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Quantifying the ecological niche overlap between two interacting invasive species: the zebra mussel (Dreissena polymorpha) *and the quagga mussel* (Dreissena rostriformis bugensis)

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ABSTRACT

1. The zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostriformis bugensis*) are two closely related invasive species. They usually occupy different habitats (e.g. shallow versus deep water) at a local scale, while occurring in the same broad regions at a large scale. The present study assesses the extent to which the habitat partitioning observed at local scales extends to niche partitioning at the global scale.

2. Species distribution models (SDMs, using MaxEnt) were used to model the potential distributions of both species based on a set of environmental and dispersal related predictors.

3. According to environmental SDMs calibrated with bioclimatic, geographic and geological factors, only 75% of the predicted quagga mussel distribution overlaps with the distribution of zebra mussel, demonstrating that the niches of the two species are moderately different at a global scale.

4. Quagga mussels were found to occur at higher average temperature and lower average precipitation, leading to the prediction that their niche includes Mediterranean and arid regions such as California and southern Spain, two areas currently unaffected by zebra mussel.

5. A second set of SDMs illustrated a notable influence of dispersal-related factors (e.g. human population density, closeness to commercial ports and reservoirs), on quagga mussel distribution. These models suggest that the distribution of quagga mussel is more constrained by dispersal-related factors than is the distribution of zebra mussel.

6. Evidence suggests that economic and environmental impacts can differ between the two species; joint accurate predictions may therefore prove important for targeting precautionary management plans at the right species.

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KEY WORDS: alien species; lake; river; modelling; benthos; invertebrates

INTRODUCTION

The zebra mussel (*Dreissena polymorpha* Pallas 1771) and quagga mussel (*Dreissena rostriformis bugensis* Andrusov 1897) are two closely related species of Ponto-Caspian origin. Over the last century they have invaded large areas of both North America

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and Europe, attracting great attention because of their adverse effects on native species and ecosystems (Mills *et al*., 1996; Ricciardi *et al*., 1998; McCabe *et al*., 2006). They also have severe consequences for industry; estimated costs to the US economy are up to $1 billion each year (US Army Corp of Engineers, 2002), while in the UK around £5 million is spent each year in boat washing, hull sealing and mechanical control of zebra mussel (Oreska and Aldridge, 2011). Zebra mussels began a dramatic spread across western Europe in the 18th century (van der Velde *et al*., 2010) and arrived in North America in 1986 (Carlton, 2008). More recently, quagga mussels have begun to invade areas previously occupied exclusively by zebra mussels. Where the two are found together, quagga mussel seems to have a competitive advantage and has quickly displaced zebra mussel as the dominant dreissenid in several lakes and rivers in North America (Mills *et al*., 1999; Ricciardi and Whoriskey, 2004), Ukraine (Mills *et al*., 1996), Russia (Orlova *et al*., 2005a) and most recently in The Netherlands (Molloy *et al*., 2007). In such cases, local habitat partitioning seems to occur as a result of differences in environmental tolerances (Spidle *et al*., 1995; Mills *et al*., 1996; Nalepa *et al*., 2010), with zebra mussels typically confined to shallow areas.

Despite these differences, at a large scale the two species tend to be found together in the same broad regions (Figure 1); zebra mussels cover a larger area at present but quagga mussels have been expanding into the zebra mussel range. The colonization of the western United States by quagga mussels is the first time a large ecosystem has been infested by quagga mussels without first being invaded by zebra mussels (Wong and Gerstenberger, 2011). This indicates that the small-scale habitat partitioning observed locally may extend to large-scale niche partitioning, and presents the possibility that quagga mussels may be able to spread into other areas that have until now been considered at low risk of dreissenid invasion.

One approach to investigate the risk of invasion by the two species on a large scale is to develop species distribution models (SDMs). These correlate observed presences of a species with the

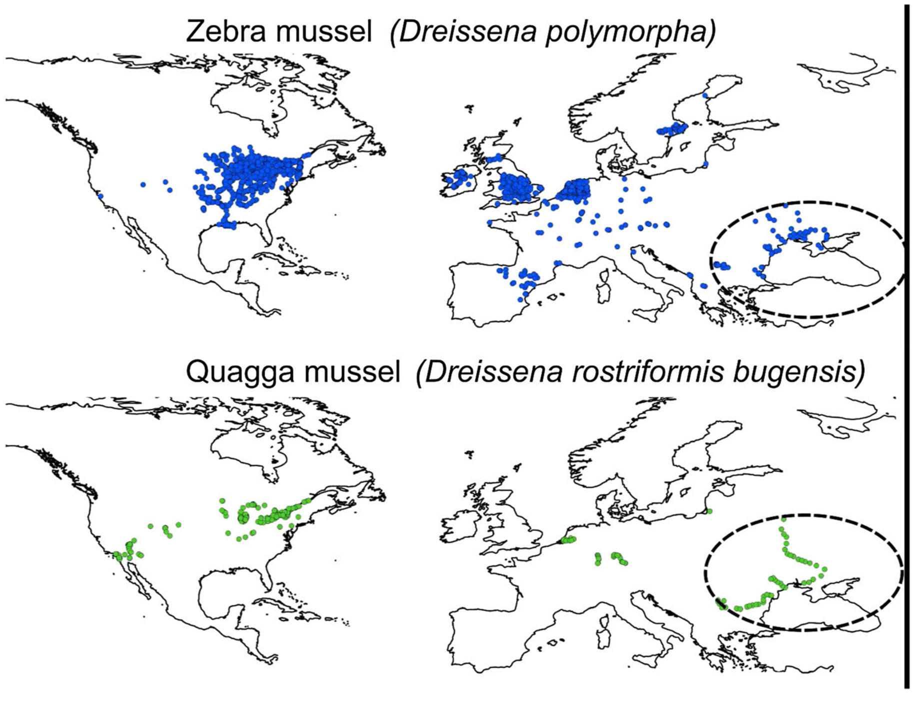

Figure 1. Location of zebra and quagga mussel presence points used in this study and extracted from GBIF (data.gbif.org) and the US Geological Survey (usgs.gov). The dashed ellipse roughly envelopes the native range of each species.

