respectively, for *P. leniusculus* and *P. clarkii* to predict their global habitat suitability under current and future climatic conditions. Both ensemble SDMs exhibited excellent predictive capacities and models showed that the two invasive crayfish species have different environmental requirements and will potentially display different responses to climate change.

4.1 | Important predictor variables

Among the selected 10 predictor variables, annual mean temperature is expected to play an important role in determining the distributions of the two crayfish species. Response curves of the relationships between occurrence probabilities of the two species and annual mean temperature indicate that *P. clarkii* has a preference for higher temperatures than

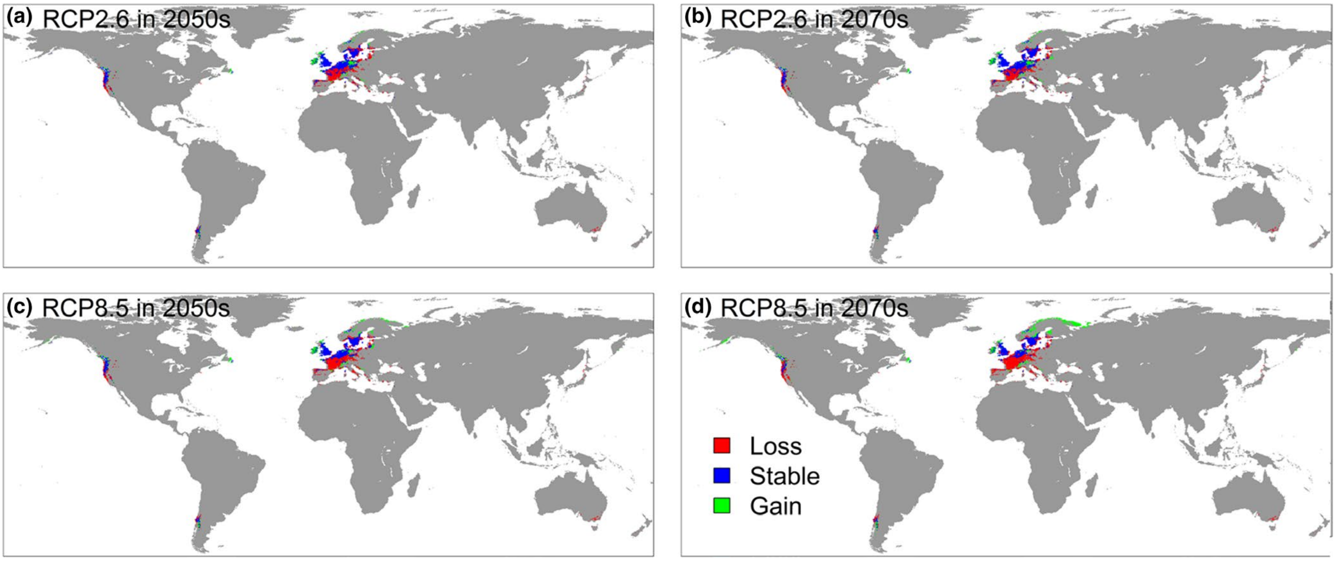

FIGURE 4 Range size changes of the signal crayfish *Pacifastacus leniusculus* under future climate scenarios. (a) In 2050 under RCP2.6; (b) in 2070 under RCP2.6; (c) in 2050 under RCP8.5; (d) in 2070 under RCP8.5. RCP: representative concentration pathway. Mean values of six global climate models were used as future climate conditions. Stable (in blue) indicates areas that are suitable for *P. leniusculus* under both present-day and future climates; Loss (in red) indicates areas which will no longer be suitable for *P. leniusculus* in future; Gain areas (in green) represent areas that will become suitable for *P. leniusculus* in future [Colour figure can be viewed at wileyonlinelibrary.com]

