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Modelling the Risk Posed by the Zebra Mussel *Dreissena polymorpha*: Italy as a Case Study

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Abstract We generated a risk map to forecast the potential effects of the spreading of zebra mussels *Dreissena polymorpha* across the Italian territory. We assessed the invader's potential impact on rivers, lakes, watersheds and dams at a fine-grained scale and detected those more at risk that should be targeted with appropriate monitoring. We developed a MaxEnt model and employed weighted overlay analyses to detect the species' potential distribution and generate risk maps for Italy. *D. polymorpha* has a greater probability of occurring at low to medium altitudes in areas characterised by fluviatile deposits of major streams. Northern and central Italy appear more at risk. Some hydroelectric power dams are at high risk, while most dams for irrigation, drinkable water reservoirs and other dam types are at medium to low risk. The lakes and rivers reaches (representing likely expansion pathways) at medium-high or high risk mostly occur in northern and central Italy. We highlight the importance of modelling potential invasions on a country scale to achieve the sufficient resolution needed to develop appropriate monitoring plans and prevent the invader's harmful effects. Further high-resolution risk maps are needed for other regions partly or not yet colonised by the zebra mussel.

Keywords Aquatic systems · Biological invasions · Mollusc · Risk map · Species distribution models

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Introduction

Biological invasions–i.e., the spread of organisms accidentally or deliberately introduced to geographic regions outside their native range (IUCN 2000)–often represent a serious threat in terms of biodiversity loss, alteration of ecosystem functions and socioeconomic impacts (Pimentel 2002; Jeschke et al. 2014). Since Elton (1958)'s early warning, the problem has grown exponentially along with the ever increasing human population size, people movement and transport of goods.

It is estimated that 5–20% of alien species may give rise to problems, some of which of especially great concern (Vilà et al. 2010; Lockwood et al. 2013). Due to the overwhelming number of alien species present virtually in all continents, setting priorities for interventions aimed to prevent, mitigate or remove the detrimental effects of such organisms has crucial importance (McGeoch et al. 2016). Once the invader has settled in a given region, priority must be given to the prevention of its spread and the protection of especially sensitive areas (McGeoch et al. 2016).

Species distribution models (hereafter SDMs) have been widely used to address a broad range of ecological applications (Elith and Leathwick 2009; Scoble and Lowe 2010; Smeraldo et al. 2017) including preparation of pest risk maps that predict the potential geographic range and impact of alien species before such effects are realised (Venette et al. 2010).

The zebra mussel *Dreissena polymorpha* (Pallas 1771) is regarded as one of the 100 most aggressive invaders on a global scale (Lowe et al. 2004). This freshwater bivalve mollusc, native to lakes and slow-moving rivers of the Caspian and Black Sea regions, is nowadays widespread in Europe and North America (e.g., Gallardo 2013). The species produces large numbers of highly mobile propagules, a feature which makes it an especially aggressive invader (Johnson and Padilla 1996). Every female can lay 30,000–40,000 eggs, from which planktonic veliger larvae develop; after 8–12 days these will adhere to hard substrates (Castagnolo et al. 1980). The species is ecologically flexible, being able to live at depths of 0–60 m b.s.l., and tolerate significant salinity ranges–it dwells in fresh to moderately salty waters–as well as mild levels of pollution (Mantecca et al. 2003). *D. polymorpha* shows high filtration performances and at high densities may have significant ecological impacts by altering the content of suspended matter, as well as of phytoplankton, chlorophyll, phosphorus and nitrate concentrations (Binelli et al. 1997), with detrimental effects on native bivalves and other macroinvertebrates (Stewart and Haynes 1994; Fincke et al. 2009), disrupting food web dynamics (Miehls et al. 2009) and leading to system-wide collapse of major predators (Kumar et al. 2016). The species may seriously damage clog water intake pipes, water filtration, and electric generating plants, leading to especially high economic losses (Pimentel et al. 2005). In Italy zebra mussels were first recorded in the early 1970s in the Garda Lake, in the north of the country (Giusti and Oppi 1972). They then spread over tributaries and nearby basins, reaching the Apennine Mountains in the 1990s, namely Tuscany (Lori and Cianfanelli 2006), Umbria (Spilinga et al. 2000), Abruzzo (pers. obs.), Molise (Bodon et al. 2005) and Sicily (Colomba et al. 2013).