environmental conditions found at those sites, and use these relationships to predict the potential geographic range of the species. The potential distribution derived from an SDM can be considered an approximation of the fundamental niche of a species (Soberon and Peterson, 2005), defined as the potential area and resources that a species is capable of using (Araújo and Guisan, 2006). The fundamental niche is broadly controlled by species' tolerances of various environmental conditions. Usually, a species is prevented from filling its fundamental niche by factors such as interaction with other species, and inability to disperse to all suitable areas (Araújo and Guisan, 2006). The area a species occupies as a result of these constraints is described as its realized niche.

The fundamental niche of zebra mussel in North America has been well studied. Drake and Bossenbroek (2004) used a genetic algorithm for rule-set prediction (GARP, a type of machine-learning algorithm) with 11 mapped climatic, geological, and topographic variables as inputs to produce three models of the potential zebra mussel distribution. More recently, Gallardo *et al.* (2013) used SDMs to explore differences in the European and North American ranges of zebra mussel. These models did not include the calcium concentration of water bodies directly, although Ramcharan *et al.* (1992) showed that pH and calcium concentration are the most important environmental factors in limiting the spread of zebra mussels. Instead, geology was used on the assumption that it is related to these factors. A relationship between bedrock geology classes and water chemical factors such as alkalinity, calcium and other ion concentrations has been shown (Geochemical Atlas of Europe, 2012); for instance, low calcium concentration and alkalinity in European waters were significantly related to acid igneous and metamorphic rocks (e.g. granite and sandstone), while sedimentary rocks (e.g. limestone and dolomite) supply most of the calcium in stream waters.

The current distribution of quagga mussel is notably smaller than that of zebra mussel (Figure 1), but it is unclear whether this reflects a smaller fundamental niche. Whittier *et al.* (2008) used direct measurements of water calcium concentrations in North America to identify areas that imply a high risk of invasion by either of the two mussels (those with more than 28 mg Ca L^{-1}), but this model includes no other factors and so provides a very incomplete picture of the quagga mussel niche. In the absence of data to the contrary, present risk assessments may treat it as identical to that of zebra mussel (Montgomery and Wells, 2010).

In the present study a multi-factorial model of quagga mussel distribution was developed for the first time, allowing a global comparison of the fundamental niches of zebra and quagga mussel. In addition, models were developed that included factors assumed to relate to dispersal, allowing the relative importance of environmental and dispersal related factors in controlling the distributions of the two mussels to be evaluated.

METHODS

Species occurrence data

Presence points for zebra and quagga mussels were obtained from the Global Biodiversity Information Facility (http://data.gbif.org) and the United States Geological Survey (http://www.usgs.gov) (Figure 1). The final data set was made up of 5893 zebra mussel points and 545 quagga mussel points.

Environmental factors

Data on nine bioclimatic and geographic relatively uncorrelated (Pearson $r < 0.8$) variables considered likely to affect mussel distributions were obtained from WorldClim (Hijmans *et al.*, 2005, available at http://www.worldclim.org) at a 30″ (*c.* 1 × 1 km) resolution and WGS1984 projection, with full coverage of North America and Europe. The rationale for the inclusion of bioclimatic and geographic variables as predictors of mussel occurrence is given in Table 1. To reduce the size of files used for modelling and thereby optimize computing time, the resolution of all layers was reduced by a factor of four, which means that layers were used at a 2′ (*c.* 4 × 4 km) resolution. At the large continental scale used in this study, such up-scaling of variables does not result in

Table 1. Environmental factors used to develop environmental species distribution models, and justification for their inclusion in models

Factor	Justification	Source
Annual mean temperature Min temperature of coldest month Max temperature of warmest month Temperature seasonality	Temperature is known to have an effect on survival and reproduction of both mussel species. Unless the temperature is above a certain level for significant periods of the year, the mussels cannot reproduce (Baker *et al.*, 1993), hence the use of mean annual temperature. At extreme water temperatures or below freezing the mussels die (Mills *et al.*, 1996). The maximum and minimum temperature data account for this fact. Frequent or severe changes in temperature can also have negative effects (Spidle *et al.*, 1995) so a measure of the variation in temperature is included. All data are for air temperature, which is assumed to correlate with water temperature (Stefan and Preud'homme, 1993).	WorldClim (2005)
Annual precipitation Precipitation of driest month Precipitation seasonality	Total precipitation may affect the discharge and depth of rivers and lakes and therefore habitat availability. The precipitation of the driest month and precipitation seasonality reflect the likelihood of drought (death by desiccation) and flooding. Precipitation is perhaps a less direct control on distribution, so these factors are expected to be less important than temperature in the models.	WorldClim (2005)
Altitude	Mussels in Europe have rarely been found above 500 m (Strayer, 1991). This may be due to the lack of suitable habitat (lakes and relatively large streams) at high altitude, as well as the difficulty for species relying largely on the current for dispersal to move upstream.	WorldClim (2005)
Surface geology	Koutnik and Padilla (1994) concluded that geology was an acceptable approximation of water chemistry to investigate the response of zebra mussel, and has been used as such in previous publications on this subject (Drake and Bossenbroek, 2004). Sedimentary rocks are associated with high alkalinity and calcium concentration of surface waters, which affects mussel shell formation.	Commission for the Geological Map of the World (2010)

discernible changes to the main environmental gradients (Gallardo *et al.*, 2013).