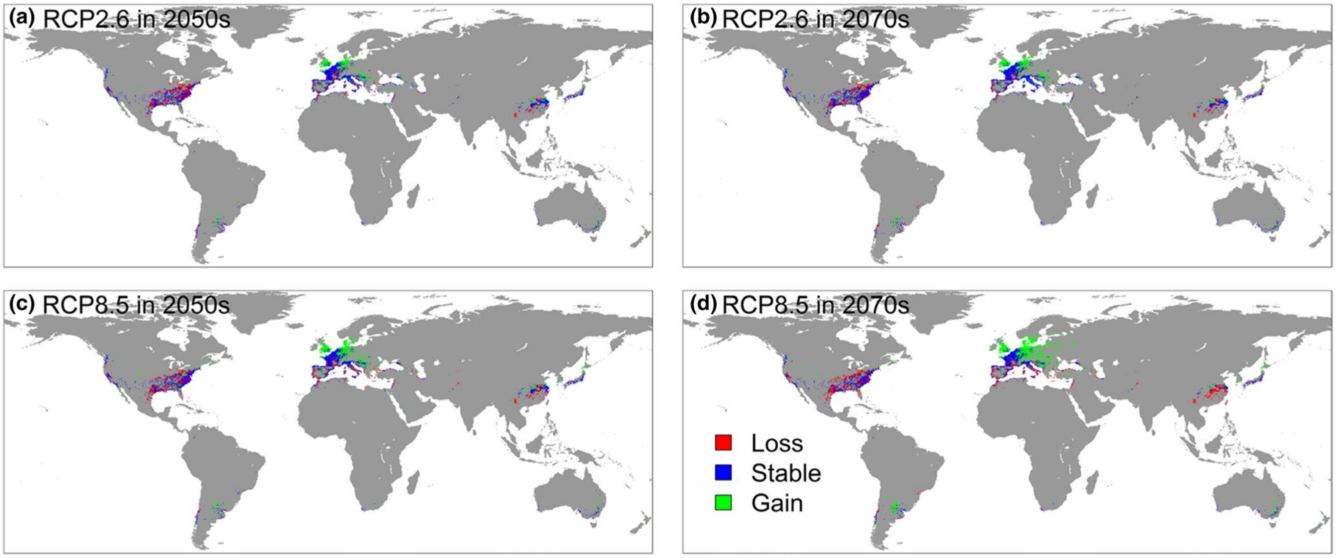

FIGURE 5 Range size changes of the red swamp crayfish *Procambarus clarkii* under future climate scenarios. (a) in 2050 under RCP2.6; (b) in 2070 under RCP2.6; (c) in 2050 under RCP8.5; (d) in 2070 under RCP8.5. RCP: representative concentration pathway. Mean values of six global climate models were used as future climate conditions. Stable (in blue) indicates areas that are suitable for *P. clarkii* under both present-day and future climates; Loss (in red) indicates areas which will no longer be suitable for *P. clarkii* in future; Gain areas (in green) represent areas that will become suitable for *P. clarkii* in future [Colour figure can be viewed at wileyonlinelibrary.com]

P. leniusculus. This result is supported by the fact that *P. clarkii* is considered a warm water species whereas *P. leniusculus* a cool water species (Paglianti & Gherardi, 2004; Usio et al., 2006). Besides, previous studies have reported that the preferred temperature for *P. clarkii* is 21–30 °C (Espina & Herrera, 1993; Suko, 1958), while the optimal temperature for the growth of *P. leniusculus* is about 15–20°C (Ackefors, 1999). Other studies have found that temperature can affect a variety of physiological processes including growth, which ultimately influences survival of the two species (Harlıoğlu, 2009; Kozák et al., 2009; Paglianti & Gherardi, 2004). Other predictor variables contribute differently to the geographical distributions of the two species, we notice that temperature seasonality and maximum temperature of warmest month are also fairly important predictors. These two temperature-related variables may reflect thermal tolerance of the two crayfishes.

