

Research Article

Predicting the risk of introduction and establishment of an exotic aquarium animal in Europe: insights from one decade of Marmorkrebs (Crustacea, Astacida, Cambaridae) releases

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Received: 15 July 2014 / Accepted: 10 September 2014 / Published online: 20 October 2014

Handling editor: Vadim Panov

Abstract

The presence of the North American Marmorkrebs (*Procambarus fallax* f. *virginalis*) in European inland waters is entirely driven by ongoing propagule pressure from the ornamental trade. Since 2003 at least 25 independent introduction events have been confirmed, of which some have eventually resulted in established populations. This study links a maximum-entropy model that forecasts the probability of Marmorkrebs introduction based on socio-economic predictors to an updated species distribution model based on environmental predictors in order to explore the risk of further Marmorkrebs establishment in Europe. In line with related research, the probability of Marmorkrebs release was largely affected by gross domestic product and human population density, i.e. predictors very likely related to the density of Marmorkrebs owners, whereas environmental suitability was mostly influenced by minimum temperature and the availability of lentic habitats, which was indirectly assessed by terrain slope. While considerable parts of Europe were predicted as potentially suitable for establishment, high probabilities of introduction were forecasted in much smaller geographic areas. The consensus map of the model predictions suggests that introduction and subsequent establishment of Marmorkrebs is likely to occur in much of Germany, the Benelux countries, England, Italy, and areas of high human population density throughout France and Spain, as well as parts of southernmost Scandinavia and Southeastern Europe. Monitoring trades of Marmorkrebs in these high-risk regions is recommended and implications for proactive measures are discussed, including the need for consistent trade regulations at the EU level.

Key words: marbled crayfish, propagule pressure, risk assessment, ornamental trade, introduction pathway

Introduction

An important introduction pathway for aquatic alien species is the growing trade of wildlife for ornamental purposes (Padilla and Williams 2004; Strecker et al. 2011; Masin et al. 2014). Alien species introductions from the ornamental trade involve notorious and harmful invaders such as bullfrog (*Lithobates catesbeianus* (Shaw, 1802)), goldfish ('*Carassius auratus*' (Linnaeus, 1758)), red swamp crayfish (*Procambarus clarkii* (Girard, 1852)), and Brazilian waterweed (*Egeria densa* Planch.) (Duggan 2011; Strecker et al. 2011; Chucholl 2013a, and citations therein). What is more, exotic species available in ornamental trades can carry exotic pathogens and parasites, including *Batrachochytrium dendrobatidis* Longcore et al., the causative agent of Chytridiomycosis in

amphibians (Mazzoni et al. 2003), and *Aphanomyces astaci* Schikora, the causative agent of crayfish plague (Kozubíková-Balcarová et al. 2013). In the case of release into open waters, these associated organisms may spill over to native and often also naive species, causing massive mortalities.

The likelihood of an exotic species to become introduced from aquaria into nature has been shown to be closely related to intrinsic ecological traits (e.g., maximum body size) and its popularity in the hobby, which may be dynamic over time (Duggan et al. 2006; Duggan 2011; Chucholl 2013a). New trends among aquarium hobbyists that result in rapid proliferation of new species in the trade and home aquaria can entail introduction of new alien species into nature. A prime example for this phenomenon is the proliferation

of the parthenogenetic Marmorkrebs (*Procambarus fallax* (Hagen, 1870) f. *virginalis*) in the Central European pet trade as part of the 'invertebrates boom' among German aquarium hobbyists since the late-1990s, which—after some delay—has resulted in introduction and establishment in at least five European countries (Chucholl et al. 2012; Bohman et al. 2013), as well as Madagascar, where it was dubbed a 'perfect invader' (Jones et al. 2009; Kawai et al. 2009).