Ideally, calcium concentration would be included directly in the model, but no data sets are currently available that encompass the scale of this study. Geology has consequently been included as a proxy. Data for onshore geological units were obtained from the Commission for the Geological Map of the World (available at http://ccgm.free.fr/) and included seven bedrock geologies: endogenous plutonic or metamorphic rocks, extrusive volcanic rocks, island, lake, ophiolitic complexes, sedimentary rocks, and undifferentiated facies. The geological map – initially in the form of a shape-file – was converted into a raster with the same resolution (2′) and projection (WGS1984) as the rest of the environmental layers. To strengthen further the predictions of this study, maps of calcium concentration for North America (USGS, available at http://www.usgs.gov) and Europe (Geochemical Atlas of Europe, available at http://www.gtk.fi/publ/foregsatlas/) were used to inform interpretation of the models (both shown in Figure 2).

Dispersal factors

To assess the extent to which the distribution of the mussels is controlled by differences in dispersal, factors considered likely to relate to dispersal were selected for inclusion in a second set of models. The relevance of these additional factors to explain the distribution of aquatic invasive species has been discussed in detail by Gallardo and Aldridge (2013c). Data were transformed to a 4 × 4 km resolution and WGS1984 projection, with full coverage of North America and Europe. The dispersal factors are shown in Table 2 along with justification for their inclusion.

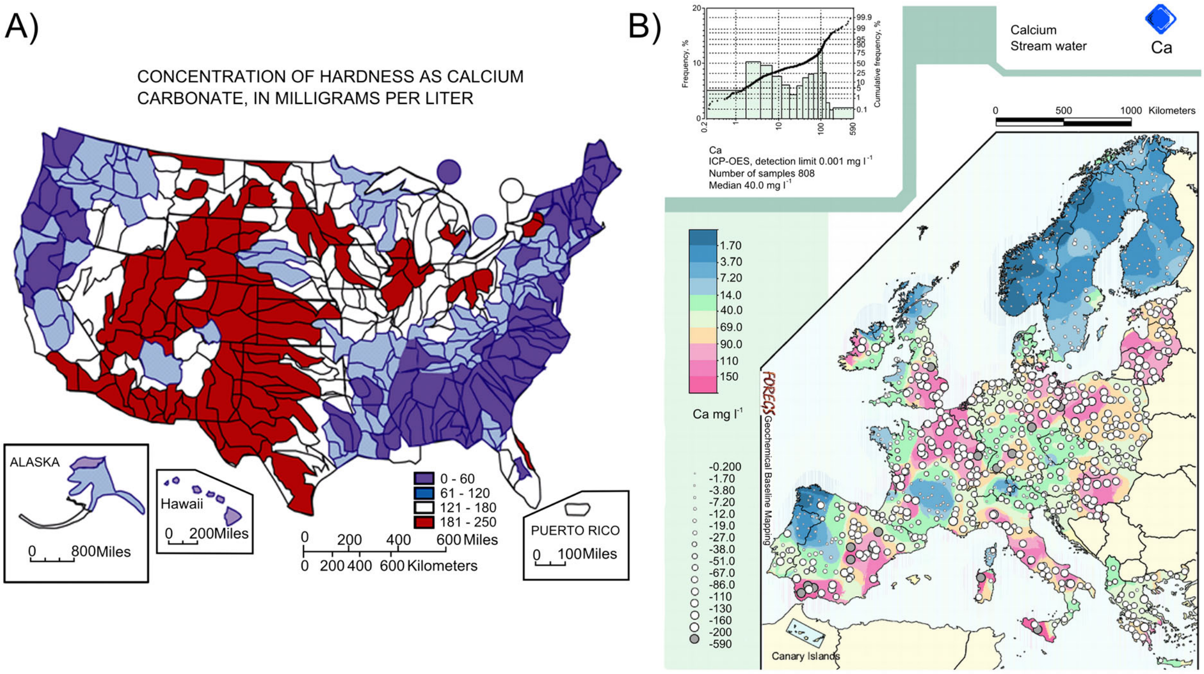

Figure 2. (A) Map of calcium hardness as calcium carbonate for North America. Note that 'calcium concentration' is equal to 'calcium hardness as calcium carbonate / 2.5.' Courtesy of the US Geological Survey. (B) Map of calcium concentrations in Europe. Circles represent sampling points used to measure water chemistry. Courtesy of the Geochemical Atlas of Europe; © 2005 the Association of the Geological Surveys of The European Union (EuroGeoSurveys)/ the Geological Survey of Finland.