Risk maps predicting the spread and effects of *D. polymorpha* may be vital to inform management in order to set up appropriate monitoring and early warning strategies. A few studies have adopted a modelling approach to investigate invasion ecology of *D. polymorpha*. Drake and Bossenbroek (2004) and Bossenbroek et al. (2007) modelled the species' potential distribution in the US, and Gallardo (2013) analysed the usefulness of the native and invaded ranges to describe the species' range somewhere else, showing the occurrence of multiple episodes of niche expansion and supporting the adoption of partial ranges for the reliable modelling of spatio-temporal invasion patterns. Quinn et al. (2014) analysed niche partitioning between *D. polymorpha* and its close relative *D. rostriformis bugensis* showing the occurrence of significant interspecific differences related to both ecogeographic variables and dispersal-related factors. Hallstan et al. (2009) performed a survey of zebra mussels in Sweden generating a risk model based on the species' potential distribution. The authors used a logistic model considering 2781 lakes, 3.9% of which were predicted to be potentially at risk of invasion.

In our study, we analysed the potential risk posed by *D. polymorpha* to the Italian territory. We assessed the invader's potential impact on rivers, lakes, watersheds and dams at a fine-grained scale and detected those more at risk that should be targeted with appropriate monitoring. To do so, we used the maximum entropy algorithm (MaxEnt, Phillips et al. 2006). The use of this approach is common in the scientific literature to address the potential distribution of biological invaders (Ficetola et al. 2007; Rödder and Lötters 2009; Bradley 2010; Gallardo 2013; McDowell et al. 2014; Yiwen et al. 2016). Moreover, in our case we dealt with a species that has long (45 years) been present in Italy, and previous work has established that its population has now reached an equilibrium in the colonised areas (Cianfanelli et al. 2010), which further legitimates our approach to investigate the potential distribution of an alien species (e.g., Václavík and Meentemeyer 2012; Yiwen et al. 2016). Our work is also the first to use *D. polymorpha* potential distribution to generate a risk map detecting the country's regions, watersheds, dams, rivers and lakes that are most likely to be affected by the species' potential presence.

Materials and Methods

Data Collection

We considered the entire Italian territory comprised between latitudes 45°N–36°N and longitudes 6–18°E (corresponding to *ca.* 301,000 km^2, elevation range = 0–4810 m a.s.l.). We used several sources to obtain presence records of *D. polymorpha* in Italy: (1) public access databases, including Global Biodiversity Information Facility (GBIF) (http://www.gbif.org) and CKmap Fauna Italiana (http://www.faunaitalia.it/ckmap); (2) scientific articles and reports (Quaglia et al. 2008; Cianfanelli et al. 2010; Colomba et al. 2013); and (3) unpublished information, including our first record for the Abruzzo region (proximity of Bomba Lake, 42.0289°N, 14.3472°E) (Fig. S1). The resulting database featured 39 records scattered across the country. Records were screened in ArcGis (version 9.2) for spatial autocorrelation using average nearest neighbour analyses and Moran's I measure of spatial autocorrelation to remove spatially correlated data points (e.g., Russo et al. 2015; Bosso et al. 2016a, 2016b, 2016c). After this selection, 16 fully independent presence records for *D. polymorpha* were used to generate SDMs.

Although we preferred to generate a local model focusing on Italy to get a finer-grained resolution in the modelling exercise, we also compared this output with that of a large-scale European model based on 6318 occurrences available in GBIF. In this case too, data were first screened for autocorrelation and 60 independent records were selected from the initial sample.

Selection of Ecogeographical Variables

For the local SDM, we used a set of 22 ecogeographical variables (EGVs). We included altitude and 19 bioclimatic variables and also employed an hydrogeological map. Altitude and the 19 bioclimatic variables were obtained from the WorldClim database (www.worldclim.org/current) (Hijmans et al. 2001). Bioclimatic variables are biologically meaningful parameters derived from monthly temperature and rainfall values that describe annual trends, seasonality and extremes for species survival. Water temperature has a chief role in influencing reproduction, growth and dispersal of *D. polymorpha* (McMahon 1996). Because water temperature layers are often unavailable for lakes and water courses, in this study, as previously done by others modelling the potential distribution of *D. polymorpha* (Drake and Bossenbroek 2004; Li et al. 2008; Gallardo 2013; Quinn et al. 2014), we adopted bioclimatic variables as a proxy for water temperature. Air temperature is directly related to water temperature (Stefan and Preud'homme 1993), which affects the reproduction, growth, dispersal, metabolism of several aquatic organisms including *D. polymorpha* (McMahon 1996). We also used hydrogeological information because it is linked to water chemical factors known to affect the species, such as alkalinity, concentration of calcium and other ions (Salminen et al. 2005). Alkalinity and calcium are particularly relevant as they influence the mussel's shell growth and hardening. The hydrogeological map was downloaded from the Environmental National Information System of Italy (http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais).