The Marmorkrebs indeed possesses several species-level traits that can promote invasiveness, including a rapid life cycle, high fecundity, polyploidy, and obligatory parthenogenetic reproduction (Seitz et al. 2005; Martin et al. 2010a; Martin et al. 2012). The latter aspect is a unique feature among the alien crayfish species in Europe and implies that even very low propagule pressure, *i.e.* one released animal, can seed a new population. Apart from species-level traits considered beneficial throughout the invasion process, the invasiveness of Marmorkrebs is clearly determined by the climate suitability of the recipient habitat. Owing to its presumed origin from the subtropical southeastern part of North America (Florida and southern Georgia; Martin et al. 2010a), climate was suggested to be a limiting factor for its establishment and spread in many parts of Europe (Martin et al. 2010b; Chucholl et al. 2012; Bohman et al. 2013). For instance, Marmorkrebs became highly invasive in Madagascar, where climatic conditions are favorable (Jones et al. 2009; Kawai et al. 2009), whereas the species is as-yet restricted to summer-warm habitats in Central Europe (summarized in Chucholl et al. 2012). At even higher latitudes in Scandinavia, it is expected that climate has a decidedly negative effect on the invasiveness of Marmorkrebs (Bohman et al. 2013).

Feria and Faulkes (2011) used niche-based species distribution models (SDMs) to predict suitable areas for Marmorkrebs in Madagascar, Europe, and North America. All of their models predicted that eastern Madagascar, the southeastern United States, Cuba, and much of Mexico are potentially suitable for Marmorkrebs. With regard to Europe, only small areas were predicted as suitable by most models; however, a model that was trained on occurrences of Marmorkrebs in Europe predicted much of Europe as suitable. Since then, new records of Marmorkrebs from Europe became available, including more established populations (Chucholl et al. 2012; supplementary Table S1).

Niche-based SDMs forecast environmental suitability, *i.e.* factors that mostly determine

establishment and spread (Elith et al. 2011). SDMs are therefore widely used to project the possible extent of biological invasions (e.g., Larson et al. 2010; Feria and Faulkes 2011; Palaoro et al. 2013), which may help risk assessment and conservation strategies. However, determinants of the first stage in the invasion sequence, *i.e.* introduction, are rarely included in model construction (but see Gallardo and Aldridge 2013). This is unfortunate in that introduction is a crucial part of any invasion process (Lockwood et al. 2007; Blackburn et al. 2011). Disregarding information related to introduction pathways may ultimately over-predict areas at risk, which, in turn, may handicap reliable conservation strategies.

The purpose of the present study is to link a maximum-entropy model that forecasts the probability of Marmorkrebs introduction based on socio-economic predictors to an updated SDM based on environmental predictors in order to advance overall risk assessment for Europe. This integrated approach acknowledges the multi-staged nature of biological invasions and the different forces that determine the likelihoods of introduction and establishment (Blackburn et al. 2011). Arising implications for proactive measures and early detection are discussed.

Rationale and model construction

I used maximum-entropy modeling (Maxent) based on (i) introduction-related socio-economic predictors and all records of free-living Marmorkrebs and (ii) environmental predictors and records of established populations only to independently forecast areas at risk of introduction and establishment, respectively. Both risk maps were subsequently combined to produce a consensus map that shows areas where both introduction into nature and successful establishment are likely.

Maximum-entropy modeling has been extensively used to model the potential distribution of invasive species and ranks among the best-performing methods for this purpose (Elith et al. 2006; Elith et al. 2011; Gallardo and Aldridge 2013). What is more, Maxent only requires presence records, which eliminates the need for any *a priori* assumptions about absences (Phillips et al. 2006; Elith et al. 2011). Maxent represents a machine learning algorithm that predicts environmental suitability for a given species as a function of predictor variables based on maximum entropy. The method correlates species records with the environmental characteristics found at the occurrence sites and uses those relationships to

forecast environmental suitability and thereby potential distribution across the landscape. The Maxent algorithm is not limited to predictions of environmental suitability though, as it is a general-purpose method for making predictions from incomplete information (Philips et al. 2006). In the present study, Maxent modeling is also used to derive the probability of Marmorkrebs introduction into nature from a set of socio-economic predictors. For a comprehensive description of the Maxent modeling algorithm and the underlying statistics please refer to Elith et al. (2011).

