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Research Article

Forecasting the distribution of Marmorkrebs, a parthenogenetic crayfish with high invasive potential, in Madagascar, Europe, and North America

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Abstract

The parthenogenetic marbled crayfish, Marmorkrebs, has high potential to become an invasive species because single individuals can establish a population. Marmorkrebs have already been introduced in several countries, have successfully established populations in at least two of them, and are rapidly expanding in one case (Madagascar). To assess the potential ecological threat arising from further Marmorkrebs introductions, we developed four species distribution models using the distribution of *Procambarus fallax* (the sexual form of Marmorkrebs) and exotic populations of Marmorkrebs in Madagascar and Europe. The models were applied to three regions where Marmorkrebs pose a conservation concern: Madagascar, where Marmorkrebs populations are growing; Europe, where individuals have been found repeatedly, and where some Marmorkrebs populations are becoming established, and; North America, where Marmorkrebs are sold as pets, which presents a risk of introduction into North American ecosystems. All models predicted that eastern Madagascar provides suitable habitat for Marmorkrebs. Most models suggested that relatively small areas of Europe are suitable habitat, although a model that includes locations of Marmorkrebs introductions in Europe predicts much of Europe could be suitable, which is supported by recent discoveries of populations in Germany. All models predicted that the south eastern United States, Cuba, and much of Mexico are also potential habitats. The climatic variable with the greatest predictive power was precipitation in the warmest quarter, which may reflect a susceptibility to drought that has been documented for *P. fallax*.

Key words: marbled crayfish, MaxEnt, *Procambarus fallax*, species distribution models

Introduction

Many crayfish species are keystone species in freshwater habitats, simultaneously acting as herbivores (Chambers et al. 1990; Creed 1994), predators (Momot 1995; Dorn and Wojdak 2004), prey (Stein and Magnuson 1976), and bioturbators (Dorn and Wojdak 2004). It is unsurprising, then, that introductions of non-indigenous crayfish species have had profound ecological impacts on several continents (Gherardi 2006). Among the ecological impacts of such introductions are conservation and biodiversity concerns. For example, North America contains about 75% of the world's crayfish species (Lodge et al. 2000a), but the introduction of non-indigenous crayfish has contributed to the loss of indigenous crayfish (Hill and Lodge 1999; Lodge et al. 2000a; Klocker and Strayer 2004). This, combined with other pressures, has created a situation where crayfish are among the most threatened animal groups in North America: nearly half of the crayfish species on the continent pose a conservation concern (Taylor et al. 2007).

Potential introductions of marbled crayfish, Marmorkrebs, present a particularly worrying scenario. Marmorkrebs is currently the only confirmed parthenogenetic decapod crustacean (Scholtz et al. 2003; Vogt et al. 2004; Martin et al. 2007; but see Yue et al. 2008 for a report suggesting parthenogenesis in *Procambarus clarkii*), which gives it unusual potential to become an invasive species, because the release of just one individual could establish a new population. The evolutionary origin of this mode of reproduction, however, has been difficult to track down. There are currently no known indigenous populations of Marmorkrebs. Marmorkrebs were first found in the pet trade in Europe in the mid-1990s (Scholtz et al. 2003), and efforts to uncover their provenance failed (Vogt et al. 2004). To the best of our knowledge, no other exotic animal has both a mode of reproduction unlike any other species in its order, and no recorded occurrence in its probable original habitat.

Marmorkrebs have been released into natural ecosystems in Madagascar (Jones et al. 2009; Kawai et al. 2009), several countries in Europe (Holdich et al. 2009; Marzano et al. 2009; Chucholl and Pfeiffer 2010; Martin et al. 2010b), and Japan (Kawai and Takahata 2010).

In Madagascar, Marmorkrebs were first found in 2003 (Heimer 2010) and populations are growing rapidly (Jones et al. 2009; Kawai et al. 2009). Madagascar has been of particular concern because of the presence of an endemic crayfish genus, *Astacoides* (Hobbs 1987; Jones et al. 2006; Jones and Coulson 2006; Jones et al. 2007). *Astacoides* may be vulnerable to competition from Marmorkrebs (Jones et al. 2009) and crayfish plague (Jones et al. 2007), which could conceivably be transmitted by Marmorkrebs.

The situation in Europe is changing rapidly. In a paper available online in early July 2010, Martin et al. (2010b) pointed out that there were no populations of Marmorkrebs larger than single individuals and suggested that the species may not pose as great a threat as feared. Less than four months later, the popular press in Germany reported a Marmorkrebs population that was apparently so crowded that crayfish were leaving the water to find new locations (Löwe 2010; Privenau 2010), followed within weeks by a technical paper describing an established population in another German lake (Chucholl and Pfeiffer 2010).

There have not yet been any confirmed introductions of Marmorkrebs into natural ecosystems in the North America, but Marmorkrebs are increasingly available through the pet trade (Faulkes 2010). The poor track record of aquarium keepers containing their pets to their tanks (Chang et al. 2009; Keller and Lodge 2009; Duggan 2010) gives reason to be pessimistic that Marmorkrebs will stay confined as pets in North America.

One approach that can assist in assessing the threat from Marmorkrebs is to examine the ecology of its most closely related sexual form, the slough crayfish, *P. fallax* (Hagen, 1870) (Martin et al. 2010a). Martin et al. (2010a) characterized Marmorkrebs as a parthenogenetic form of this species, and suggested a scientific name of *P. fallax* f. *virginalis* for Marmorkrebs. Here, we use the common name "Marmorkrebs" for the parthenogenetic form to minimize possible confusion between the forms and to emphasize the difference between the indigenous sexual populations in Florida, and the introduced exotic parthenogenetic populations elsewhere.

