

Is Great Britain heading for a Ponto–Caspian invasional meltdown?

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Summary

1. The outcome of multiple invasions from a common origin may lead to facilitative interactions because the invaders have co-evolved under similar environmental conditions. This outcome is often referred to as invasional meltdown, with a resultant increase in invasive species and a decline in native species richness and abundance.
2. This study seeks to assess the full scope of the threat posed by a high-risk group of 23 freshwater invaders originating from the Ponto–Caspian region (south-east Europe) across Great Britain. Ponto–Caspian invaders constitute a group of special concern because they have recently caused a large-scale invasion into western Europe.
3. According to a literature review, 76% of reported interactions between Ponto–Caspian invaders are positive (mostly provision of food and commensalism) or neutral (habitat partitioning). Negative interactions (mostly predation) were rare, thus highlighting the ability of Ponto–Caspian invaders to coexist.
4. At least 14 out of the 23 Ponto–Caspian organisms investigated are well-established in the Rhine estuary and Dutch ports. Four of them (*Hemimysis anomala*, *Dikerogammarus villosus*, *D. haemobaphes* and *Hypania invalida*) have recently established in Great Britain. Regression models suggest the rest are under a critical risk of being transported, with four species predicted to have arrived already to Great Britain: *Echinogammarus ischnus*, *Jaera istri*, *Limnomyces benedeni* and *D. bispinosus*.
5. According to species distribution models, the cumulative risk of invasion of multiple Ponto–Caspian species, thus invasional meltdown, is highest in the south-east of England and decreases to the north and west.
6. Great Britain might be on the brink of invasional meltdown, and as a consequence, confronting the problem of Ponto–Caspian invasive species is a vital element for national biosecurity.
7. *Synthesis and applications.* The predictive models and maps developed in this study provide a means for an evidence-based prioritization of species and habitats for the management of existing and future invasions of Ponto–Caspian species. This integrated approach can be easily applied to risk assess other groups of species and habitats.

Key-words: biosecurity, human influence index, invasion lag, invasional meltdown, MAXENT, quagga mussel, species distribution models

Introduction

The invasional meltdown hypothesis (IMH) predicts ecosystems to become gradually more disrupted as colonization by multiple invasive species progresses, since many invaders facilitate each other's establishment, potentially leading to an accelerating increase in the rate of invasion

and thus compounding their deleterious impacts on recipient ecosystems (Simberloff & Von Holle 1999; Simberloff 2006). The IMH is one of the invasion-related hypotheses with the widest scientific support (77% empirical tests: Jeschke *et al.* 2012) across terrestrial (e.g. O'Dowd, Green & Lake 2003), freshwater (e.g. Ricciardi 2001) and marine systems (e.g. Levin *et al.* 2002).

A classic example of invasional meltdown is posed by the introduction of the zebra mussel *Dreissena polymorpha* (Pallas 1771) in the Great Lakes of North America

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(Ricciardi 2001). By providing habitat complexity, food and shelter, mussels have facilitated the introduction of at least 14 invasive species, including plants (e.g. *Myriophyllum spicatum*, *Potamogeton crispus*), invertebrates (e.g. *Echinogammarus ischnus*, *Gammarus fasciatus*, *Dugesia polychroa*, *Bithynia tentaculata*, *Valvata piscinalis*) and fish (e.g. *Alosa pseudoharengus*, *Cyprinus carpio*, *Osmerus mordax*, *Neogobius melanostomus*, *Proterorhinus marmoratus*) (Ricciardi 2001). The invasion of the zebra mussel in North America is relatively recent (ca. 30 years), yet no similar facilitation process has been described in western Europe, where this species has been slowly spreading over the last two centuries (der Van Velde, Rajagopal & de Bij Vaate 2010). Furthermore, the zebra mussel's native Ponto–Caspian region, located within the basins of the Black, Azov and Caspian Seas, is an exceptional 'donor hot spot' of freshwater invaders towards western Europe, with over 100 species currently known to be spreading out of their native range (Ketelaars 2004). Yet, very little is known about their interspecific interactions. This is worrying, since invasional meltdown is more likely between species from the same native region that have co-evolved under similar environmental conditions and have developed strategies that facilitate their coexistence (Ricciardi 2001). Ponto–Caspian species therefore constitute a group of high concern for environmental managers and stakeholders requiring specific strategies that take into account pathways of introduction, interspecific interactions, habitat preferences and potential impacts.