The Maxent models for probability of introduction and environmental suitability were calibrated and evaluated with 15 European Marmorkrebs records taken from Chucholl et al. (2012) and 6 additional, validated and geo-referenced records that became known since then (Table S1), including the first finding of Marmorkrebs in Scandinavia (Bohman et al. 2013). Seven out of the 21 records were considered as established populations, following the rationale of Chucholl et al. (2012). Records of free-living Marmorkrebs from Madagascar were not used for model calibration because a preliminary analysis based on multivariate environmental similarity surfaces (MESS; Elith et al. 2010) showed that most of Europe represents a non-analog climate relative to Madagascar, which limits the predictive ability of Madagascan Marmorkrebs records for European climates. The native range of the probable parent species of Marmorkrebs, *Procambarus fallax*, was also excluded since the origin of Marmorkrebs from this area is as yet speculative (*cf.* Martin et al. 2010a). What is more, previous niche-based models of invasive crayfish distribution, including Marmorkrebs, suggest little climate niche conservatism between native and invaded ranges (Larson et al. 2010; Fera and Faulkes 2011). The present analysis was therefore explicitly restricted to European climates and species records.

Socio-economic and environmental predictors were selected according to related research on the introduction pathway and Marmorkrebs biology (Duggan et al. 2006; Copp et al. 2010; Fera and Faulkes 2011; Perdikaris et al. 2012; Chucholl 2013a; Gallardo and Aldridge 2013; Patoka et al. 2014a). Because the analysis was based on relatively few presence records ($N = 21$), and to avoid over-fitting and multicollinearity, the number of predictor variables was limited to seven (four for probability of introduction and three for environmental suitability), following the suggestion of Elith and Leathwick (2009; *cf.*

Elith et al. 2011). To this end, all candidate variables were scaled to the same resolution (30", which corresponds to a grid cell size of approximately 1×1 km) and checked for correlation using ENMTools (v.1.3; Warren et al. 2010). Of highly correlated variable pairs ($R > 0.8$) only the ecologically most meaningful variable was retained. The remaining predictor variables were only weakly correlated (Pearson correlation: $R < 0.5$). Finally, a jackknife test of variable importance was employed and variables with a contribution < 0.05 were removed. The final predictor variables are summarized in Table 1, including justification for inclusion in the respective model and the data source.

The model that forecasts the probability of Marmorkrebs introduction was calibrated on the whole of Europe, whereas the environmental suitability model was only trained on the area delimited by records of Marmorkrebs introductions and then projected to the whole of Europe. The rationale behind this training region was that the underlying assumption of equilibrium of Marmorkrebs distribution with environmental variables can't be met in areas where it was not introduced (*cf.* Elith et al. 2011). MESS analysis was carried out to identify non-analog environments in which projections of environmental suitability from the training region are unreliable (Elith et al. 2010).

All models were run in the software Maxent (v. 3.3.3k; Phillips et al. 2006). To allow for better generalization of the models and to avoid over-fitting, the regularization multiplier was set to 1.5 (Gallardo et al. 2013; Quinn et al. 2013). All other parameters were left at default settings, including the auto features function, which automatically limits the number of model parameters and feature types (link functions) according to the number of training occurrences (Elith et al. 2011). Accuracy of the model prediction was assessed by the area under the receiver operating characteristic curve (AUC), averaged over replicate runs with cross-validation (20-fold cross-validation for probability of introduction and 7-fold cross-validation for environmental suitability). The AUC tests model accuracy based on presence points and pseudo-absences drawn from background points and ranges from 0.5 (random prediction) to 1 (excellent prediction). Finally, the average model output was visually checked for its ability to capture the introduced and established range of Marmorkrebs in Europe and the response curves of the predictor variables were inspected for plausible behavior (*cf.* Philips et al. 2006).

Table 1. Predictor variables used in the Maxent models, including justification for inclusion in the respective model and the data source.