Given that the available evidence strongly suggests that Marmorkrebs and *P. fallax* are the same species, it is reasonable to use information from one to make models and predictions about the other. At the broad scale, *P. fallax* is widely distributed across the Florida peninsula (Hobbs 1942), but the factors limiting its distribution at this macro level have not been identified. At the fine scale, the key factor influencing distribution of *P. fallax* is a need for a constant supply of water (Hendrix and Loftus 2000). *Procambarus fallax* is particularly susceptible to surface waters drying out, because it only rarely builds burrows (Dorn and Trexler 2007), which other crayfish species use to reach the water table during dry periods. Competition with a sympatric species, *P. alleni*, may be a secondary factor influencing the distribution of *P. fallax* (Dorn and Trexler 2007). Hobbs (1942) also noted *P. fallax* abundance was correlated with vegetation, and that he never collected it from sand bottomed streams. Although constrained by the presence of water, *P. fallax* does not appear to be highly constrained by water quality: it is tolerant of low oxygenation and fairly high acidity (Hobbs 1942). Ovigerous females can be found most months of the year, and *P. fallax* is extremely variable in its form (Hobbs 1942). If these features are also true of Marmorkrebs, they could pose problems for conservation and management. Year round reproduction suggests that this an r-selected species, which may outcompete more K-selected species by dint of numbers. Morphological variation may make it difficult to identify an individual as Marmorkrebs, which is key to early detection of an introduction. Although Marmorkrebs are genetically identical (Martin et al. 2007), their morphology can vary substantially (Vogt et al. 2008; Martin et al. 2010b).

Martin et al. (2010a) discussed extrapolating from the ecology of *P. fallax* to make qualitative predictions about the potential distribution of Marmorkrebs that are released into new habitats, focusing on temperature requirements. To make more explicit, quantitative predictions about the regions where Marmorkrebs might thrive, we developed species distribution models (SDM), using nineteen climatic variables, for the three regions where Marmorkrebs currently pose the greatest conservation concern: Madagascar, Europe, and North America. Species distribution models have been used to assess species' invasive potential (Broennimann et al. 2007; Rödder et al. 2009). Invasive potential can be modelled in three ways. First, it can be modelled using the native distribution of a species. In this case, we used the distribution of *P. fallax* in Florida as a proxy for the distribution of Marmorkrebs. Second, invasive potential can be modelled using the distribution of introductions where new populations are successfully established. We used the distribution of Marmorkrebs in Madagascar, which were the only known established populations at the time this manuscript was being prepared. Third, the data from both the native and the introduced populations can be combined. We used all of these three approaches because each has its own pros and cons (Bradley et al. 2010). Finally, we also generated a more speculative model using both the distributions of Marmorkrebs in Madagascar and the locations of individuals in Europe (where there were no confirmed populations at the time; Martin et al. 2010a), on the premise that it was at least plausible that Marmorkrebs could establish populations from those individuals, which has since proved to be correct (Chucholl and Pfeiffer 2010).

Methods

The geographic distribution of *Procambarus fallax* and Marmorkrebs were estimated from previous publications on these species. The level of information available required different approaches to estimate the distributions for each species.

Because the indigenous Madagascar crayfish are most at risk from the introduction and growing populations of Marmorkrebs, we extracted information about the distribution of crayfish species in the genus *Astacoides* to compare with the current and predicted ranges of Marmorkrebs. This was not done for Europe or North America, because the number of species now present in these regions is so much greater (particularly in North America) that extracting information about all indigenous and exotic species present on these continents was impractical.

Procambarus fallax

Hobbs (1942) thoroughly surveyed the distribution of all known crayfishes in Florida, including *P. fallax*. In most cases, he described the distribution by naming the counties in which *P. fallax* were found. Later, the distribution of *P. fallax* was extended to two additional southern counties (Hendrix and Loftus 2000). County names were searched though Google Earth v. 5.2.1.1547 (*http://earth.google.com*), which provided latitude and longitude measurements in the approximate center of the counties. The wide distribution and high densities of this species should compensate somewhat for the coarseness of the available location data. Hobbs noted, "Practically all of the streams within the range of *(P.) fallax* seem to be inhibited by it, in at least some of their reaches." Additionally, Hobbs's survey was completed before massive urbanization and development that occurred in Florida in the mid to late twentieth century. Thus, Hobbs's data document the distribution of *P. fallax* in environments less disturbed than present.

Marmorkrebs and Astacoides

Latitude and longitude measurements were taken from published GPS values (Kawai et al. 2009) or estimated from published maps (Jones et al. 2009 for Marmorkrebs; Hobbs 1987 for *Astacoides*). When published maps were used, they were superimposed on the relevant geographic location in Google Earth using the "Add Image Overlay" tool, and the transparency of the map was adjusted using "Properties" option for the image to view both the published map and the Google Earth image simultaneously. Placemarks were put onto points indicated on the published map, from which latitude and longitude were recorded.