We investigate the interaction between Ponto–Caspian invaders and the risk of invasional meltdown in Great Britain, an island where invasive freshwater species have caused large ecological and economic impacts (Oreska & Aldridge 2011). Freshwater invaders from the Ponto–Caspian region are likely to arrive in Great Britain through the central and southern European corridors described by Bij de Vaate *et al.* (2002). These two corridors lead species from their native range towards the Rhine River and coastal areas of the Netherlands, from where they are eventually transported to Great Britain in ballast water or as contaminants of ornamental plants, animals and aquatic equipment (e.g. attached to boats, fishing gear). The zebra mussel, first reported in Great Britain in 1824 and currently widely distributed (Aldridge, Elliott & Moggridge 2004), is thought to have facilitated the establishment of subsequent Ponto–Caspian invaders, including the killer shrimp *Dikerogammarus villosus* (Mac-Neil *et al.* 2010) and the demon shrimp *D. haemobaphes* (Kobak *et al.* 2009). Gallardo & Aldridge (2013a,b) report that climatic conditions and water chemistry similar to continental Europe, and a high propagule pressure, increase the risk of invasion of multiple Ponto–Caspian invaders in the south-eastern part of England. They warned that facilitation between Ponto–Caspian invaders may further amplify the risk of invasional meltdown in this region, although facilitative interactions between species were not specifically evaluated.

We assessed the full scope of the threat posed by Ponto–Caspian invaders in Great Britain through the integration of predictive models that allows the inference of likely future scenarios of invasion. Data extracted from global, European and national data bases were used to investigate (i) interspecific interactions among Ponto–Caspian species giving support to the IMH, (ii) spatiotemporal patterns of freshwater invasions in Great Britain that may help to anticipate the potential routes of new invasions and (iii) the likely spatial distribution of Ponto–Caspian species in Great Britain based on their propagule pressure and environmental preferences. This integrated approach can be easily applied to risk assess other groups of species and habitats, and has potentially broad utility in helping to focus the most efficient use of resources.

Materials and methods

The list of Ponto–Caspian species assessed in this study included 23 organisms identified as potential threats to British freshwaters in previous horizon risk assessments (e.g. Godard *et al.* 2012; Gallardo & Aldridge 2013b) (Table 1). The list included five species already recorded in Great Britain: the Caspian mud shrimp *Chelicorophium curvispinum* G.O. Sars (1895), the bloody red mysid *Hemimysis anomala* G. O. Sars (1907), the killer shrimp *Dikerogammarus villosus* Sowinsky (1894), the demon shrimp *Dikerogammarus haemobaphes* Eichwald (1841) and the polychaete worm *Hypania invalida* Grube (1960). These organisms were included in our assessment because they are considered to have the potential for considerable increase in distribution and abundance across Great Britain. In addition, these five species can serve as important controls to check the reliability of predictive tools developed within this study.

INTERACTION BETWEEN PONTO–CASPIAN INVASIVE SPECIES

A literature search was undertaken utilizing each species scientific name within the ISI Web of Knowledge to summarize interactions among the 23 species of Ponto–Caspian origin investigated in this study. Additionally, Google Scholar was used to locate other scientific papers from non-indexed journals (such as *Aquatic Invasions*) and grey literature (e.g. national reports, PhD dissertations). The literature review included all reported field and experimental interactions with no geographic restrictions; therefore, assuming that relationships between Ponto–Caspian invaders in Europe are similar throughout their ranges. As a result, information regarding the co-occurrence and interaction of Ponto–Caspian species was retrieved from 42 publications (Table S1, Supporting Information).