Model	Predictor	Justification	Source
Probability of introduction	Gross Domestic Product	Gross domestic product and human population density have been previously shown to correlate with introductions of aquatic alien species (Perdikaris et al. 2012). Population density was also suggested as surrogate predictor of propagule pressure (Copp et al. 2010). Both factors are only weakly correlated ($R < 0.5$).	Center for International Earth Science Information Network (2002, 2005)
	Population Density		
	Land Cover	Releases of exotic pets may be linked to certain land use types, such as parks or urban areas (van Ham et al. 2013).	Hansen et al. (1998)
	Human Influence Index	The Human Influence Index is a composite measure of human population pressure, human land use, infrastructure, and human access. Most of those factors can be related to introduction of alien species (Gallardo and Aldridge 2013). The Index shows only a weak correlation with gross domestic product and population density ($R < 0.4$).	Last of the Wild Data Version 2 (2005)
Environmental suitability for establishment	Min Temperature of Coldest Month	Temperature is known to affect growth, survival, and reproduction of Marmorkrebs (Seitz et al. 2005). Low temperature has been frequently cited as a limiting factor for Marmorkrebs establishment in Europe (Martin et al. 2010b, Bohman et al. 2013). Data are for air temperature, which is assumed to correlate with water temperature. Min. temperature correlates strongly with mean temperature of coldest quarter, annual mean temperature, and isothermality ($R > 0.8$), and moderately with mean temperature of warmest quarter, max. temperature, and temperature seasonality ($R > 0.6$).	Hijmans et al. (2005), WorldClim
	Slope	Marmorkrebs establishment success in Europe has been linked to lentic habitats (Chucholl et al. 2012). Terrain slope was used as surrogate predictor for the availability of lentic habitats.	Hijmans et al. (2005), WorldClim; derived from elevation data
	Precipitation of Driest Month	Feria and Faulkes (2011) showed a clear effect of minimum precipitation on climate suitability for Marmorkrebs. They concluded that the species has a low tolerance towards drying-out of habitats. The factor was used together with slope as surrogate predictor for availability of permanent lentic habitats. Precipitation of driest month correlates strongly positively with precipitation of warmest quarter ($R > 0.8$), and moderately negatively with mean temperature of warmest quarter ($R > 0.7$).	Hijmans et al. (2005), WorldClim

For construction of the consensus map, the logistic output maps were converted into binary maps using average minimum training presence thresholds (Elith et al. 2011). This threshold rule was chosen because both models are based on relatively few presence records, which have all been verified by photos or voucher specimens (*cf.* Chucholl et al. 2012). Any bias from erroneous records that would advise against this threshold rule can therefore be excluded. To produce the consensus map, binary grid cell values of the environmental suitability model were multiplied by two and then added to the binary grid cell values of the introduction model. Possible grid

cell values of the consensus map were then: 0 – no risk of introduction and establishment, 1 – risk of introduction only, 2 – risk of establishment only, and 3 – risk of introduction and establishment.

Results and discussion

Model predictions and evaluation

The resulting model outputs and the consensus map are shown in Figure 1 and the respective model statistics are summarized in Table 2. Following the rough classification of model accuracy of Araújo and Guisan (2006), the models