Potential distribution

Several ecological, evolutionary, and historical factors determine geographic areas in which a species occur. These factors can be (1) abiotic (e.g., climate); 2) biotic (i.e., species interactions: competition, parasitism, trophic interactions); 3) historical (e.g., barriers, speciation process); 4) dispersal capabilities; 5) accessible regions for dispersal; 6) evolutionary capacity of species' populations to adapt to new conditions; and 7) anthropogenic factors (e.g., land use transformation, translocation of organisms; Pulliam 2000; Soberón and Peterson 2005). From these, climatic variables (abiotic factors) are frequently used to estimate species' distributions (Brown et al. 1996; Austin 2002).

Climate can limit distributions directly by affecting growth or survival (e.g., lower and upper lethal temperatures), and indirectly via interacting species (e.g., food sources, pathogens, competitors, or predators). Species distribution models can be used to model the potential distribution of species by correlating occurrence data (measure in latitude and longitude) and climatic variables (temperature, precipitation; Araújo and Guisan 2006; Kearney 2006). There are many ways to model a species' potential distribution (Guisan and Zimmermann 2000; Elith et al. 2006), but we used MaxEnt (Phillips et al. 2004; Phillips et al. 2006) because it discriminates suitable and unsuitable areas better than other methods (Elith et al. 2006; Hernandez et al. 2006; Phillips et al. 2006; Phillips 2008).

MaxEnt models a probability distribution (potential distribution) of habitat suitability over the study area using only species presences (Phillips et al. 2004; Phillips et al. 2006). The modelled potential distribution must agree with everything that is known about the environment and the known distributional data of the species, thereby avoiding placement of any unfounded constraints. The best potential distribution of the species is the one that is nearest to having equal probabilities of occurrence across the entire study area (closest to uniform), subject to the constraint that the expectation for each environmental variable included in the modelled distribution must match its empirical average over the known distributional data. The probability calculated in MaxEnt represents the relative suitability of the environmental conditions for the target species in each pixel in the study area as a function of the environment in all of the known distributional units. MaxEnt assigns a probability of habitat suitability per each grid cell in the study area, ranging from 0 (least suitable) to 1 (most suitable).

We used MaxEnt version 3.06 (*http://www.cs.princeton.edu/~schapire/maxent/*) to estimate the potential distribution of *P. fallax* and Marmorkrebs, with the default modelling parameters (convergence threshold = 10^5, maximum iterations = 500, regularization value β = auto) following Phillips et al. (2006). We used nineteen bioclimatic variables available at *http://www.worldclim.org* as predictors: annual mean temperature, mean diurnal range (mean of monthly (maximum temperature – minimum temperature)), isothermality, temperature seasonality (standard deviation ×100), max temperature of warmest month, min temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality (coefficient of variation), precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter.

The bioclimatic variables result from global land area interpolation of climate point data (years 1950–2000) at a spatial resolution of 2.5 arc-min (Hijmans et al. 2005) at a resolution of approximately 0.0083333 (1×1 km^2 grid cells). All the probability thresholds of the potential distributions were considered in order to analyze the habitat suitability of the areas in Madagascar, Europe, and North America. Model results were processed and visualized using the GIS software ArcView 3.2 (ESRI 1999) and ArcGIS 9.1 (ESRI 2005).

The choice of geographic region to be modelled was determined by a combination of factors. For Madagascar, the entire island was modelled because it is reasonably self-contained. For Europe, most continental countries were included because these included most regions where Marmorkrebs have been found in natural habitats (Holdich et al. 2009; Marzano et al. 2009; Martin et al. 2010b) and adjoining ones where Marmorkrebs might be expected to be sold or distributed. Great Britain and Ireland were also included, because Marmorkrebs have been discovered in the pet trade in England at least once (Anonymous 2007). For North America, the southern 48 states of the United States and southern Canada were included in the model because Marmorkrebs are sold as pets in these locations (Faulkes 2010). Other American countries such as Mexico and Cuba were included because these regions have endemic crayfish species for which the introduction of Marmorkrebs could create a conservation concern (Hobbs 1984).

We created four models. The first model was based on the distribution of the indigenous populations of *P. fallax* in the United States; the second was trained on the distribution of the exotic, growing populations of Marmorkrebs in Madagascar; the third used a combination of both known viable populations, and; the fourth used both viable populations, plus the documented introductions in Germany, Italy, and the Netherlands that were known before October 2010 (i.e., excluding populations described by Chucholl and Pfeiffer 2010; Löwe 2010; Privenau 2010).

Model predictivity was evaluated by splitting available occurrence data using 70% of known occurrences to train and 30% to evaluate (testing data) the model. We evaluated models by calculating the Area Under the Curve (AUC) in Receiver Operating Characteristics plots (ROC; Fielding and Bell 1997). ROC is a threshold–independent measure that evaluates the probability that the model produces a positive result in a positive locality (sensitivity) versus the probability that the model produces a negative result in a negative locality (specificity) when presented with new data. A ROC plot is obtained by plotting all sensitivity values on the *y*–axis against their equivalent (1–specificity) values for all available decision thresholds on the *x*–axis. The theoretically perfect result is AUC = 1, whereas a test performing no better than random yields AUC = 0.5. AUC and ROC plots were calculated in SPSS 12.0. Since AUC calculations require absences, we created pseudo-absences using the random point generator extension in ArcView 3.2 (ESRI 1999). The number of pseudo-absences was equal to the number of known occurrence data that was used to run the models (Mateo et al. 2010).