Species interactions were categorized following Ricciardi (2001): (i) commensalism, in which one species benefits from the presence of another species that is unaffected by the interaction (tabulated as +/0); (ii) coexistence, when both species are reported to co-occur exhibiting certain habitat partitioning (0/0); (iii) exploitation, in which one species benefits at the expense of another (e.g. predation) (+/–); (iv) amensalism, in which one species is inhibited while the other is unaffected (0/–); and (v) antagonism, which is defined as any mutually detrimental interaction

Table 1. Ponto–Caspian invasive species reviewed in this study (in alphabetical order)

Scientific name	English name	Order
<i>Cercopagis pengoi</i>	Fish-hook water flea	Cladocera
<i>Chaetogammarus warpachowski</i>		Amphipoda
<i>Chelicorophium curvispinum*</i>	Caspian mud shrimp	Amphipoda
<i>Chelicorophium robustum</i>		Amphipoda
<i>Chelicorophium sowinskyi</i>		Amphipoda
<i>Dikerogammarus bispinosus</i>		Amphipoda
<i>Dikerogammarus haemobaphes*</i>	Demon shrimp	Amphipoda
<i>Dikerogammarus villosus*</i>	Killer shrimp	Amphipoda
<i>Dreissena r. bugensis</i>	Quagga mussel	Veneroida
<i>Echinogammarus ischnus</i>		Amphipoda
<i>Echinogammarus trichiatus</i>		Amphipoda
<i>Hemimysis anomala*</i>	Bloody red shrimp	Mysida
<i>Hypania invalida*</i>		Canalipalpata
<i>Jaera istri</i>		Isopoda
<i>Limnomyces benedeni</i>	Mysid shrimp	Mysida
<i>Lithoglyphus naticoides</i>	Gravel snail	Neotaenioglossa
<i>Neogobius gymnotrachelus</i>	Racer goby	Perciformes
<i>Neogobius melanostomus</i>	Round goby	Perciformes
<i>Obesogammarus crassus</i>		Amphipoda
<i>Obesogammarus obesus</i>		Amphipoda
<i>Pontogammarus robustoides</i>		Amphipoda
<i>Proterorhinus marmoratus</i>	Tubenose goby	Perciformes
<i>Proterorhinus semilunaris</i>	Freshwater tubenose goby	Perciformes

*Species already recorded in Great Britain but showing a limited distribution.

(e.g. resource competition, intraguild predation)(−/−). No case of mutualism, a situation where the interaction is beneficial to the survival of both species (+/+), was reported in the literature. In some instances, interactions were reported for groups of species. For instance, Ponto–Caspian amphipods generally prefer dreissenid beds as habitat, which provides them with food and shelter; amphipods serve in turn as prey for invasive gobies (Van der Ploeg *et al.* 2002; Campbell *et al.* 2009). Consequently, all 13 amphipods included in this assessment were assigned the same interaction score with respect to dreissenids and the four investigated gobies, respectively. Because the effects of the zebra mussel *Dreissena polymorpha*, Pallas (1871) and the quagga mussel *Dreissena rostriformis bugensis* Andrusov (1897) are difficult to differentiate, and the former is already widespread in Great Britain, we decided to include both species together under a common ‘Dreissenids’ category. This extrapolation may not always hold true, since *D. r. bugensis* inhabits greater depths than *D. polymorpha* (Mills *et al.* 1996), and may therefore not provide suitable habitat for some of the investigated species.

The effect of each species on the establishment and survival of the rest of organisms investigated was finally tabulated as net

positive (+), negative (−) or neutral (0) to conform a matrix of species × species (Table S2, Supporting information). In cases where one invader had various reported effects on another’s occurrence, positive or negative interactions were favoured over neutral effects. To give support to the IMH, the total number of positive and neutral interactions should exceed the number of negative interactions. While this approach provides a useful summary of interactions between two species (Ricciardi 2001), it is important to recognize that more complex interactions at the community level may contribute to the overall facilitation or suppression of species establishment.