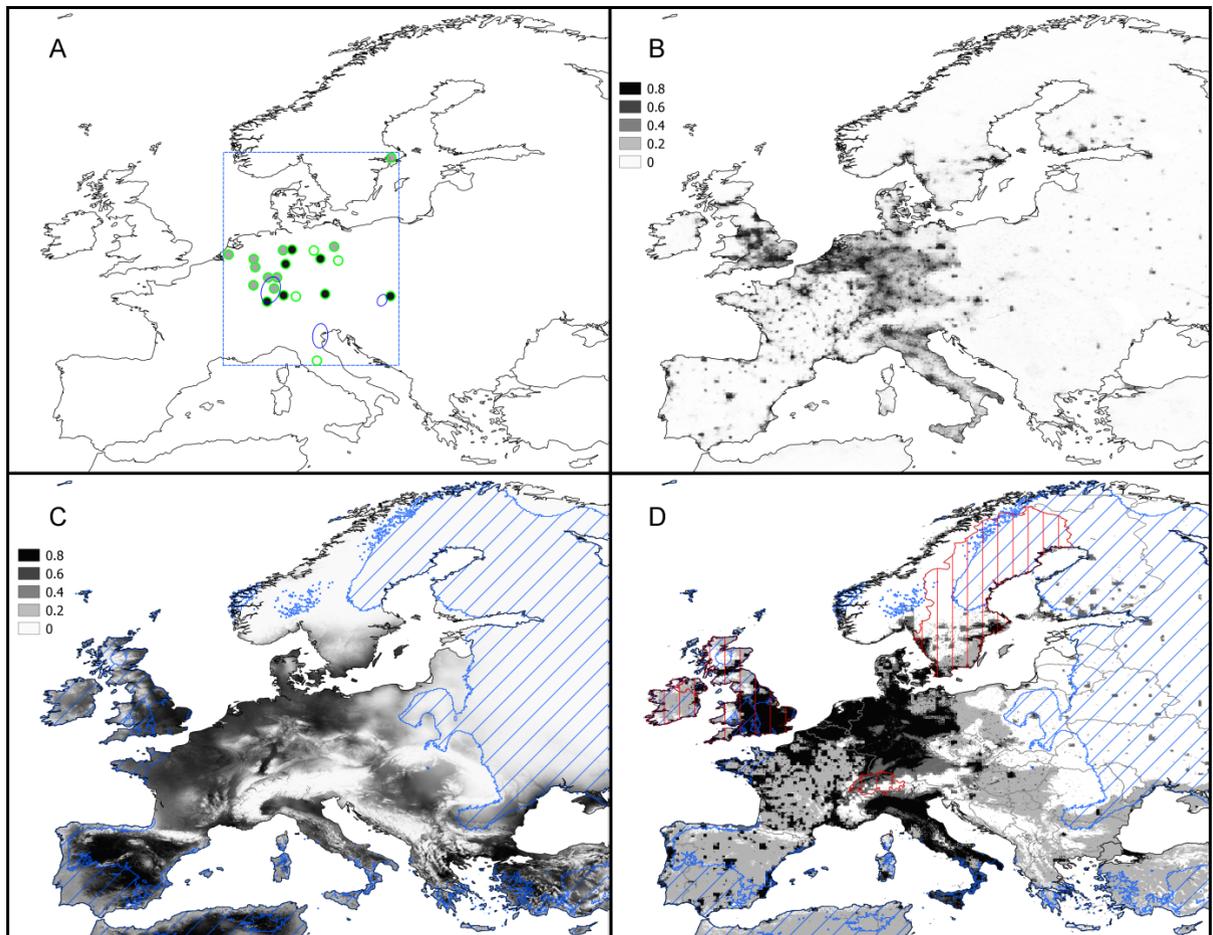


Figure 1. A – Marmorkrebs records used to calibrate the models (green dots); black fill color indicates established populations, grey indicates records involving several Marmorkrebs individuals but with an unknown population status, and white indicates single specimens. Blue ellipses enclose the approximate location of four additional records of Marmorkrebs populations that were used for model evaluation (see discussion for details). B – Probability of Marmorkrebs introduction into open waters based on socio-economic predictors (point-wise mean of 20-fold cross-validation); C – Environmental suitability for Marmorkrebs establishment based on environmental predictors (point-wise mean of 7-fold cross-validation); and D – consensus map, showing areas at risk of (i) introduction only (dark grey), (ii) establishment only (light grey), and (iii) introduction and establishment (black). Hatched blue areas in C and D indicate regions with non-analog climates compared to the training region (blue rectangle in A), as indicated by MESS analysis. Predictions of environmental suitability in regions with non-analog climates should be carefully interpreted. Hatched red areas in D highlight territories, where import, trade or keeping of Marmorkrebs is prohibited. Iceland is not shown, since it features a non-analog climate throughout.

attained good (environmental suitability) to excellent (risk of introduction) AUC values and the average output maps are in good accordance with our knowledge of the introduction pathway, Marmorkrebs biology, and previous research (*cf.* Duggan et al. 2006; Copp et al. 2010; Chucholl et al. 2012; Perdikaris et al. 2012).

The predicted likelihood of Marmorkrebs introduction was strongly positively related to gross domestic product and human population density, and—to a lesser extent—land cover and the Human Influence Index (Figure 2). This

finding is in line with previous research that identified positive correlations between gross domestic product and human population density and the overall number of alien crayfish species present in European countries (Perdikaris et al. 2012), as well as the general notion that dumping of exotic pets into the wild occurs more frequently in or near urban areas than remote areas (van Ham et al. 2013). Gross domestic product and human population density probably mainly affect the overall density of Marmorkrebs owners in a given area, which, in turn, is very likely directly