Results

Maps of potential distribution for both *P. fallax* and Marmorkrebs obtained high performance scores with AUCs > 0.9. The factor with the greatest predictive power in all four models was precipitation during the warmest quarter (Table 1), which explained 36.2-60.6% of the variation in the data. Despite its high predictive power in all four models, the values for precipitation in the warmest quarter used to train the models did not overlap for *P. fallax* and the Madagascar Marmorkrebs population (Figure 1); other climatic variables associated with these two populations showed more overlap. The model in which this variable had the lowest predictive power was when the model was trained on the most restrictive dataset, i.e., Marmorkrebs in Madagascar only. This variable's greatest predictive power occurred in the model with the largest dataset for which we have reasonable confidence that it is drawn from viable populations, namely the endemic range of *P. fallax* and the introduction of Marmorkrebs in Madagascar.

Madagascar

All models showed eastern Madagascar as being suitable habitat for Marmorkrebs (Figure 2). Even the model with the smallest predicted distribution, trained on *P. fallax* data alone (Figure 2a), predicted at least one location where Marmorkrebs are known to occur as suitable habitat. The *P. fallax* model, however, did not predict that the region near the capital of Antananarivo is suitable habitat, when this region in fact contains many Marmorkrebs (Jones et al. 2009).

Even though the known distribution of Marmorkrebs in Madagascar is relatively small, all three models incorporating those data of Marmorkrebs in Madagascar predicted that most of Madagascar is highly suitable habitat for Marmorkrebs. The predicted distribution from all three models completely overlaps the distribution of the endemic *Astacoides* species.

Europe

Only a few regions in Europe were predicted to be suitable habitat for Marmorkrebs in three of the four models we ran (Figure 3a-c). Using *P. fallax* data alone (Figure 3a), no western European regions are predicted to be suitable habitat. When data on Marmorkrebs in Madagascar are used (Figure 3b), relatively small areas of suitable habitat are predicted to exist in several countries, including Germany (where there have been several documented releases of Marmorkrebs and one confirmed population; Chucholl and Pfeiffer 2010) and the United Kingdom.

The predicted habitat changes substantially when the model is trained using *P. fallax* locations, and both the Madagscar and European locations of Marmorkrebs (Figure 3d). Almost all of Europe is predicted to be suitable habitat for Marmorkrebs, except southern Spain and Portugal.

North America

All four models indicate that Mexico, Cuba, and south eastern and south central states in the United States are suitable habitat for