Table 2. Dispersal-related factors used to develop integrated species distribution models, and justification for their inclusion in models

Factor	Justification	Source
Human influence index	This combines factors relating to human influence, including road density, population density, land use, railways, and light emitted at night, to score areas from 0 (pristine) to 64 (very heavily influenced by human activity). More human activity in an area increases the likelihood that invasive species will be brought there by humans (Pyšek *et al.*, 2010). Has been used in previous models (Gallardo and Aldridge, 2013c).	Last of the Wild Data Version 2 (WCS and CIESIN, 2005).
Human population density	High population density has previously been found to increase likelihood of invasion (Pyšek *et al.*, 2010).	Gridded Population of the World Version 3 (CIESIN, 2005).
Distance to nearest major port	Transport is the typical vector of human introductions of invasive species (Hulme, 2009). In the case of these mussels, they are known to be transferred largely in the ballast water of ships (Carlton, 2008), hence the distance to major ports may influence their distribution.	A list of ports with > 30 megatonnes total cargo volume in 2009 was obtained from the American Association of Port Authorities (2012). The euclidean distance to the closest port was then calculated using ArcGIS 10.0 ©ESRI.
Distance to nearest major reservoir	Distance to major reservoirs may be important because mussels often become established in reservoirs and then spread outwards from there (Orlova *et al.*, 2005b).	A list of reservoirs >0.1 km^3 was obtained from the Global Water System Project (2012). The euclidean distance to the closest reservoir was calculated using ArcGIS 10.0 ©ESRI.

Modelling methods

The free software MaxEnt (Phillips *et al.*, 2004) was used to create distribution models for the two mussel species. This technique has been used before to model the potential distribution of zebra mussel in Spain (Gallardo and Español, 2011), Great Britain (Gallardo and Aldridge, 2013c) and North America (Gallardo *et al.*, 2013). The predictive performance of the MaxEnt algorithm is consistently competitive with other species modelling methods (Elith *et al.*, 2006). Version 3.3.3 k was used with default settings

(10 000 background points, automatic selection of features, logistic output, removing duplicate occurrence records, 500 maximum interactions) except that a regularization multiplier of 1.5 was used (default = 1) to reduce the likelihood of over-fitting models, thus increasing their ability to predict beyond the training region (Gallardo *et al*., 2013). A five-way cross-validation was used to evaluate the predictive power of the model. This technique splits the occurrence data into five equal-size groups called ‘folds’, and models are created leaving out each fold in turn. The omitted folds are then used for evaluation, and the five models are combined to create the final model. Average values from the five replicates were used for reporting and mapping potential distributions.

The area under the Relative Operating Characteristic (ROC) curve (AUC) was calculated based on 10 000 background points to evaluate the accuracy of the models (Hirzel *et al*., 2002). The AUC tests whether the predicted distribution is significantly different from a random prediction (Broennimann *et al*., 2007) and ranges from 0.5 (very poor) to 1 (excellent). To calculate the importance of variables in the model, a variable is added in each iteration of the training algorithm, and the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. Final values are the percentage contribution of the variable to the model.

Two models were developed for each species, one including environmental factors only, and a second model integrating dispersal factors. This second model was intended to account for dispersal limitations of the species, thereby adjusting their predicted distribution. The resulting maps describe the probability of occurrence of the two species on a scale of 1–100%, with a pixel size of 4 × 4 km. The ‘equate entropy of thresholded and original distributions’ threshold rule was applied to convert this to a simple presence–absence output, allowing the predicted niche to be clearly characterized. Jiménez-Valverde and Lobo (2007) concluded that such a threshold can be appropriate when, as here, accuracy in predicting presence rather than absence is the objective and the prevalence is high. This threshold was also used in a recent risk assessment of Ponto-Caspian invasive species reaching Great Britain (Gallardo and Aldridge, 2013b). The more commonly used minimized difference threshold (MDT) and maximized sum threshold (MST) in this case led to presence–absence maps that did not extend beyond the current range of either species, and in some cases excluded already well-colonized areas.

RESULTS

Table 3 provides a summary of the data set used. The mean and standard deviation for each variable were calculated from the 5893 zebra mussel presence points and the 545 quagga mussel presence points. For all variables used except temperature seasonality, distance to nearest major port, and human population density, the differences between the two species were significant (Table 3). Quagga

Table 3. Mean ± standard deviation of factors used in models, and results of two-tailed t-test. Analysis conducted using R version 2.15.0

Factor	Zebra mussel	Quagga mussel	t	*P*-value
Mean temperature (°C)	8.5 ± 2.8	9.9 ± 5.0	−8.4	<0.00001
Max temperature (°C)	25.4 ± 5.3	27.772 ± 6.8	−6.5	<0.00001
Min temperature (°C)	−7.9 ± 5.7	−6.9 ± 6.0	−8.5	<0.00001
Temp seasonality (as standard deviation, °C)	8.3 ± 2.4	8.6 ± 2.0	1.3	0.18
Annual precipitation (mm)	843.7 ± 202.9	708.8 ± 306.3	15.1	<0.00001
Precipitation driest month (mm)	45.5 ± 14.9	39.9 ± 21.9	13.7	<0.00001
Precipitation seasonality (mm)	20.1 ± 9.0	22.9 ± 17.1	−7.8	<0.00001
Altitude (m)	130.2 ± 128.1	181.9 ± 282.4	−4.3	<0.0001
Human influence (measured from 1 (least) to 64 (most))	27.8 ± 16.4	14.5 +15.8	8.2	<0.00001
Distance to nearest major reservoir (km)	117.1 ± 83.3	88.1 ± 73.3	7.5	<0.00001
Human population density (no. km^{-2})	219.8 ± 635.4	127.7 ± 483.1	2.1	0.039
Distance to nearest major port (km)	335.5 ± 282.9	336.4 ± 226.6	−1.8	0.070

mussels were on average found at a higher mean altitude, higher temperatures, and in areas with less precipitation. Zebra mussels were found in areas with higher population densities and human influence indices, while quagga mussels tended to occur closer to reservoirs. Figure 3 shows the distribution of occurrence points along four of the environmental gradients making key contributions to the models.