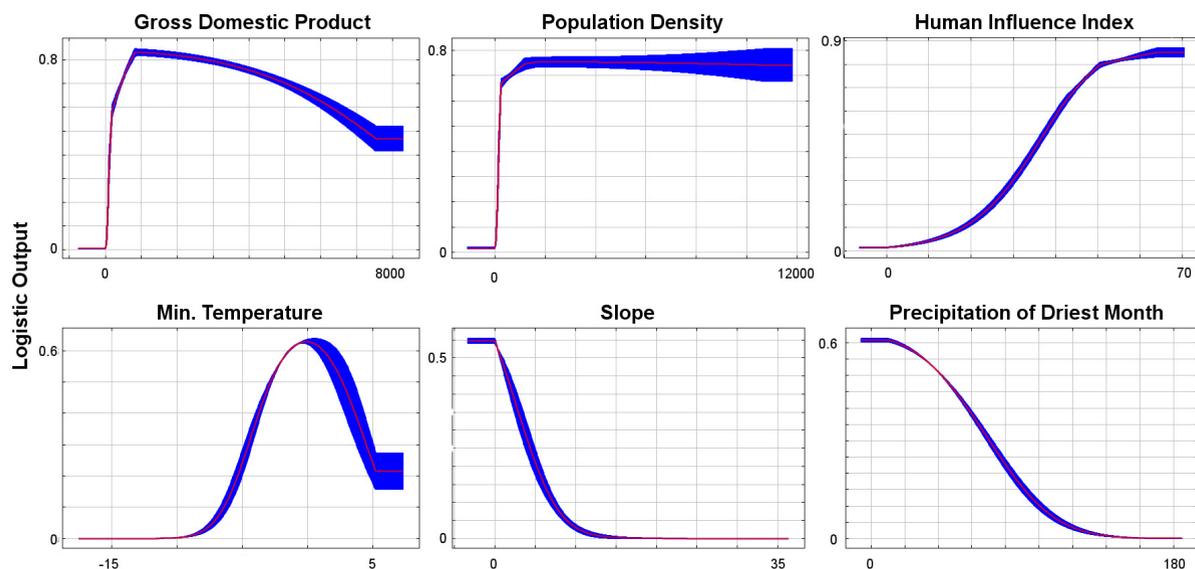


Figure 2. Response curves of the continuous socio-economic predictors (top row) and environmental predictors (bottom row) used to predict probability of Marmorkrebs introduction and environmental suitability for Marmorkrebs establishment, respectively. The curves show the mean response of 20 (top row) and 7 (bottom row) replicate Maxent runs (red) \pm SD (blue).

Table 2. Mean area under the receiver operating characteristic curve (AUC) of the Maxent models, niche breadth and estimates of relative contributions of the predictor variables. Values shown are averages over replicate runs.

Model	Cross-validation	Mean AUC (\pm SD)	Niche breadth	Predictor variable	Percent contribution	Permutation importance
Probability of introduction	20-fold	0.96 (\pm 0.05)	0.12	Gross Domestic Product	74.3	81.4
				Population Density	12.7	4.7
				Land Cover	9.9	9.4
				Human Influence Index	3.1	4.5
Environmental suitability	7-fold	0.80 (\pm 0.16)	0.48	Min Temperature	58.5	60.4
				Slope	26.7	22.2
				Precipitation of Driest Month	14.8	17.4

related to Marmorkrebs propagule pressure (*cf.* Copp et al. 2010; Patoka et al. 2014a). The risk of Marmorkrebs introduction into nature was consequently predicted to be highest throughout densely populated regions of Central Europe, the Benelux countries, England, and Italy, as well as urban centres in Western, Southern, and Eastern Europe (Figure 1B).

Environmental suitability for Marmorkrebs was largely determined by temperature during winter, terrain slope and precipitation of driest month (Figure 2). A positive association with mild winter temperatures was expected due to the presumed subtropical origin of Marmorkrebs (Martin et al. 2010a) and the latter two variables reflect the previously recognized preference of Marmorkrebs

for lentic habitats in Europe (Chucholl et al. 2012). MESS analysis indicated several areas with non-analog climates relative to the training region in which predictions of environmental suitability are unreliable (highlighted as blue hatched areas in Figure 1C and D).