More recently, Krause et al. (2019) explored climate change impacts on habitat suitability of 10 crayfish species in the Mobile

TABLE 4 Range size change (%) of the signal crayfish *Pacifastacus leniusculus* and the red swamp crayfish *Procambarus clarkii* in different areas under future climate conditions

	Pacifastacus leniusculus				*Procambarus clarkii*			
	RCP2.6 2050	RCP2.6 2070	RCP8.5 2050	RCP8.5 2070	RCP2.6 2050	RCP2.6 2070	RCP8.5 2050	RCP8.5 2070
North America	−18.8	−23.9	−15.3	−26.1	−36.1	−28.0	−33.0	−40.7
Europe	−27.5	−23.5	−30.7	−29.7	22.0	35.1	35.3	68.6
Asia	−79.6	−78.5	−79.6	−95.0	−13.7	−17.3	−19.4	−45.0
South America	−15.7	−18.0	−23.0	−29.3	12.6	21.0	31.7	77.4
Africa	NA	NA	NA	NA	0.5	4.7	4.7	−8.4
Oceania	−95.4	−87.8	−98.9	−99.5	22.5	23.0	32.1	37.3

Note: Mean values of six global climate models were used as future climate conditions (see Material and Methods). RCP: representative concentration pathway. Positive values indicate habitat will expand in future while negative values suggest habitat will contract. NA indicates that Africa is unsuitable for *P. leniusculus* under present-day and future climates.

River Basin in the south-eastern USA using maximum entropy modelling approach. Contrary to our results, they reported that geology, slope, and streamflow contributed more to crayfish distributions than water temperature. In our study, we initially also considered two topographic variables (elevation and slope), but the two variables contributed little to crayfish distribution (Table S1). Given this result, together with potential altitudinal shifts of species in response to climate change, we excluded elevation and slope from our analyses. Previous studies have demonstrated that SDM projections can be influenced by a variety of factors including the scale of the study area (Barve et al., 2011; VanDerWal, Shoo, Graham, & Williams, 2009). Given that Krause et al. (2019) focused on a single river basin in the south-eastern U.S.A., we suspect that climatic variation within this region might be more or less uniform, which may lead to the low contribution of water temperature to crayfish distributions.

4.2 | Potential distributions under current and future climate scenarios

The two ensemble SDMs suggest that the present global suitable habitat for *P. leniusculus* and *P. clarkii* is much larger than their current known distribution ranges. Our results highlight extents of agreements with predictions from previous SDM studies on the two species (Capinha et al., 2011; Capinha et al., 2013; Gallardo & Aldridge, 2013; Larson & Olden, 2012; Liu et al., 2011), but there are also noteworthy differences in several regions. For instance, Capinha et al. (2011) predicted the current global potential distribution of *P. leniusculus* and *P. clarkii* and reported that the two species have not fully occupied their suitable habitat. Our results agree with those of Capinha et al. (2011) but also indicate that the extent of currently suitable areas may be narrower than what could be apparent in the results of Capinha et al. (2011). In particular, areas receiving probability values in the mid-range of the variation gradient (e.g. much of central and southern of North America, eastern Europe, and central and south Asia for *P. leniusculus*, and of central and northern Australia, northern Africa, and Middle East for *P. clarkii*) are currently unsuitable.

Liu et al. (2011) investigated the impacts of climate change on the global potential distribution of *P. clarkii* using maximum entropy modelling and their results showed that this species will expand its distribution in Europe and contract in range in other continents. Although our results confirmed the range expansion of *P. clarkii* in Europe, they showed that range contraction only occurs in North America and Asia. Gallardo & Aldridge (2013) studied the impact of climate change on the distribution of *P. leniusculus* in Europe by machine learning techniques (i.e. generalised boosting model and random forest), while Capinha et al. (2013) examined these impacts also for Europe but concerning the two crayfish species and using Mahalanobis distance. For *P. leniusculus*, both studies found indications of a noteworthy range contraction as time progresses, with suitable habitat shifting mainly north-eastward. Based on the study by Gallardo & Aldridge (2013), range contraction is expected to be up to 32% by 2050. Habitat contraction and the north-eastward shift were also found for *P. leniusculus* in Europe in our study. Our predictions suggest that future climate change will lead to about 23–30% loss of habitat in Europe. These differences might be due to differences in modelling techniques and selection of current and future climate conditions. For *P. clarkii*, Capinha et al., (2013) show patterns of range expansion in Europe that are very similar to the ones identified here, and which corresponds mainly to an expansion of suitable climates in north-eastern regions, while most of currently suitable areas will remain stable.