For the European model, we used the same variables except the hydrogeological map which was downloaded from http://www.bgr.bund.de/EN/Themen/Wasser/Projekte/laufend/Beratung/Ihme1500/ihme1500_projektbeschr_en.html.

All variable formats were converted in ASCII files with a 30-arc second resolution ($0.93 \times 0.93\,\text{km} = 0.86\,\text{km}^2$ at the equator). To decrease the number of variables for the final distribution models, we first eliminated the highly correlated predictors and retained those with a Pearson's $|r| < 0.80$ (Elith et al. 2010). From this first set of predictors, we considered those most relevant to the ecological requirements according to expert opinion and current knowledge (Drake and Bossenbroek 2004; Li et al. 2008; Gallardo 2013; Quinn et al. 2014). This led to a final set of nine variables (Table 1) used to model the distribution of zebra mussel in Italy and the rest of Europe.

Table 1 List of ecogeographical variables used in this study, type and measurement unit

Type	Ecogeographical variable	Unit
Topographical	Altitude	m
Geological	Hydrogeology	–
Climatic	Annual mean temperature	°C
	Maximum temperature of the warmest month	°C
	Minimum temperature of the coldest month	°C
	Temperature seasonality	°C
	Annual precipitation	mm
	Precipitation of the driest month	mm
	Precipitation seasonality	mm

Species Distribution Models

To model *D. polymorpha* distribution we employed Maxent ver. 3.4.0 (http://biodiversityinformatics.amnh.org/open_source/maxent/) (Phillips et al. 2017). This algorithm usually results in good predictive models compared with other presence-only models and is especially suited to deal with scarce presence-only data (e.g., Elith et al. 2006). Because it is based on a generative approach, rather than a discriminative one, this technique performs well when the amount of training data is limited. Moreover, it has a good ability to predict new localities for poorly known species (Russo et al. 2015; Bosso et al. 2016a, 2016b, 2016c). To build the models, we used the presence records (defined "sample" in Maxent) of *D. polymorpha* selected as described above and the EGVs (defined "environmental layers" in Maxent) listed in Table 1. In the setting panel, we selected the following options: auto features; random seed; write plot data; remove duplicate presence records; give visual warming; show tooltips; regularisation multiplier (fixed at 1); 10,000 maximum number of background points; and, finally, we used a cross-validation run type as suggested by Pearson et al. (2007) to test small samples that makes it possible to replicate n sample sets removing each time one locality; 1000 maximum iterations. All other parameters were left by default. These settings are conservative enough to allow the algorithm to get close to convergence and the best performance (Phillips et al. 2006; Phillips et al. 2017). The average final map obtained had a logistic output format with suitability values from 0 (unsuitable habitat) to 1 (suitable habitat). The 10th percentile (the value above which the model classifies correctly 90% of the training locations) was selected as the threshold value for defining the species' presence. This is a conservative value commonly adopted in species distribution modelling studies, particularly those relying on data sets collected over a long time by different observers and methods (e.g., Russo et al. 2015; Bosso et al. 2016a, 2016b, 2016c). This threshold was used to reclassify our model into binary presence/absence maps. We used Jackknife sensitivity analysis to estimate the actual contribution that each variable provided to the geographic distribution models in relation to the area under curve (AUC) values. During this process, Maxent generated three models: first, each EGV was excluded in turn and a model was created with the remaining variables to check which one of the latter was the most informative. Second, a model was created for each individual EGV to detect which variable had the most information not featuring in the other variables. Third, a final model was generated based on all variables. Response curves derived from univariate models were plotted to know how each EGV influences presence probability.

Model Validations

We tested the predictive performance of the models with different methods: the receiver operated characteristics, analysing AUC (Fielding and Bell 1997); the true skill statistic (TSS) (Allouche et al. 2006); and the minimum difference between training and testing AUC data (AUC_{diff}) (Warren and Seifert 2011). Such statistics were averaged across the 20 replicates run on the 70% (training) versus 30% (testing) data set split. These model evaluation statistics range between 0 and 1 (AUC and AUC_{diff}) and between −1 and 1 (TSS): excellent model performances are expressed, respectively, by AUC and TSS values close to 1 and AUC_{diff} close to 0.