SPATIOTEMPORAL PATTERNS OF INVASION INTO GREAT BRITAIN

We analysed spatial and temporal patterns of freshwater invasion into Great Britain to calculate the probability of introduction of new invaders. We extended the investigation to all freshwater invasive species present in Great Britain, regardless of their native origin, so that there were sufficient data to perform spatiotemporal analysis. We therefore assumed that invasion pathways from the Netherlands towards Great Britain are relatively similar irrespective of native origin and should not affect the results of calculations. Criteria used for selecting data for analyses are described below.

First, we assumed the Netherlands is the most likely origin of Ponto–Caspian invasive species towards Great Britain. While Ponto–Caspian species may also originate from other North Sea ports and coastal regions such as France and Belgium, the Netherlands is currently the European country that exchanges the greatest volume of trade with Great Britain, with the largely freshwater port of Rotterdam accounting for 7.6% of total tonnage loaded and unloaded at British ports in 2008 (Talbot *et al.* 2009). Location and dates of first observation of freshwater invasive species in Great Britain and the Netherlands were obtained from the literature (Agence de l’Eau Rhin Meuse 2005; Hill *et al.* 2005; Keller, Ermgassen & Aldridge 2009) and internet accessible data bases (e.g. Great Britain-Non-Native Species Secretariat: <http://www.nonnativeSpecies.org/>).

Secondly, we limited our analyses to those invasive species recorded after 1900 because spatiotemporal patterns of introduction might change over time (Keller, Ermgassen & Aldridge 2009). Although the introduction of freshwater invaders into Great Britain depends largely on stochastic events, we also assumed that the longer an invasive species is present in donor areas (the Netherlands in this case), the higher the probability that such random event occurs.

Thirdly, we used information from freshwater invasive species that were first identified in the Netherlands and only afterwards in Great Britain to calculate time-lags (i.e. difference between years of first report) between both countries.

Consequently, data from a total 48 freshwater invaders of various native origins were finally included in the calculation. Table S3 (Supporting information) lists their respective times of introduction.

Data from the four Ponto–Caspian species that are already located in Great Britain (*D. villosus*, *D. haemobaphes*, *H. invalida* and *H. anomala*) were held out to test model accuracy. The Caspian mud shrimp (*C. curvispinum*) could not be used as control because it was detected in Great Britain in 1935, earlier than in the Netherlands (1987).

Regression models were used to investigate the relationship between time-lag (response variable) and the year in that the species was reported from the Netherlands (explanatory variable). The analyses were based on generalized additive models (GAMs, Wood 2006), instead of other regression procedures because GAMs allow the shape of the response curves to be estimated from the data instead of fitting an *a priori* parametric model which is limited in its available shape of response (Lehmann 1998). Model fit was checked through visual inspection of residual plots (Q-Q plot, residuals vs. linear predictor, histogram of residuals and response vs. fitted values) (Wood 2006). The regression model was used to predict the likely time frame of introduction for 10 Ponto–Caspian species that are already present in the Netherlands, and tested against data from the four held out species.

POTENTIAL DISTRIBUTION OF PONTO–CASPION INVADERS ACROSS GREAT BRITAIN

We used species distribution models (SDM) to locate areas in Great Britain that might be most vulnerable to the establishment of the 23 Ponto–Caspian species. SDM are a statistical technique often used to locate areas at continental or regional scale which are environmentally most similar to the current range of an invasive species, and thus are most susceptible to successful colonization in the event of an introduction (Guisan & Thuiller 2005).

Information on the current spatial distribution of invasive species was obtained from the Global Biodiversity Information Facility (GBIF, <http://data.gbif.org>), the Netherlands Biodiversity Information Facility (NLBIF, <http://www.nlbif.nl>) and the National Biodiversity Network (NBN, Gateway <http://data.nbn.org.uk>). Additionally, we used occurrence points gathered for the modelling of Ponto–Caspian invaders in previous studies (Gallardo & Aldridge 2012, 2013a,b; Gallardo, Zieritz & Aldridge 2013; Quinn, Gallardo & Aldridge 2014). Once we obtained the most accurate distribution map for a species, the software ENMTOOLS v1.3 (<http://enmtools.blogspot.co.uk>, Warren, Glor & Turelli 2010) was used to remove duplicate records. This procedure leaves only one occurrence point per pixel of 5 arcminutes (c. 10×10 km at the equator), thereby avoiding data redundancies that may bias output predictions.