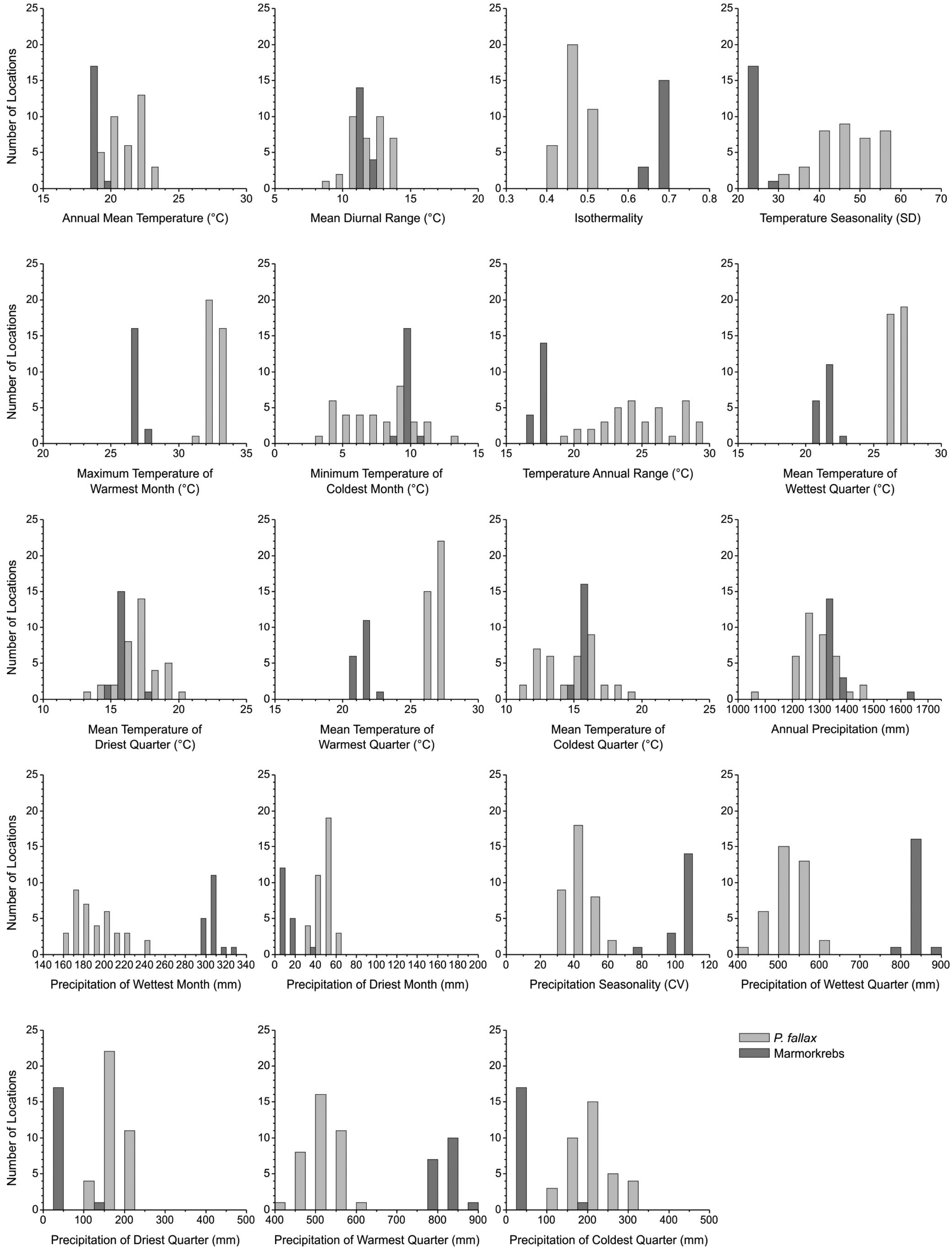

Figure 1. Histograms of nineteen climatic variables associated with the locations of *Procambarus fallax* in Florida (light gray) and Marmorkrebs in Madagascar (dark gray) used to train models 1, 2, and 3.

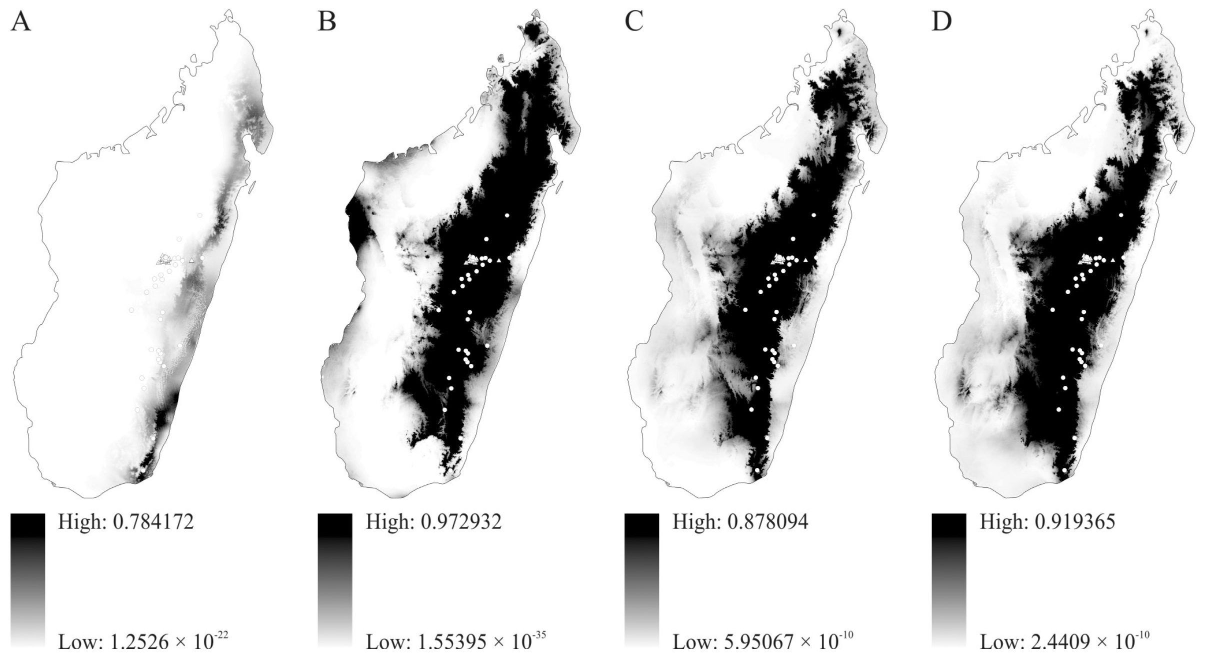

Figure 2. Potential distribution of Marmorkrebs in Madagascar predicted using model trained with data from (**a**) *Procambarus fallax* only; (**b**) Marmorkrebs in Madagascar; (**c**) *P. fallax* and Marmorkrebs in Madagascar, and (**d**) *P. fallax*, and Marmorkrebs in Madagascar and Europe. Triangles = distribution of Marmorkrebs (Jones et al. 2009; Kawai et al. 2009); circles = distribution of *Astacoides* (Hobbs 1987). Legend: Gray scale indicates the similarity between known and predicted habitats; "high" and "low" values represent the highest and lowest probability of habitat suitability.

Table 1. Major predictive variables in climate models.

	Florida only		Madagascar only		Florida and Madagascar		Florida, Madagascar, and Europe	
Rank	Variable	%	Variable	%	Variable	%	Variable	%
1	Precipitation of warmest quarter	42.6	Precipitation of warmest quarter	36.2	Precipitation of warmest quarter	60.6	Precipitation of warmest quarter	49.7
2	Mean temperature of wettest quarter	11.8	Temperature annual range	25.1	Mean temperature of coldest quarter	11.6	Temperature annual range	18.7
3	Precipitation seasonality	10.7	Annual mean temperature	13.2	Isothermality	9.2	Mean temperature of coldest quarter	8.6
4	Precipitation of driest quarter	10.4	Precipitation of coldest quarter	12.8	Annual precipitation	5.7	Precipitation of driest month	4.2

Marmorkrebs. The model trained using *P. fallax* data alone (Figure 4a) predicts a larger distribution for *P. fallax* than is observed. The model trained using the Madagascar Marmorkrebs data shows the most restricted distribution (Figure 3b), but predicts southern Florida as potential habitat, overlapping slightly with the known distribution of *P. fallax*.