Comparison Between Local and European Models

We compared statistically the local model with that generated for the entire European territory. To do so, we used a *t*-test to compare the surfaces of the presence and absence, respectively, obtained for each of the 20 replicates generated by MaxEnt at both local and European scales. The comparison was performed for both the whole Italian territory and, respectively, the north (between lats 47.06°–43.63°), centre (between lats 43.63°–41.90°) and south (between lats 41.90°–36.66°) of the country.

Risk Maps

We generated risk maps to identify (a) Italian regions, (b) watersheds, (c) dams and (d) rivers and lakes potentially more exposed to invasion risk. To generate risk maps for *D. polymorpha* in Italy, we used the Maxent logistic map and the shapefiles of Italian regions, dams, hydrographical network, primary and secondary watersheds and lakes. The administrative boundaries of the Italian regions were downloaded by Italian national statistical institute (ISTAT) (http://www.istat.it/ambiente/cartografia). The distribution of the dams was obtained from the interactive cartography of the Italian dam register (http://www.registroitalianodighe.it/maps/GisSND/GisSNDfrm.html). The distributions of the primary and secondary watersheds, the hydrographical network and the lakes were downloaded from the Environmental National Information System (http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais). These feature 495 lakes and 61,630 river reaches. Risk maps for *D. polymorpha* in Italy were obtained by weighted overlay using spatial analyst tools in ArcGIS 9.2. Weighted Overlay is a technique used to apply a common measurement scale of values to diverse and dissimilar inputs in order to create an integrated analysis (further details on how weighted overlay works are available at the following website: http://webhelp.esri.com/arcgisdesktop/9.3/index.cfm?TopicName=How%20Weighted%20Overlay%20works). Because weighted overlay use only the raster data, all shapefiles employed in this study were converted to raster format. The input raster data for weighted overlay must contain discrete integer or continuous values and these values must be on a common scale. The weighted overlay tool reclassifies values in input raster onto a common evaluation scale of suitability or preference i.e. on the basis of their relative contribution to the central theme (Iqbal and Khan 2014). In this study, all input raster data were reclassified to assign equal intervals of discrete values and then the final maps were reclassified into five categories representing different risk classes, respectively, low, medium low, medium, medium high and high. We used the binarised map and the shapefiles of the hydrographical network to identify the river traits that connect *D. polymorpha*'s suitable areas in Italy.

Results

Both models (at local and European scales) showed high levels of predictive performances. For the local model (Fig. 1), we obtained the following validation values: AUC (training, 0.821 ± 0.014; test, 0.798 ± 0.069), AUC_{diff} (0.023 ± 0.011) and TSS (0.802 ± 0.031). For the European model (Fig. S2), these were as follows: AUC (training, 0.935 ± 0.031; test, 0.798 ± 0.129), AUC_{diff} (0.137 ± 0.024) and TSS (0.855 ± 0.019).

The statistical comparison between the local and European models showed the absence of significant differences between them, both for the analysis done considering the whole Italian territory (presence, $t = 1.32$, n.s.; absence, $t = 1.45$, n.s.; Fig. S3) and for that addressing north, centre and south separately (north, presence, $t = 0.48$, n.s., absence, t