Nine environmental layers were used at a 5-arcminute resolution to calibrate the environmental preferences of Ponto–Caspian invaders: altitude (m), annual mean temperature ($^{\circ}$ C), temperature seasonality ($^{\circ}$ C), maximum temperature of the warmest month ($^{\circ}$ C), minimum temperature of the coldest month ($^{\circ}$ C), annual precipitation (mm), precipitation of the driest month (mm), precipitation seasonality (mm) and geology (categorical: endogenous plutonic or metamorphic rocks, extrusive volcanic rocks, island, lake, ophiolitic complex, sedimentary rocks and undifferentiated facies). Altitude and bioclimatic variables were obtained from WORLDCLIM (<http://www.worldclim.org>), and geology from the Commission for the Geological Map of the World (CCGM-CGMW, Paris 2010, <http://ccgm.free.fr/>). Variables showed a Pearson correlation $r < |0.8|$, as checked with ENMTOOLS v1.3 (Table S4, Supporting information). Plisoff *et al.* (2014) showed that the use of different sets of climatic predictor variables did not have a significant effect on overall metrics of model performance, but had significant effects on spatial predictions. Thus, when selecting bioclimatic variables to calibrate our models, we had to consider the trade-off of choosing variables that are ecologically meaningful (e.g. maximum and minimum annual

temperatures, annual precipitation) at the expense of increased collinearity.

In addition to environmental factors, we introduced five human-related factors at a 5-arcminute resolution: the human influence index (HII), land use (categorical: forest, shrubland, savanna, grassland, wetland, cropland/natural vegetation, urban, snow/ice and barren/sparsely vegetated), density of human population (habitants per square m), distance from the closest commercial port (km) and distance to primary roads (km). The first three human variables were obtained from internet gateways (Socio-Economic Data and Applications Centre, <http://sedac.ciesin.columbia.edu/>; IGBP – International Geosphere–Biosphere Programme, <http://www.modis.bu.edu/landcover/>; Oak Ridge National Laboratory, <http://www.ornl.gov/sci/landscan/>, respectively). These three layers are expected to reflect the intensity of human activity directly and indirectly related to freshwater introductions (e.g. fishing, boating, water sports and aquaculture). Closeness to primary ports and roads maps was generated from vector maps using ARCVIEW 10.0©ESRI (see more information in Gallardo & Aldridge 2013a) and was expected to reflect potential accessibility to water bodies. Despite the inclusion of HII, which may partially account for some of the other four human footprint proxies selected, collinearity levels were low (Pearson $r < |0.5|$, Table S4, Supporting information). The relevance of selected environmental and human variables as potential predictors of Ponto–Caspian species potential distribution has been already demonstrated by Gallardo & Aldridge (2013b) and Gallardo (2014).

MAXENT version v3.3k (www.cs.princeton.edu/~schapire/maxent) was used to calibrate distribution models. Modelling settings follow those described by Gallardo & Aldridge (2013a). For input, MAXENT models used the data set of species occurrences and the set of environmental and socio-economic predictors that might affect the likelihood of species establishment. To test the accuracy of predictions, occurrence data were split into two sets: 70% of the data was used for modelling and the remaining 30% for testing the model. Because no absence data were available, a total of 10 000 random background points were generated. To assess model performance, the area under the receiving operating characteristic (ROC) curve (AUC) (Hanley & McNeil 1982) was used. After calibration, models were projected onto Great Britain to obtain suitability maps, ranging from 0= conditions completely different to those of the current range of the species, to 100%= complete match with the current range of the species. The threshold maximizing the sensitivity (i.e. number of presences correctly predicted) and specificity (i.e. number of background points correctly predicted) of the model was used to transform suitability maps into presence/absence maps (Liu *et al.* 2005). Thresholded maps provided a simple absence/presence prediction for each species allowing identification of broad geographic regions whose propagule pressure and environmental conditions may facilitate the successful establishment of an invasive species. Finally, all maps were combined together into a single ‘heat map’ reflecting the cumulative risk of invasion of the study area for all evaluated species together.