Environmental models

The accuracy scores of models using environmental factors as predictors were higher for quagga mussel (mean AUC = 0.96) than for zebra mussel (mean AUC = 0.87). For both species average annual temperature and altitude were identified as important contributors to models (Table 4). For quagga mussels, the maximum temperature reached also seemed to be an important factor. As can be seen in the histograms in Figure 3(A–C), while the distribution of both mussels with altitude seemed broadly similar, the temperature distribution of the two species was noticeably different, with quagga mussels found at higher mean and maximum temperatures. This observation is largely due to the relatively high proportion of quagga mussel presence points in western North America. Geology also made a considerable contribution to the quagga mussel model, illustrating higher suitability scores within lacustrine (suitability > 90%) and sedimentary (>40%) regions.

The zebra mussel model (Figure 4(A)) showed that environmental factors are suitable for zebra mussel to spread further into France, Italy, Denmark, Scandinavia, central Europe and the Balkans, as well as into the west coast of Portugal and the south east of the United States. However, the European

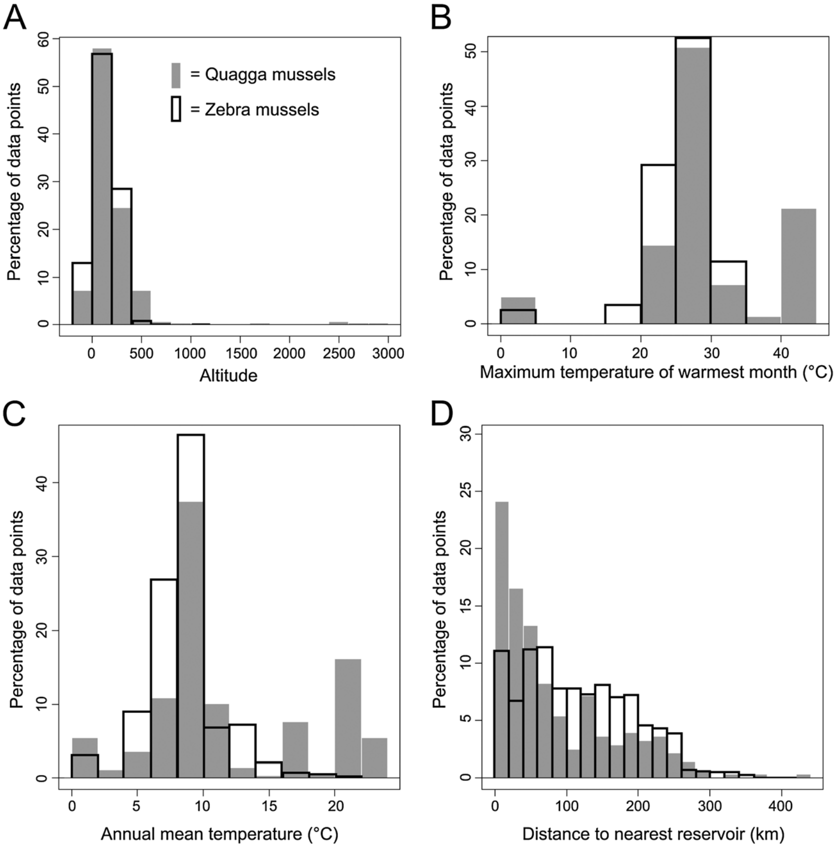

Figure 3. Histograms of zebra and quagga mussel occurrence along a gradient of (A) altitude, (B) maximum temperature of the warmest month, (C) annual mean temperature, and (D) distance to nearest reservoir.

Table 4. Results from species distribution models (SDMs) performed with environmental factors only (environ. SDM) and incorporating environmental and dispersal related factors (integrated SDM)

	Zebra environ. SDM	Quagga environ. SDM	Zebra integrated SDM	Quagga integrated SDM
Model statistics				
AUC	0.87 ± 0.00	0.96 ± 0.00	0.88 ± 0.00	0.96 ± 0.01
Minimum training presence	0.01 ± 0.00	0.03 ± 0.02	0.01 ± 0.01	0.06 ± 0.02
Threshold	0.30 ± 0.00	0.23 ± 0.01	0.30 ± 0.00	0.24 ± 0.01
Importance of factors (% contribution to model)				
Annual mean temperature	46.9 ± 0.71	25.6 ± 4.05	44.6 ± 1.26	26.0 ± 1.63
Temperature seasonality	2.4 ± 0.09	3.3 ± 1.05	3.8 ± 0.26	4.6 ± 0.73
Maximum temperature of warmest month	1.2 ± 0.04	15.9 ± 0.70	0.8 ± 0.98	11.1 ± 0.13
Minimum temperature of coolest month	0.0 ± 0.00	4.9 ± 0.84	0.4 ± 0.16	4.6 ± 0.44
Annual precipitation	15.5 ± 1.03	7.4 ± 1.14	12.7 ± 1.22	8.3 ± 0.51
Seasonality in precipitation	6.9 ± 0.67	4.7 ± 0.96	4.3 ± 1.31	4.5 ± 0.48
Precipitation of driest month	7.5 ± 1.06	1.3 ± 0.41	8.8 ± 1.41	3.5 ± 0.20
Altitude	18.5 ± 1.07	17.3 ± 0.23	16.5 ± 1.47	16.7 ± 1.59
Geology	1.0 ± 0.18	19.8 ± 2.33	0.7 ± 0.20	7.2 ± 0.66
Human influence	—	—	1.9 ± 0.08	0.4 ± 0.19
Distance to nearest reservoir	—	—	1.2 ± 0.96	7.0 ± 1.54
Distance to nearest major port	—	—	0.3 ± 0.26	1.4 ± 0.64
Human population density	—	—	4.0 ± 0.37	4.8 ± 0.42