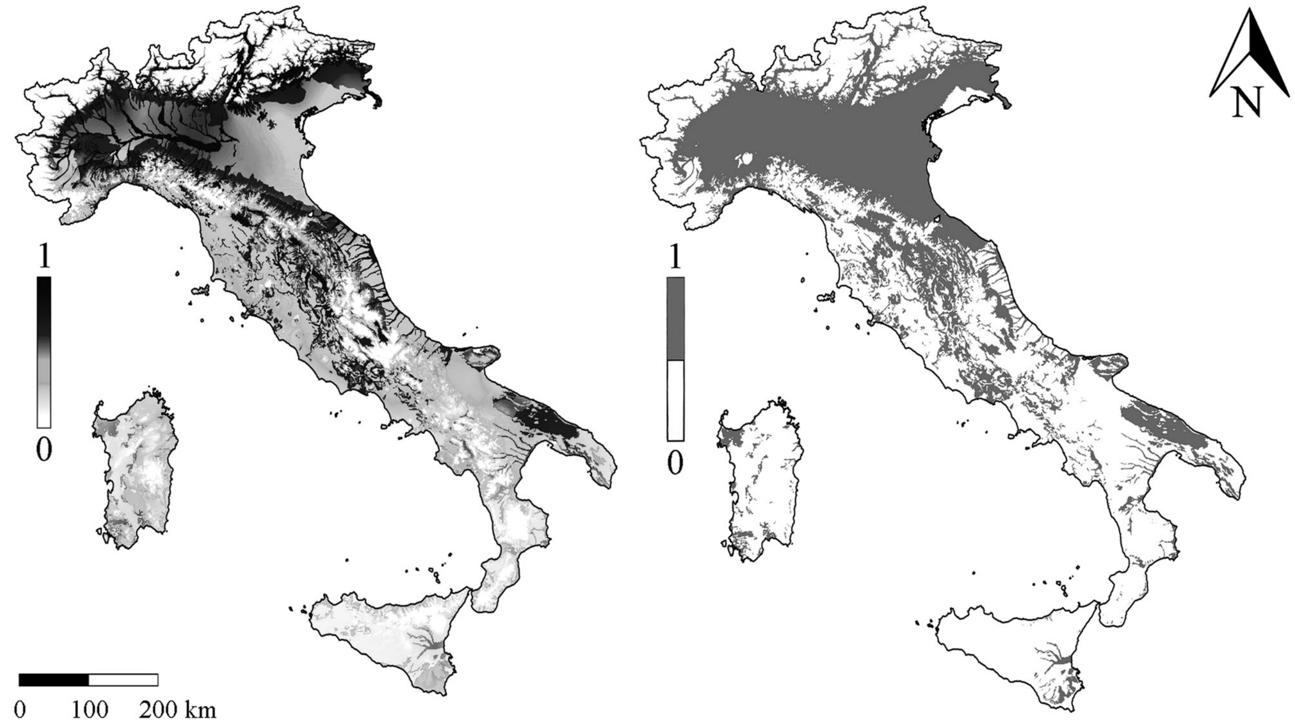

Fig. 1 Species distribution models of *D. polymorpha* in Italy. *Left*: logistic map; *right*: binary map. Scales show the probability of presence ranging from 0 to 1

= 0.46, n.s.; centre, presence, $t = 0.99$, n.s., absence, $t =$ 0.52, n.s.; south, presence, $t = 1.13$, n.s., absence, $t = 0.98$, n.s., Fig. S4). Furthermore, a visual assessment of the suitable areas detected by both models showed no relevant differences (Figs. 1 and S2). Therefore, further analyses only used the local model.

Six variables contributed for 99% of model prediction. Hydrogeological map (44.3%) and temperature seasonality (30.1%) were the main factors influencing model performance. Altitude, precipitation seasonality, minimum temperature of coldest month and maximum temperature of warmest month provided a 24.6% total contribution. Based on the model's predictions, *D. polymorpha* has a greater probability of occurring at relatively low altitudes (0–500 m a.s.l.) in areas characterised by fluviatile deposits of major streams, temperature seasonality >7.5 °C, precipitation seasonality <20%, minimum temperature of coldest month of −5 to −10 °C and maximum temperature of warmest month >25 °C.

The Jackknife sensitivity analysis of the AUC plot (Fig. S5) showed that the variable of minimum temperature of coldest month had an AUC of 0.75 when it was used individually. On the other hand, altitude, temperature seasonality and hydrogeological map showed an AUC of *ca.* 0.78 when they were individually omitted by the models. Finally, Maxent obtained an AUC value of 0.82 when all the EGVs were used in the models.

Overall, northern and central Italy appear more at risk, where the potential distribution of *D. polymorpha* showed high logistic values (Fig. 1), especially in the Po River Valley, near the central Apennines and eastern coasts. In such areas primary and secondary watersheds with high or medium high risk were found (Fig. 2).

Piedmont, Lombardy, Veneto, Friuli-Venetia Julia, Emilia-Romagna, Umbria and Marche were the regions at highest invasion risk while Valle d'Aosta, Calabria and Sicily were those at lowest risk (Fig. 3).

Lombardy (23,070 km^2), Emilia-Romagna (21,286 km^2), Piedmont (18,870 km^2), Veneto (14,911 km^2) and Tuscany (10,342 km^2) were the regions encompassing the largest potentially suitable surface for the species while Sicily (1898 km^2), Calabria (1443 km^2), Molise (1336 km^2), Basilicata (976 km^2) and Valle d'Aosta (284 km^2) were those including the smallest amount of it (Table S1).

We found 23 out of 274 hydroelectric power dams to be at high risk, all in northern Italy (Table 2). Most dams for irrigation, drinkable water reservoirs and other dam types were classified as at medium to low risk and occur in central and southern Italy (Table 2). The lakes ($n = 107$) and rivers reaches ($n = 11,414$) classified as at medium-high to high risk occur in northern and central Italy (Table 3).