Discussion

The four models of the potential distribution of Marmorkrebs all agree that Madagascar and the southern part of North America are highly suitable habitat for Marmorkrebs. Models built on the distribution of *P. fallax* predicted a

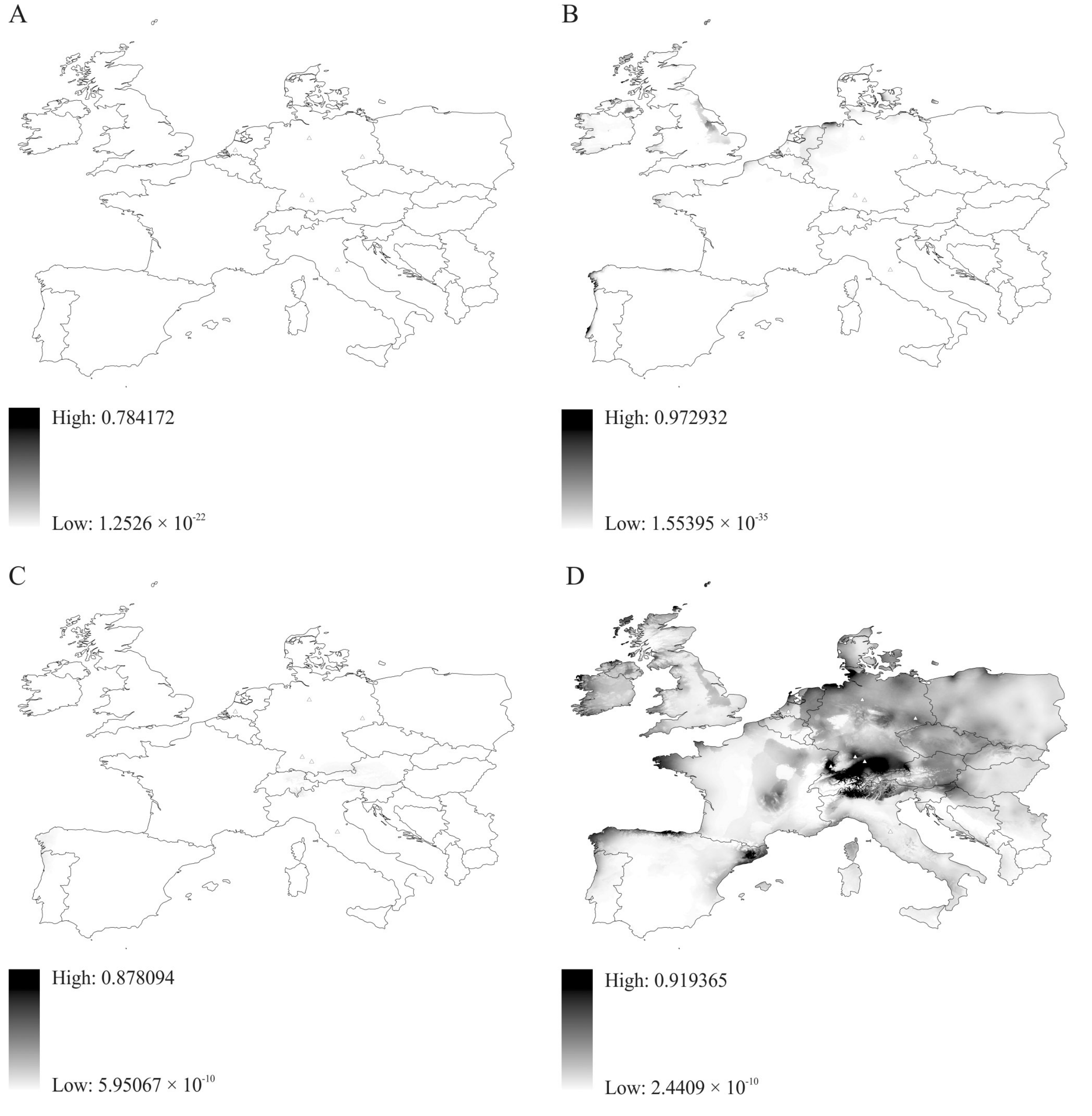

Figure 3. Potential distribution of Marmorkrebs in Europe predicted using model trained with data from (**a**) *Procambarus fallax* only; (**b**) Marmorkrebs in Madagascar; (**c**) *P. fallax* and Marmorkrebs in Madagascar, and (**d**) *P. fallax*, and Marmorkrebs in Madagascar and Europe. Triangles = releases of Marmorkrebs (Holdich et al. 2009; Marzano et al. 2009; Martin et al. 2010b). Legend: Gray scale indicates the similarity between known and predicted habitats; "high" and "low" values represent the highest and lowest probability of habitat suitability.

distribution that overlapped of the known range of Marmorkrebs in Madagascar, and vice versa, but only partially. For example, the model trained on *P. fallax* data alone (Figure 2a) did not predict the Antananarivo region to be suitable habitat, but this location is the epicenter of the Marmorkrebs population (Jones et al. 2009). This is similar to other modelling studies where the native distribution of a species did not predict the precise distribution of that species following introductions to new habitats (e.g., Broennimann et al. 2007; Larson et al. 2010). Marmorkrebs may be undergoing a niche shift that sometimes occurs when exotics are