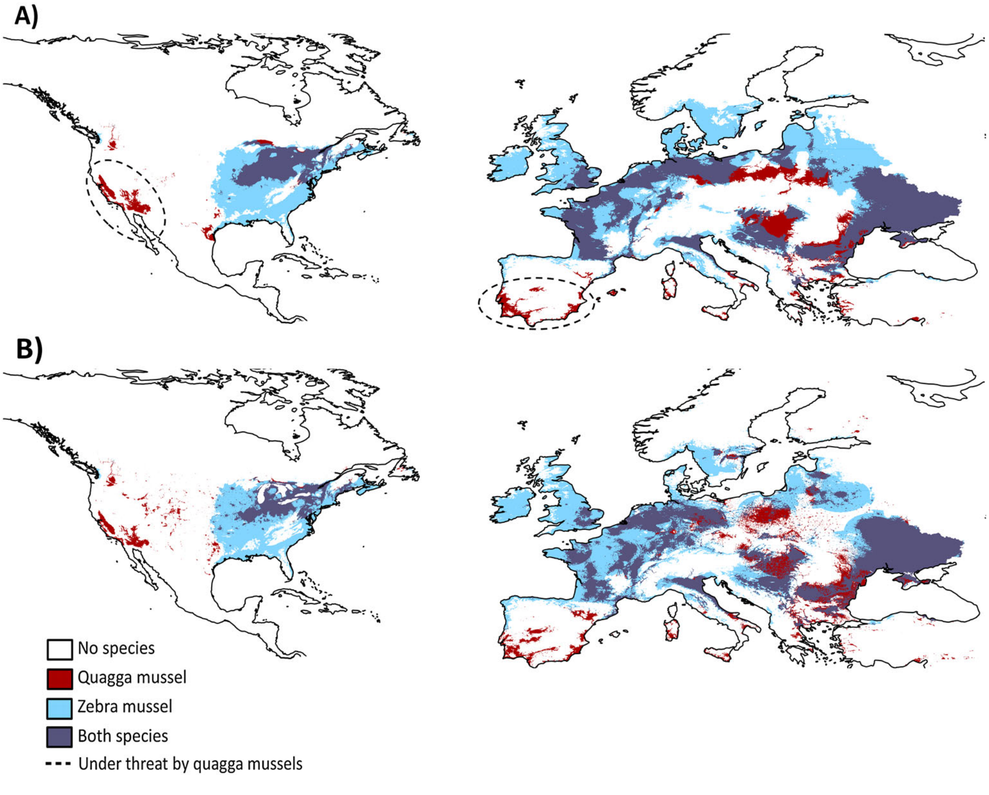

Figure 4. Species distribution models (SDMs) calibrated with (A) environmental factors only (e.g. bioclimatic, geographic, and geology), and (B) environmental and dispersal-related factors (e.g. population density, closeness to ports and reservoirs). The dashed ellipses highlight the dreissenid-free areas threatened with quagga mussel invasion. Model settings are described in Methods, and results are summarized in Table 4.

(Figure 2(A)) and North American (Figure 2(B)) calcium concentration maps show that of these areas, Portugal, Scandinavia and the south-eastern United States are unlikely to be suitable.

Within Europe, the quagga mussel model (Figure 4(A)) showed suitable environmental conditions in France, Britain, Germany, Italy, central Europe and the Balkans, all of which have already been invaded by zebra mussels. The south of Spain, which is currently free of zebra mussels, was also identified as vulnerable to invasion by quagga mussels. In North America, conditions were shown to be suitable for quagga mussel in the northern half of the zebra mussel range, Texas and parts of California. The calcium concentrations in these areas are suitable (Figure 2(A), 2(B)). Globally, 75% of the predicted quagga mussel distribution overlaps with the predicted zebra mussel distribution, although only 43% of the latter is expected to contain quagga mussels.

Integrated models

Although AUC values remained similar (mean 0.88 and 0.96 for the zebra and quagga mussel integrated models respectively; Table 4), there were notable differences between the environmental and integrated models. For zebra mussels, the two models predicted occurrence in roughly the same regions, but the predicted total area occupied was reduced by 6% when dispersal-related factors were included (Figure 4 (B)). In the case of quagga mussels, the same was true but the reduction in area when dispersal-related factors were included was greater at 10%. The most important contributors to the models were again annual average temperature and altitude.

Dispersal-related factors contributed nearly twice as much to the quagga mussel model as the zebra mussel model (13.6% compared with 7.4%; Table 4). The dispersal-related factor making the greatest contribution to the quagga mussel model was the distance to the nearest reservoir (7%). Indeed, quagga mussel distribution was clustered near to reservoirs, with a sharp drop in the presence points found beyond 60 km, while the zebra mussel presence points were more evenly spread between 0 and 200 km from reservoirs (Figure 3(D)). Human population density was less important, contributing 4% to the zebra mussel model and 5% to the quagga mussel model. Distance to nearest port and the human influence index were not relevant factors, making contributions of less than 2%.

DISCUSSION

Zebra mussels invaded significant areas of Europe as long as 300 years ago (van der Velde *et al.*, 2010). Nonetheless, the invasion has continued to the present day, with zebra mussels first recorded in Spain as recently as 2006 (Rajagopal *et al.*, 2009). The major prediction within Europe according to the distribution models is for continued spread through France, Scandinavia, central Europe, the Baltic and the UK. This is in accordance with predictions made by Gallardo and Aldridge (2013a) for Europe. The European calcium concentration map (Figure 2(A)) shows that the west of Portugal and southern Scandinavia, while otherwise suitable, are unlikely to be threatened owing to the low calcium concentration of the water there.