The environmental suitability model output is ecologically plausible in that it is in general accordance with the European distribution of a closely related invader with comparable ecological requirements—*Procambarus clarkii*. *Procambarus clarkii* originates from subtropical regions of North America, comparable in climate to the presumed native range of Marmorkrebs (Souty-Grosset et al. 2006; Martin et al. 2010a). *Procambarus clarkii* is an old crayfish invader in Europe and was first

introduced into the Iberian Peninsula in 1973, where its widespread distribution presumably reflects its fundamental niche by now (Souty-Grosset et al. 2006; Holdich et al. 2009). It became one of the worst aquatic invasive species throughout Southwestern Europe, France and Italy and these areas were also predicted as generally suitable for Marmorkrebs (Figure 1C). In addition, there's a growing number of records from higher latitudes, including Germany, Belgium, The Netherlands and England, of which most stem from lentic or slow flowing habitats (Boets et al. 2009; Chucholl 2011; Ellis et al. 2012; van der Wal et al. 2013). The latter aspect coincides with the apparent link between Marmorkrebs establishment success and summer-warm lentic habitats (Chucholl et al. 2012) and suggests that subtropical *Procambarus* species may be able to colonize summer-warm habitats throughout most of Central Europe and parts of England, as indicated by the environmental suitability model for Marmorkrebs (Figure 1C). This view is further supported by ecological niche models for *P. clarkii* (Mestre et al. 2013), which are remarkably consistent to the SDM for Marmorkrebs.

The consensus map correctly predicted five out of the seven established Marmorkrebs populations that were used for model calibration and provided a spatially close fit to the remaining two populations (cf. Figure 1A and D). The grid cell of a population in Slovakia (cf. Janský and Mutkovič 2010) was predicted to be suitable for establishment but the risk of introduction was predicted slightly lower than the average minimum training presence threshold. However, several grid cells in proximity (~ 2 km) were predicted to be at high risk of introduction and establishment and the nearby populations mentioned by Stloukal (2009) were correctly forecasted (see below). In the second instance, the grid cell of a semi-feral population in a garden pond in Bavaria was predicted to be at high risk of introduction but environmental suitability fell just below the average minimum training presence threshold. This might be due to a favorable microclimate in the garden pond that is not well represented by the grid cell values of the environmental variables.

A high accuracy of the consensus map prediction is ultimately corroborated by four independent records of established Marmorkrebs populations that were not used for model calibration due to a lack of precise locality information and that were nonetheless correctly forecasted (blue ellipses in Figure 1A): Stloukal (2009) reported that Marmorkrebs formed

breeding populations in garden ponds in or near to Bratislava, Slovakia. The greater area of Bratislava was correctly predicted to be at high risk of introduction and establishment. Likewise there are two records of populations from southwestern Germany, one in a garden pond and one in a gravel pit lake, that are situated in an area that is generally predicted to be at high risk of introduction and establishment (A. Martens pers. comm. 2013). Finally, it was recently suggested that an established population of Marmorkrebs occurs in the lower River Po drainage, close to Venice, Italy (Z. Ďuriš, cited in Kouba et al. 2014). This area was also correctly predicted to be at high risk of Marmorkrebs introduction and establishment (cf. Figure 1B and C).

Implications for risk mitigation

Owing to the different forces that drive probability of introduction and environmental suitability (Lockwood et al. 2007; Copp et al. 2010; Perdikaris et al. 2012), the risks of introduction and establishment can considerably differ from each other in a given region. Indeed, the model output for probability of introduction was only very weakly correlated to the model output for environmental suitability (Pearson correlation: $R = 0.18$).

An invasion stage-specific modeling approach, as implemented in Figure 1, may therefore improve conservation planning. For instance, while considerable parts of Europe were predicted as potentially suitable for establishment (Figure 1C), high probabilities of introduction occur in much smaller geographic areas (Figure 1B; niche breadth as assessed by ENMTools = 0.48 and 0.12 for environmental suitability and probability of introduction, respectively). Such information is relevant for risk mitigation and early detection efforts, and is hard to extract when predictors of introduction and establishment/spread are combined into a single model. Overall, the consensus map suggests that introduction and subsequent establishment of Marmorkrebs is likely to occur in most of Germany, the Benelux countries, England, Italy, and areas of high human population density throughout France and Spain, as well as parts of southernmost Scandinavia and Southeastern Europe (Figure 1D).