Our study forecasted the distributions of *P. leniusculus* and *P. clarkii* under future changing climate conditions at a global scale using an ensemble model approach, which has three major advantages over previous projections made for these species. First, we obtained current climate data from CHELSA, which represents average climate data for 1979–2013 by a quasi-mechanistic statistical downscaling method (Karger et al., 2017). The WorldClim provides an interpolated dataset of global terrestrial surface climate (Fick & Hijmans, 2017; Hijmans et al., 2005), it has been frequently used in SDM studies including recent SDMs for crayfishes (see Gallardo & Aldridge, 2013; Liu et al., 2011). However, the current climate conditions from WorldClim represent the average climate data for 1970–2000 (Fick & Hijmans, 2017), which failed to properly match with temporal range of occurrence records (since 2000) of the two crayfishes. In addition, Bobrowski and Schickhoff (2017) suggest that species distribution models based on predictor variables from CHELSA showed higher predictive performance than models using WorldClim climate data.

Second, we adopted an ensemble forecasting approach to construct the SDMs for the two species. There are a number of modelling approaches available for SDM studies including classification, regression, and machine learning methods. Previous SDMs on *P. leniusculus* and *P. clarkii* were mainly developed by single modelling algorithms, such as the artificial neural network approach (Capinha et al., 2011) and the maximum entropy modelling method (Liu et al., 2011). Previous studies have revealed that different single modelling algorithms have different predictive ability and can produce largely variable results (Elith & Graham, 2009; Pearson et al. 2006; Qiao et al., 2015). This inter-model variability in predictive accuracy was also found in our study. We should notice that the maximum entropy modelling approach might be the most widely used SDM algorithm, plausibly because of its easy-to-use features. In our study, this algorithm was not considered for *P. clarkii* due to its lower predictive performance. To reduce the model-based uncertainty and produce reliable predictions, the ensemble modelling technique has been proposed and frequently used, which combines prediction results of multiple modelling algorithms thus can reduce the uncertainties in model predictions (Araújo & New, 2007; Guisan et al., 2017; Thuiller et al., 2014, 2019).

Third, a range of future climate projections from six GCMs were utilised to forecast future distributions of the two crayfish species. It has been revealed that high uncertainties in future projections of species distributions would arise from differences among GCMs (Goberville, Beaugrand, Hautekèete, Piquot, & Luczak, 2015; Tang et al., 2018; Thuiller et al., 2019). Therefore, it is recommended that multiple emission scenarios and multiple GCMs should be used to predict the impact of climate change on species distribution. For instance, Luo et al. (2015) examined the effect of climate change on distributions of 22 ungulate species on the Tibetan Plateau by using three GCMs and three emissions scenarios. Yan et al. (2017) selected five GCMs and two emissions scenarios to evaluate the range shifts of Chinese caterpillar fungus (*Ophiocordyceps sinensis*) in response to climate change. In our present study, six GCMs and two emissions scenarios were chosen and the variabilities in results of range size change were also detected; average outputs of the six GCMs were used as future climates which is believed to reduce uncertainties associated with different GCMs (Yan et al., 2017).

Previous studies have demonstrated that future climate change could result in extensive loss of coastal wetlands due to sea-level rise (Hinkel et al., 2018; Schuerch et al., 2018; Spencer et al., 2016). Therefore, we should notice that our SDM projections may overestimate future habitat availability of the two crayfish species in the coastal areas. In addition, niche modelling cannot consider thermal flexibility of some species. Thermal flexibility has also been reported in crayfishes (Haubrock et al., 2019; Veselý, Buřič, & Kouba, 2015); for instance, Veselý et al. (2015) reported from laboratory experiments that *P. clarkii* can persist low water temperature that simulated winter water temperature in temperate Europe. Therefore, niche modelling may underestimate the actual predicted distributions of the two species as these models generally show suitable habitats rather than tolerant habitats. Likewise, flexibility of the crayfishes to other climatic factors can also be expected. Recently, an established population of *P. clarkii* was reported from Indonesia (Putra et al., 2018), a region where our SDMs suggest the absence of suitable climates. This might be potentially explained by a niche shift of *P. clarkii* (i.e. the capacity to occupy climates where it was not observed before), but we also highlight that the existing population of *P. clarkii* in Indonesia remains local in extent, and occurs in natural ponds where it is semi-intensely cultivated. So the general suitability of climatic conditions in the area remains to be investigated.