Within North America, the only areas outside the present range of zebra mussel identified as suitable were New England, the Piedmont, the Coastal Plains ecoregions along the Atlantic, and much of the south east. These areas were also identified as at risk of zebra mussel invasion by Drake and Bossenbroek (2004) more than 8 years ago, but have still not been invaded. However, the calcium-based model developed by Whittier *et al.* (2008) classifies these areas as being at low risk of invasion. The continued absence of zebra mussels, despite apparent climatic suitability, emphasizes the importance of calcium concentration in controlling distribution and the need to take this into account when interpreting models. Overall the North American part of the zebra mussel environmental model was very similar to that produced by Drake and Bossenbroek (2004). This is not surprising, as the same set of variables was used to predict the distribution of the mussel in both cases. The similarity between the models is important though, because it shows that a further decade of data collection and opportunity for zebra mussel to spread has not resulted in any notable change to the predicted distribution. Gallardo *et al.* (2013) showed that zebra mussel initially colonized the parts of North America most similar to its native range, then later underwent a niche expansion allowing it to occupy a wider range of conditions. The similarity of this study's predictions to those of Drake and Bossenbroek (2004) suggests that zebra mussel has undergone no further niche expansion. Moreover, the limited further expansion predicted across both continents suggests that zebra mussel is close to filling its fundamental niche, and that the slowdown in expansion may be a natural occurrence.

In contrast to zebra mussel, quagga mussel does not at present inhabit much of its predicted distribution. This suggests that quagga mussel has not filled its fundamental niche, and is compatible with the observation that it is currently expanding its distribution (Orlova *et al.*, 2005a, b). Within Europe, quagga mussel is predicted to follow zebra mussel into France, Italy and Great Britain, in accordance with other risk assessments (Gallardo and Aldridge, 2013c). Parts of the southern coast of Spain are identified as vulnerable. Southern Spain is at present unoccupied by either species, and would thus suffer entirely new economic and ecological losses were quagga mussel to invade, so measures to prevent spread here are especially advisable.

In North America the model predicted that quagga mussels will continue to spread into much of the area currently occupied by zebra mussels. Further expansion by quagga mussel in the western part of North America, particularly throughout California, was also predicted.

How similar are the fundamental niches of zebra and quagga mussels?

The environmental models showed that 75% of the predicted quagga mussel distribution overlaps with the predicted zebra mussel distribution, suggesting that the niches of the two species are similar but nonetheless significantly different. This emphasizes the importance of modelling the two species separately when attempting to predict their future spread. Only 43% of the zebra mussel distribution was predicted to be invaded by quagga mussels, suggesting that the niche of quagga mussel is much smaller. However, if quagga mussel is still at an early stage of its invasion, it is probable that the model is not predicting its full potential distribution. Broennimann and Guisan (2008) and later Gallardo *et al.* (2013) showed that the native range of a species cannot predict its invaded range, and argued that new occurrence points should be added as an invasion proceeds to increase the accuracy of predictions. Models of the quagga mussel niche will therefore need to be updated as it continues to spread.

The most important factors in the models for both species were annual mean temperature and altitude, suggesting that the broad distributions of both species are limited by the same factors. The annual mean temperatures at which the two species occur differs, however, with quagga mussels generally found at higher temperatures and lower precipitation levels. This result is driven by the relatively high density of quagga mussel presence points in the western US, where air temperatures are higher than elsewhere in the range. Finer controls on distribution also seem to differ, with maximum temperature making a larger contribution to quagga mussel distribution, and annual precipitation having a greater control on zebra mussel. The means for all of the environmental variables used in modelling were significantly different between the two species (Table 3), with the exception of temperature seasonality. It should be noted that all temperature data used in modelling were for air temperature, which may not fully reflect the temperature conditions the mussels experience (see 'Model considerations' for a discussion).

A number of studies have compared the environmental tolerances of zebra and quagga mussels experimentally. Quagga mussels are more tolerant of low dissolved oxygen concentrations and can reproduce at lower temperatures (Karatayev *et al.*, 1998; Nalepa *et al.*, 2010), which may explain their dominance in the deeper regions of lakes and reservoirs. The response of the two species to high temperatures is less clear. Studies in North America have shown consistently that zebra mussel populations have a higher thermal tolerance than quagga mussel populations (Mills *et al.*, 1996; Karatayev *et al.*, 1998). In Europe, however, the thermal tolerance of quagga mussel populations has been shown to be equal to or higher than that of zebra mussels (Antonov and Shkorbatov, 1990), and Shevtsova (1968) noted that increasing temperatures from north to south in the Dneiper river basin were correlated with the more southerly distribution of quagga mussel.

What conclusions can be drawn from the inclusion of dispersal-related factors in models?

For both species, the inclusion of dispersal factors reduced the area of the predicted distribution, essentially removing from the predictions areas that are most difficult for the mussels to reach. The reduction was greater for quagga mussel, and dispersal-related factors contributed twice as much to the quagga mussel model as the zebra mussel model. Thorp *et al*. (2002) suggested that dispersal factors may underlie the current differences in the distributions of the two species, with quagga mussel being confined to a smaller portion of its fundamental niche as a result of its inferior ability to disperse. There is some evidence to support this idea. Ricciardi *et al*. (1995) found that zebra mussels tolerate aerial exposure better than quagga mussels, and may therefore be able to move larger distances overland, for instance when attached to the hulls of trailered boats. Wilson *et al*. (1999) suggested that the tendency of quagga mussels to live in deeper waters than zebra mussels means they have less contact with boat traffic, and therefore less opportunity to be transported overland. In addition, zebra mussels have a greater rate of byssal thread production and higher attachment strength than that of quagga mussels (Peyer *et al*., 2009), which may have contributed to the higher rate of zebra mussel spread, particularly by recreational boats. Whether quagga mussel will remain constrained by dispersal factors into the future is uncertain. Its present clustering around certain reservoirs may be attributed to an inability to disperse further. Alternatively, it may be because quagga mussel is in an early stage of its invasion and will eventually spread further from such locations. The present study, being correlational, cannot distinguish between these two alternatives.