Specifically, we detected 53 river reaches representing likely expansion pathways for *D. polymorpha* in Italy (Table S2).

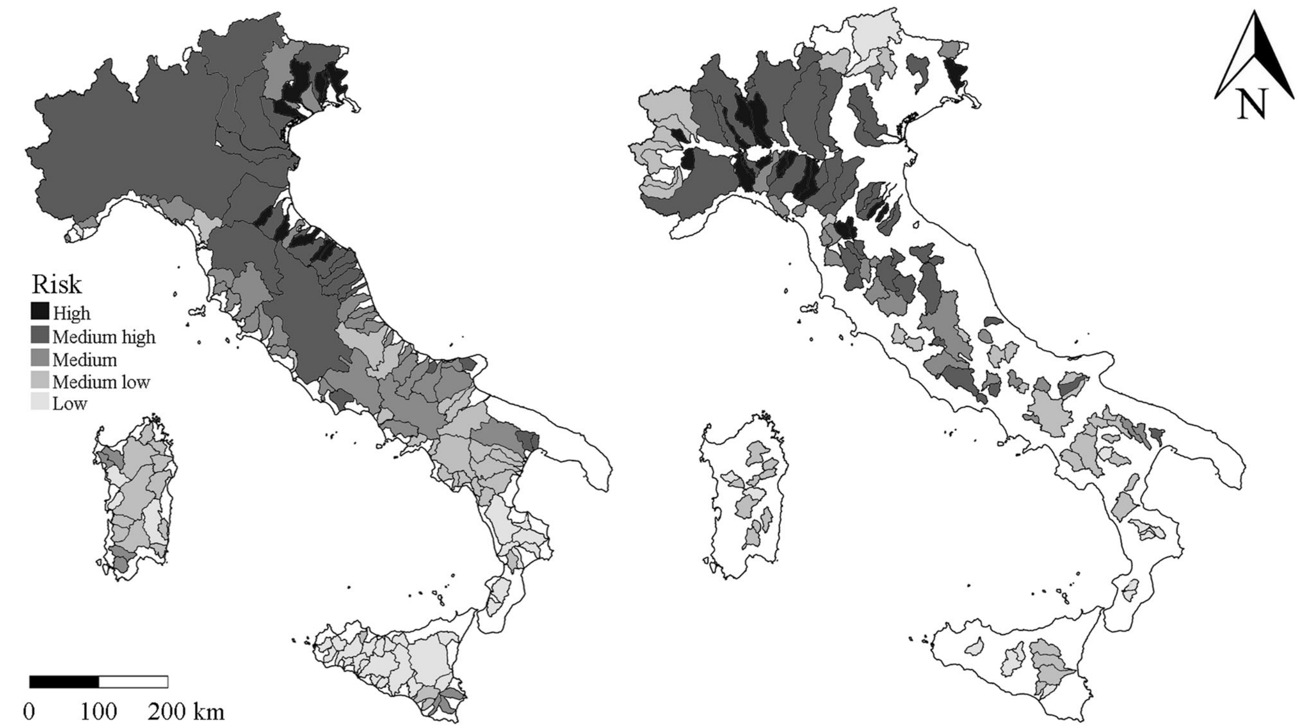

Fig. 2 Risk map of exposure to *D. polymorpha* of primary and secondary watersheds in Italy

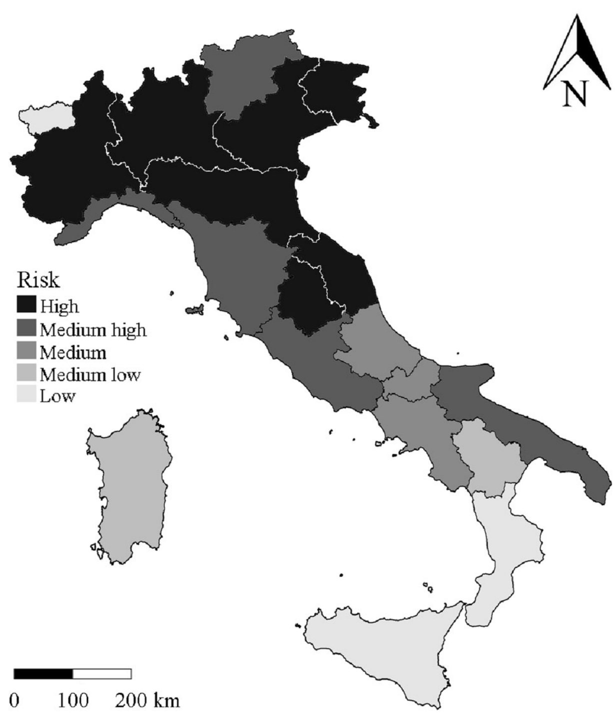

Fig. 3 Risk map of exposure of Italian regions to *D. polymorpha*

Table 2 Numbers of hydroelectric, irrigation, drinkable water and other dams in Italy classified according to the invasion risk posed by *D. polymorpha*