Invasive *Procambarus* species can build up high population densities and act as polytrophic keystone species, exerting multiple pressures on lentic ecosystems, even at higher latitudes (Chucholl 2013b; van der Wal et al. 2013). These effects

were shown to be not functionally redundant to the effects of native European crayfish (Dunoyer et al. 2014). What is more, competition and crayfish plague transmission by Marmorkrebs pose an additional threat to imperiled native crayfish (Chucholl et al. 2012; Kozubiková-Balcarová et al. 2013), and Marmorkrebs might also carry the causative agent of Chytridiomycosis, as it was shown for the closely related congener *P. alleni* (Faxon, 1884) and *P. clarkii* (McMahon et al. 2013). Established Marmorkrebs occurrences in Central Europe are mostly localized to isolated lentic habitats and have not substantially spread yet (Chucholl et al. 2012). However, potential for high population growth, active spread *via* surface waters and migration over land as well as secondary introductions have been repeatedly demonstrated (summarized in Chucholl et al. 2012; A. Martens pers. comm. 2013). In regions with high environmental suitability (Figure 1B) and abundant lentic habitats, such as wetlands and rice paddies in southwestern and southern Europe, Marmorkrebs releases might readily pave the way for substantial spread (*cf.* Jones et al. 2009; Kawai et al. 2009).

Monitoring trades of Marmorkrebs in the identified high-risk regions is therefore recommended and proactive measures should be adopted where necessary. Previous research has established a clear link between species' availability in the ornamental trade and the likelihood of release into nature, *i.e.* propagule pressure (Duggan et al. 2006; Strecker et al. 2011; Chucholl 2013a). Limiting the availability of Marmorkrebs is therefore in all likelihood one of the most effective strategies for risk mitigation (*cf.* Holdich et al. 2009; Chucholl 2013a).

However, this strategy is significantly hindered by the fact that only 4 out of the 17 European territories that harbor high-risk regions for Marmorkrebs introduction and establishment have as yet implemented trade regulations for ornamental alien crayfish species (Figure 1C, territories hatched in red; *cf.* Holdich et al. 2009). Germany in particular, which represents the largest market for ornamental crayfish in Europe, hasn't adopted any regulations for import, trade, and keeping of alien crayfish species (Chucholl 2013a, and citations therein). Such large and unregulated markets also provide plenty of opportunities for illegal introductions into countries where there are trade regulations in place. This is exemplified by black markets for ornamental crayfish in Switzerland, Sweden and Great Britain, which are most likely fueled by imports from

neighboring countries without trade regulations, including Germany (Peay et al. 2010; Bohman et al. 2013; Chucholl pers. obs.). In order to provide effective trade regulation within EU territory, consistent regulations at the EU level are needed to overcome the regulatory inconsistencies among member states (Hulme et al. 2009; Caffrey et al. 2014). In the meantime, public education and voluntary self-regulation of the trade offer the presumably best possibilities for proactive risk mitigation in the identified high-risk regions (Chucholl 2013a; Patoka et al. 2014a,b).

Finally, it is important to acknowledge that recent invasiveness screening studies have concordantly reported the presence of several high-risk alien crayfish species (*i.e.* species with a high potential invasiveness), mostly originating from North America, in the European aquarium market (Peay et al. 2010; Chucholl 2013a; Patoka et al. 2014b). While the Marmorkrebs clearly represents a focal species to assess releases of ornamental crayfish—due to its exclusive and common availability in the aquarium trade as well as its track record of introductions—efforts for risk mitigation, as outlined above, should be directed at all of the available high-risk species (*cf.* Chucholl 2013a; Patoka et al. 2014b).

Acknowledgements

I'd like to thank the organizers (T. Kawai and Z. Faulkes) and participants of the Crayfish Biology session at the SICB meeting in San Francisco 2013 for many interesting presentations and discussions on Marmorkrebs. I'm very grateful to H. Groß (Edelkrebsprojekt NRW) and A. Martens (PH Karlsruhe) for providing additional Marmorkrebs records and to A. Brinker (Fisheries Research Station) and three anonymous referees for adding valuable suggestions and comments that helped to improve this paper. The views expressed in this article are those of the author and not necessarily those of his parent organization.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Validated geo-referenced Marmorcrebs records used for Maxent model calibration and evaluation, excluding the records previously reported by Chucholl et al. (2012).

This material is available as part of online article from:

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