The use of other factors more directly related to species dispersal, such as boat movements and hydrological connectivity could improve the predictions and conclusions drawn from distribution models, allowing areas at particular risk owing to high propagule pressure to be identified. At present, however, such data are not available at the scale and resolution necessary for modelling.

Model considerations

The most effective distribution modelling techniques, including MaxEnt, require absence as well as presence data. Although presence–absence data were preferred (Phillips *et al*., 2009), they were not available for this study, so instead 10 000 pseudo-absences were randomly selected during modelling. The accuracy of the model is probably lower using pseudo-absences than it would be with real absence data. There was a high concentration of zebra mussel observations in the UK and The Netherlands, which may be the result of higher sampling effort and propagule pressure in these countries rather than higher suitability. Methods exist which try to account for spatial bias (Phillips *et al*., 2009; Gallardo *et al*., 2013). However, as no data for quantifying the sampling effort across the study area existed, such methods could have the opposite effect of wrongly attributing high suitability to high sampling effort. The observation data were therefore used with minimum alteration, but it is possible that the suitable locations predicted by the model are unfairly skewed towards areas with conditions similar to the UK and The Netherlands.

Although water chemistry, water temperature and habitat structure would ideally be used to calibrate SDMs for aquatic species, these factors are rarely available at the necessary spatial resolution and coverage. There is, however, evidence to suggest that climatic variables may act as proxies for these factors. For example, air temperature is directly related to water temperature (Stefan and Preud'homme, 1993), which affects the reproduction, growth, dispersal, metabolism and oxygen consumption of aquatic organisms (Griebeler and Seitz, 2007). Although climatic variables cannot account for habitat on a fine scale, aquatic ecosystems do respond to climate through changes in their physical characteristics – for instance, stratification and mixing regimes of lakes, catchment hydrology, extension and depth of water bodies. These in turn influence the chemistry of habitats (e.g. oxygen concentration, nutrient cycling) and the phenology and distribution of most aquatic organisms

(Nickus *et al*., 2010). Considering the lack of other relevant factors at a large enough scale and high enough resolution to model the distribution of aquatic species, globally available bioclimatic variables offer reasonable means for developing distribution models (Theissinger *et al*., 2011; Gallardo *et al*., 2013).

Nonetheless, the use of air temperature as a proxy for water temperature may have influenced conclusions. The data set used shows that the observed average and maximum temperatures of sites inhabited by quagga mussel are higher than for zebra mussels. This result is driven largely by the relatively high concentration of quagga mussels in the western USA, where air temperatures are higher than in most of the rest of the mussels' distributions. The concentration of quagga mussel presence points in the western USA also drives the prediction that the quagga mussel niche includes southern Spain, which has a similar climate. The observed results may reflect a real difference in temperature tolerance between the species, or may be caused by air temperature data not accurately reflecting the actual conditions the mussels face. While air temperature correlates well with water temperature (Stefan and Preud'homme, 1993), it is important to emphasize that the deep water temperature will be much colder than that at the surface. If quagga mussels are living only in deeper waters then they may be relatively unaffected by air temperature. In fact, quagga mussels are not confined to deep water in the warmer parts of their range; they have been observed living in the surface waters of Lake Mead (Morse, 2009) where water temperature reaches 28°C, above the generally accepted upper tolerance limit of North American quagga mussels. The higher air temperature here does seem to reflect a higher temperature experienced by the mussels, which is the assumption that the use of air temperature data is based on. This supports the suggestion that the quagga mussel niche may include warmer areas apparently unsuitable for zebra mussels, but field studies are needed to assess whether quagga mussels in the western USA do indeed have a higher temperature tolerance than previously documented for the species (Morse, 2009).

Management implications

Dreissenid invasion has severe economic and environmental consequences. The global distribution of quagga mussel has not previously been modelled, and areas at risk of quagga mussel invasion are identified here. For regions unaffected by zebra mussels, a quagga mussel invasion would have new severe economic and ecological consequences. In addition, the spread of quagga mussels into areas already occupied by zebra mussels, such as France, Great Britain and Italy, may cause further damage. There is evidence to suggest that the economic and ecological risks associated with invasion by quagga mussels are not identical to those associated with zebra mussels. Quagga mussels may be able to foul intake pipes that take in water too cold for zebra mussels to tolerate (Cornell University, 2005). Their impact on native species can also differ; Nalepa *et al*. (2009) monitored the benthic community in Lake Michigan and noted that the population of the native amphipod *Diporeia* underwent a severe decline after the zebra mussel invasion of the lake, but then stabilized. When quagga mussels began to colonize the lake they replaced most of the zebra mussels in the shallow areas, but were also able to colonize the deeper areas of the lake, which led to a further decline in the *Diporeia* population and extirpation of the species from much of the lake. The fact that zebra mussels are already present should not lead to complacency, therefore, about invasion by quagga mussels. The importance of early detection and proactive development of a rapid response plan in repelling dreissenid invasion has been shown (Wimbush *et al*., 2009), and such plans should be developed for areas at risk.

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