Risk class	Dam type											
	Hydroelectric			Irrigation			Drinkable water			Others		
	N	C	S	N	C	S	N	C	S	N	C	S
High	23	0	0	2	0	0	0	1	0	4	0	0
Medium high	16	14	0	4	5	0	1	1	0	0	2	2
Medium	19	8	1	9	8	10	6	1	0	5	2	3
Medium low	30	19	5	1	17	35	3	2	13	1	9	4
Low	115	6	18	0	0	40	2	0	7	1	0	11

N Northern Italy, *C* Central Italy, *S* Southern Italy

Table 3 Numbers of lakes and rivers in Italy classified according to the invasion risk posed by *D. polymorpha*

Risk class	Lakes			Rivers		
	N	C	S	N	C	S
High	52	6	0	4046	301	0
Medium-high	24	25	0	4867	2200	104
Medium	76	8	10	7383	2682	1531
Medium-low	51	40	50	5593	7034	8098
Low	72	14	67	8384	797	8610

N Northern Italy, *C* Central Italy, *S* Southern Italy

Discussion

Model Performances and Limitations

The SDMs that we implemented for *D. polymorpha* in Italy showed considerable power, mainly supported by the good gain value (1.1) achieved. AUC such as those we obtained (>0.8) are among the highest reported for published models (e.g., Rebelo and Jones 2010; Domíguez-Vega et al. 2012; Russo et al. 2015; Di Febbraro et al. 2015; Smeraldo et al. 2017) and demonstrate a high predictive capacity (Swets 1988; Elith et al. 2010). Our study was further supported by the AUC_{diff} and TSS values (Russo et al. 2015; Smeraldo et al. 2017). Although both local and European models performed well and no significant differences occurred between them, we chose to carry out the study on the local model since the hydrogeological map available for the country-scale is especially detailed and all Italian occurrences had a finer resolution and were validated by previous work (Cianfanelli et al. 2010).

The Jackknife sensitivity analysis of the AUC plot provides an alternative method to determine which variables are most important in the model (Phillips et al. 2006; Phillips and Dudik 2008; Phillips et al. 2017). The minimum temperature of the coldest month showed a reasonably good fit to the input data and proved to be the most effective single variable to predict the distribution of *D. polymorpha* in Italy. On the other hand, altitude, temperature seasonality and hydrogeological map were those variable including a substantial amount of useful information not covered by the other variables. In fact, we recorded a decrease of AUC values when such variables were omitted from the model. Overall, the AUC obtained using all the variables was higher than any other AUC value associated with subsets of variables, showing that predictive performances improved when all variables were employed (Phillips et al. 2006; Phillips and Dudik 2008; Phillips et al. 2017).

Some limitations to our predictions may arise from the necessity of using proxy variables (air temperature and hydrogeological information), respectively, for water temperature and chemistry, whose actual values are not available for the scale at which we did our analysis. However, many previous studies on *D. polymorpha* as well as other aquatic species have also employed bioclimatic variables obtaining satisfactory results (Drake and Bossenbroek 2004; Loo et al. 2007; Li et al. 2008; Capinha et al. 2012; Gallardo 2013; Gallardo and Aldridge 2013; Quinn et al. 2014).

Ecological Considerations

According to our results *D. polymorpha* may successfully colonise all Italian regions, but those more at risk are in the northern and central parts of the country. So far, the species has been reported for 11 out of 20 regions (Quaglia et al. 2008; Cianfanelli et al. 2010; Colomba et al. 2013; this study) but insufficient monitoring may have caused substantial underestimation of its real presence. The potential distribution we obtained had a much finer resolution than did that shown by Gallardo (2013) on which basis Italy would be uninterruptedly suitable except Sardinia and Sicily and other small territory portions. Such a high resolution results from the regional level of our analysis as well as the greater number of occurrences we considered for Italy.