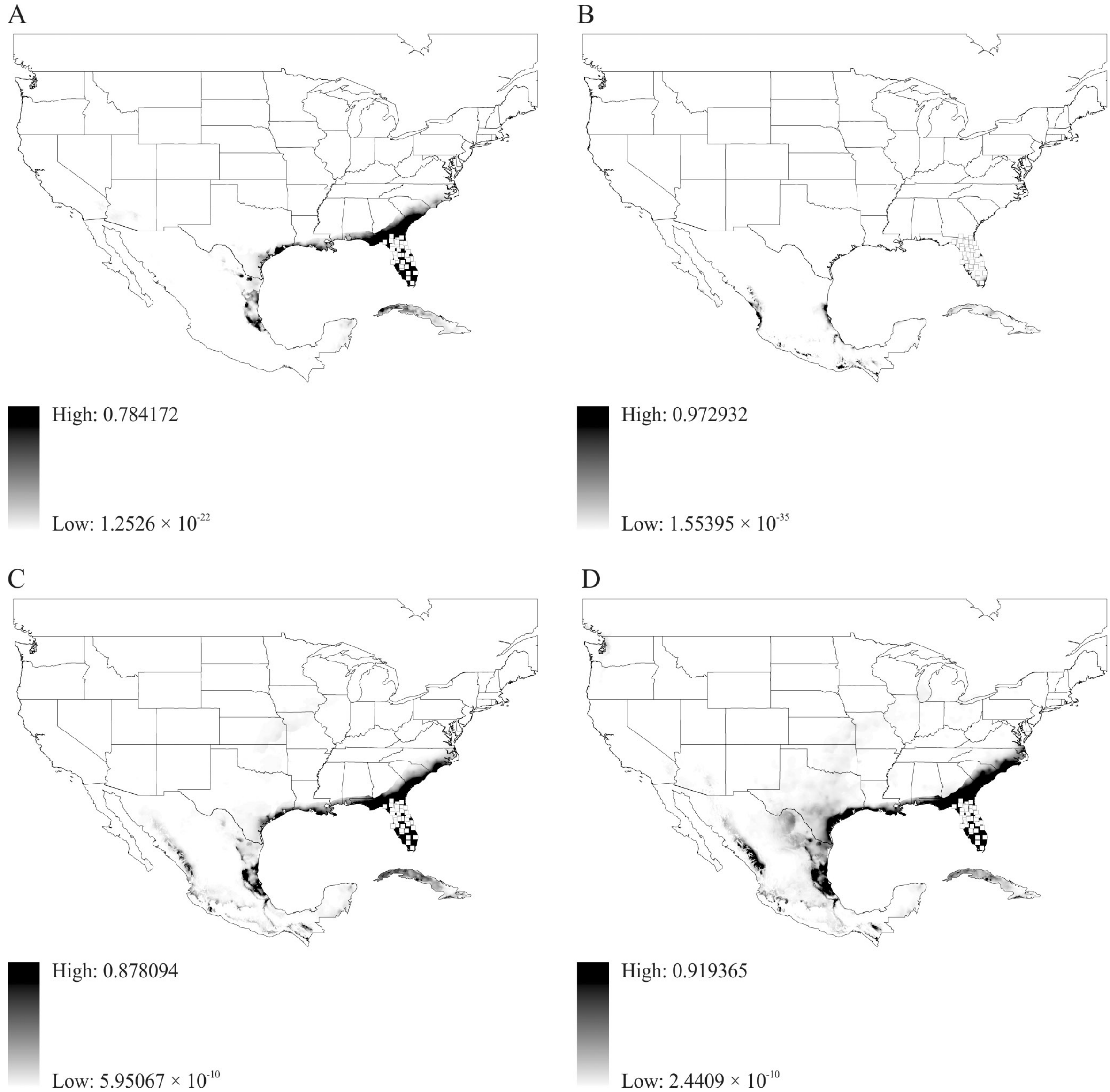

Figure 4. Potential distribution of Marmorkrebs in North America predicted using model trained with data from (**a**) *Procambarus fallax* only; (**b**) Marmorkrebs in Madagascar; (**c**) *P. fallax* and Marmorkrebs in Madagascar, and (**d**) *P. fallax*, and Marmorkrebs in Madagascar and Europe. Squares = distribution of *P. fallax* (Hobbs 1942; Hendrix and Loftus 2000). Legend: Gray scale indicates the similarity between known and predicted habitats; "high" and "low" values represent the highest and lowest probability of habitat suitability.

introduced into new habitats (Broennimann et al. 2007; Broennimann and Guisan 2008; Larson et al. 2010). Also, the current distribution of crayfish is often influenced by past geologic events, which may have shrank distribution, and the low mobility of crayfish (Rahel 2007), which limits the rate of expansion back to the maximal distribution of the species, which is largely determined by the physiological limits of the species to climatic conditions. For example, the rusty crayfish, *Orconectes rusticus*, has tremendously expanded its distribution because its dispersal has been aided by humans (Olden et al. 2006).

The model that included European Marmorkrebs data was considered to be speculative, because at the time we performed the analyses, there was no clear published evidence that any of the locations used contained ongoing populations (Martin et al. 2010b); an established population of Marmorkrebs in Europe (Chucholl and Pfeiffer 2010) was reported only late in the process of preparing this manuscript.

That the precipitation of the warmest quarter explains such a large proportion of the data may be related to the probability of sloughs drying out, which significantly harms *P. fallax* populations (Dorn and Trexler 2007; Dorn and Volin 2009).