4.3 | Management implications

Our results have important implications for the management of both invasive species. Under global warming, the distribution of *P. leniusculus* and *P. clarkii* is predicted to expand northward in Europe where this species already occurs. Early monitoring programmes and preventative measures should be considered to control spread of the two invasive species in Europe. In this sense, the European Union (EU) is committed with this environmental problem and has regulated a set of measures across the EU that includes prevention, early detection–eradication, and management of invasive species, as well as the financial support systems to implement such measures (European Parliament, 2014). However, the implementation of such measures depends on societal and political issues in each EU member country, which can reduce their effectiveness. Early detection of alien crayfish species may be performed using environmental DNA (eDNA) techniques (Muha, Rodríguez-Rey, Rolla, & Tricarico, 2017). Species-specific eDNA primers are available for both *P. leniusculus* (Larson et al., 2017) and *P. clarkii* (Tréguier et al., 2014). In areas where the dispersal of invasive crayfish species seems unavoidable, mitigation management strategies to conserve vulnerable wildlife may also be planned prior to the arrival of the invaders. For example, both *P leniusculus* and *P. clarkii* have been reported to displace native crayfish through predation, competitive exclusion or transmission of diseases in Japan and Europe. In such areas, captive populations of native crayfish may be established before extirpation by crayfish invaders.

Regarding Australia and New Zealand, these areas are considered suitable for both invasive crayfish species, but they have not been reported yet. These two countries are taking biosecurity extremely seriously and have strict regulations regarding importation of species (see the Biosecurity Act 2015 and the Biosecurity 2025 Direction Statement for New Zealand's biosecurity system for details). Existing biosecurity measures should be kept in place, and the ban on aquarium and ornamental trades of these invasive species in Australia and New Zealand should be continued.

Even though various control methods have been attempted to control nuisance crayfish, crayfish eradication is almost impossible except in limited circumstances (Gherardi, Aquiloni, Diéguez-Uribeondo, & Tricarico, 2011; Hansen, Ives, Vander Zanden, & Carpenter, 2013; Holdich, Gydemo, & Rogers, 1999; Manfrin, Souty-Grosset, Anastácio, Reynolds, & Giulianini, 2019). However, Hansen et al. (2013) pointed out that more frequently droughts in the future may facilitate eradication of invasive rusty crayfish (*Orconectes rusticus*) in Wisconsin lakes. Under the future climate change scenarios, southern Europe will become less suitable for *P. leniusculus* as time progresses, and existing eradication programmes in these areas should become more effective (Gallardo & Aldridge, 2013). Recently, the economic exploitation of invasive crayfish has been proposed as a measure for population control (Conde & Domínguez, 2015). However, there are also concerns that harvested crayfish may transmit crayfish plague to native crayfish species (Souty-Grosset et al., 2016); in addition, similar to what has been verified for the invasive Chinese mitten crab in the River Thames, economic exploitation might result in intentional releases of individuals into new watersheds for the sake of financial benefits (Clark, 2011). As a result, the derived economic activity and societal pressure might run counter population control or the eradication of the species in southern Europe.

Considering the potentially high costs and risks associated to crayfish eradication programmes, more efforts may be directed towards the prevention of species introductions into new regions. Our results highlight areas that are highly susceptible to the establishment of two highly problematic crayfishes under current and future conditions. These results could help in the development of strategies aiming to prevent further invasions.

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CONFLICTS OF INTEREST

Authors have no conflict of interest to declare.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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