The niche occupied by *D. polymorpha* in Italy is, in terms of temperatures and precipitation, closer to that of the native Ponto-Caspian regions and other European parts of the invaded range than to that known for North America, whose environmental ranges are consistently broader (Gallardo 2013). As observed elsewhere, our analysis showed that the species may tolerate cold water corresponding to air temperatures as low as −10 °C. *D. polymorpha* has shown a high capacity of rapid environmental adaptation within 20 years, due to a combination of evolutionary and ecological processes that render its niche especially flexible (Astanei et al. 2005; May et al. 2006; Rajagopal et al. 2009; Gallardo 2013). As somewhere else in Europe, where *D. polymorpha* is uncommon above 500 m a.s.l (Drake and Bossenbroek 2004; De Ventura et al. 2016), for Italy too we found this elevation to represent the upper distributional limit.

The frequent presence of fluviatile deposits in the north and centre of Italy emerged as an important factor favouring *D. polymorpha*'s presence and reminds conditions found in the species' native range, dominated by sedimentary rocks (Gallardo 2013), whereas in southern Italy volcanic, metamorphic and plutonic rocks determine less suitable environmental conditions.

The presence of *D. polymorpha* can modify habitats and affect biodiversity, sometimes radically, at different levels (Charavgis and Cingolani 2004; Cianfanelli et al. 2010). Our models showed that the potential distribution of *D. polymorpha* in Italy matches the distribution of several species of Unionidae and Veneroida of conservation importance (Ruffo and Stoch 2006). Due to its high rate of reproduction, dispersal and capacity to form high-density populations, zebra mussel reduces the phytoplankton population competing with the autochthonous fauna (Meier-Brook 2002; Lancioni and Gaino 2005; Cianfanelli et al. 2010), and such effects are already visible in some Italian regions (Fabbri and Landi 1999; Niero 2003). Extensive overgrowth by *D. polymorpha* of unionids, resulting in mass mortality of the latter, is characteristic of periods of rapid population growth of zebra mussels when the species invades a new waterbody (Karatayev 1981). After this period, if the environmental and food conditions are suitable for both organisms, native bivalves may mitigate competition and achieve coexistence with *D. polymorpha*.

Risk Map

Our models showed that *D. polymorpha* may colonise all Italian regions and watersheds and that the northern and central regions are more at risk. *Ca*. 30% of hydroelectric, irrigation and industrial dams fall within medium to high-risk areas. These structures could be seriously damaged by *D. polymorpha* due to its tendency to form large clusters anchored to rigid substrates, often obstructing or damaging water inlets, pipes, filters, pumps, turbines and drains (Franchini 1980). The dams placed in areas assessed as medium or high risk should be regularly checked and cleaned to avoid damage to equipment and structures.

Ca. 40% and 37% of lakes and rivers, respectively, were classified by our model as at medium or high risk. *D. polymorpha* is preyed upon by several vertebrate (Negra and Lipparini 2003; Charavgis and Cingolani 2004) and invertebrate (Bignami et al. 1978) species that might be subjected to biomagnification of toxic compounds the bivalve accumulates by filtration. This may compromise the predators' vital functions leading to detrimental consequences for the native fauna. Lakes and watercourses also represent a preferential way through which *D. polymorpha* spreads and colonises new areas either naturally (e.g., aquatic animals, aquatic plants and current water) or carried by boats (Johnson et al. 2001; Minchin et al. 2003; De Ventura et al. 2016). In the latter case, the hulls, motor surfaces, anchors or material snagged by the anchor of the boats should be checked and cleaned before navigation. The river traits that we highlighted as at special risk should be monitored to prevent the species' further dispersal. Water body management should consider all possible ways of avoiding accidental introduction into environments which have not yet been colonised. In particular, hydrographic systems and lakes should be subject to inspection. Early detection and proactive development of a rapid response plan in countering *D. polymorpha* invasion is of utmost importance (Wimbush et al. 2009) so appropriate planning is needed to maximise its effectiveness especially in northern and central Italy where according to our analysis most basins are at significant risk.

D. polymorpha may have severe economic and environmental consequences outside its native range but the species' ecological plasticity implies that the magnitude of such effects may differ greatly according to the region considered. Our study is the first to generate a risk map for *D. polymorpha* through SDMs implemented at a country-wide scale and provides useful information to prevent the spread of *D. polymorpha* to sectors of the country's territory not yet colonised. Our work remarks the importance of modelling potential invasions on a country scale to achieve the sufficient resolution needed to develop appropriate monitoring plans and prevent the invader's harmful effects. For this reason, we urge that further high-resolution risk maps be generated for other countries not yet invaded, or only partly colonised, by *D. polymorpha*.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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