Madagascar

Of the three locations tested by our models, Madagascar presents the most troubling scenario. The Marmorkrebs introduction in Madagascar has advanced further along the stages followed by an invasive species (Theoharides and Dukes 2007; Hellmann et al. 2008) than any other introduction of Marmorkrebs. From a conservation and management standpoint, there are probably few *worse* locations on the planet that Marmorkrebs could have been introduced into. First, all four models we ran indicated that eastern Madagascar is a highly suitable habitat for Marmorkrebs. This suggests that it will probably be difficult, if not impossible, to eradicate established populations, based on experiences with exotic crayfish in locations like Great Britain (Freeman et al. 2010). Although exotic vertebrate species have been eradicated successfully from many small islands (Donlan 2008; Anonymous 2010), there are not similar examples of success in eliminating small aquatic invertebrates from a large island. Probably the best that can be hoped is to slow and contain the spread of Marmorkrebs across watersheds. Given that *P. fallax* is susceptible to drying out (Dorn and Trexler 2007), they are likely to have minimal mobility from one watershed to another if they are not aided by humans. Second, the predicted suitable habitat in some models largely overlaps the distribution of the endemic crayfish species in Madagascar, increasing the possibility of detrimental interactions between the indigenous and exotic species. It is not clear how much the small scale niches of Marmorkrebs and *Astacoides* species may overlap, however. Most *Astacoides* species appear to prefer rivers and streams (Jones et al. 2007), while Marmorkrebs and *P. fallax* appear to prefer lakes and ponds (Hendrix and Loftus 2000; Chucholl and Pfeiffer 2010). Third, rice is grown in Madagascar (Barrett and Dorosh 1996; Jones et al. 2007), and crayfish significantly reduce productivity of rice paddies (Barnes and Baldridge 2009). Finally, Madagascar is currently politically unstable (Bearak 2010), which may make it difficult to implement or enforce any policies to curb the spread of Marmorkrebs until the political situation has stabilized.

Europe

The predicted Marmorkrebs distribution for Europe varied the most of the three regions examined here across our four models. Three models suggested few regions in Europe were suitable habitat for Marmorkrebs (Figure 3a-c), which was consistent with the suggestion by Martin et al. (2010b) that the threat posed by Marmorkrebs to European waterways may have been overestimated. When data for the locations where Marmorkrebs have been found in Europe are incorporated into the model, however, the picture changed dramatically. Given that two established populations have now been described (Chucholl and Pfeiffer 2010; Löwe 2010; Privenau 2010) in locations near the single individuals used to train our model, this model probably represents a better prediction of the potential distribution of Marmorkrebs in Europe than the models trained using Madagascar and Florida data alone. This model is also consistent with the suggestion of Chucholl and Pfeiffer (2010) that the population they describe in Germany may only be a tiny fraction of the actual established populations in Europe. This clearly indicates the need to monitor Marmorkrebs introductions around the globe closely: if Marmorkrebs are discovered in locations far from the current known introductions, the predicted distribution could change substantially, and the assessment of risk would change.

North America

Although Marmorkrebs are widely distributed throughout the North American pet trade (Faulkes 2010), all four models suggest that the most probable locations where Marmorkrebs might become established if released are in the south eastern and south central United States (a hotspot for crayfish biodiversity; Lodge et al. 2000a), Mexico, and Cuba (both of which contain endemic crayfish species; Hobbs 1984). These jurisdictions should quickly review their policies concerning crayfish imports and sales

(Lodge et al. 2000b; Padilla and Williams 2004; Keller and Lodge 2009). To date, the only North American jurisdictions that we are aware of that are considering regulating Marmorkrebs are Missouri (Missouri Department of Conservation 2010) and Maryland (Thomson 2010; Maryland Department of Natural Resources 2011), neither of which is predicted to contain suitable habitat in our models.

The large scale models in this paper are only a first attempt to assess the possible problems posed by Marmorkrebs. To develop models that could predict the distribution of Marmorkrebs on a smaller scale, information on the following would be needed. First, we have limited knowledge about the fine-scale distribution of *P. fallax* and the best physiological conditions for *P. fallax* and Marmorkrebs, although Seitz et al. (2005) have made a reasonable start on the latter. Second, there appear to be relatively few attempts to model the distribution of aquatic species that consider multiple physical variables (but see Lehmann et al. 1997; Naura and Robinson 1998 for examples of studies that do consider such variables). For example, flow regimes can be important to determining habitat suitability for some crayfish (Jones and Bergey 2009). Naura and Robinson (1998) provide an example of the level of detail needed to develop fine scale models of crayfish distribution. Chucholl and Pfeiffer (2010) point out that Marmorkrebs are more likely to thrive in lentic habitats, such as lakes and ponds, rather than streams or rivers.

A major advantage of quantitative species distribution models is that they can be refined as new information becomes available, such as occurred during the preparation of this paper. To refine large scale models like those presented here, the spread of Marmorkrebs in regions where it has been introduced needs to be monitored closely, and regions where Marmorkrebs are likely to be introduced would benefit from close surveillance of natural ecosystems. Additionally, these models can help to direct attention and policy in the jurisdictions at greatest risk of introductions, which are the most likely to need increased efforts in surveillance (e.g., monitoring waters for exotic crayfish, such as Marmorkrebs), policy (e.g., passing regulations concerning the sale of Marmorkrebs), and public education (e.g., informing pet owners of the threats posed by Marmorkrebs).

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