Results

INTERACTION BETWEEN PONTO–CASPION INVASIVE SPECIES

After the literature review, 157 effects between Ponto–Caspian invasive species were recorded, including 64

negative (56 predation, 7 amensalism and 1 antagonism), 48 neutral (habitat partitioning) and 71 positive interactions (19 commensalism, 52 provision of food) (Tables S1 and S2, Supporting information). Negative interactions apart from fish predation were rare, with coexistence through habitat partitioning as the commonest strategy. Fourteen species showed a positive net balance (i.e. they affect more species positively than negatively), and this came mostly from crustaceans that serve as prey for fish and dreissenids that provide food and habitat to other species (Table S1, Supporting information). The four fish showed a negative balance (i.e. they affect more species negatively than positively), predating on amphipods and mussels.

SPATIOTEMPORAL PATTERNS OF INVASION INTO GREAT BRITAIN

We obtained the year and location of first report in the wild of 48 freshwater invasive species (see Table S3, Supporting information for their dates of introduction). Of these, 33% (16 species) were reported for the first time from the Thames River Basin District (RBD), mostly in the London, Wey, Loddon and Medway management catchments. The second RBD in number of first records was the Anglian (19%, 9 species), which included the Nene, Great Ouse and the Broadland Rivers. The Humber RBD also recorded a high number of first introductions (15%, 7 species), concentrated along the River Trent.

The GAM was highly significant and able to explain 37% of the variance in the response variable (time-lag between report dates) (Fig. 1). The model residuals were normally distributed (Shapiro–Wilk normality test, $W = 0.96$, $P > 0.05$) and were graphically unbiased (Fig. S1, Supporting information). The model showed a negative linear trend, illustrating the tendency towards shorter time-lags in more recent years. Predicted 95% confidence intervals of introduction according to this model are shown in Table 2. Dates of first report in the wild of Ponto–Caspian species already located in Great Britain were used to test the robustness of this model: while the introduction of *H. anomala*, *H. invalida* and *D. haemobaphes* agreed with our model, the prediction regarding *D. villosus* failed by 2 years.

POTENTIAL DISTRIBUTION OF PONTO–CASPIAN INVADERS ACROSS GREAT BRITAIN

The accuracy of models ranged from 0.97 to 0.99 AUC, which can be considered a very high quality. Environmental variables were able to explain on average 60% of the current geographic distribution of Ponto–Caspian species, whereas the contribution of human factors reached a notable 40% on average. A summary of modelling outputs, including the contribution of each variable to the model, can be consulted in Table S5 (Supporting information).

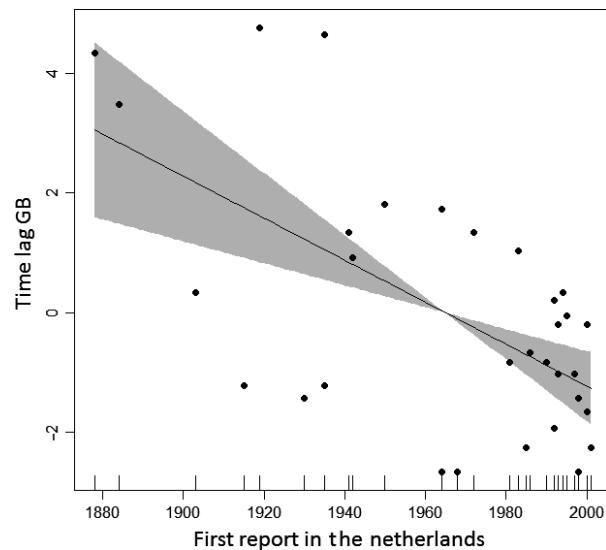


Fig. 1. Modelled relationship between the year of report of freshwater invasive species in the Netherlands and Great Britain. The y-axis represents the partial residuals of the model. The shaded area delimits error bounds (95% confidence interval). The GAM regression model explained 37% of the variance in the data set.

Table 2. Predicted year of introduction of Ponto–Caspian invasive species currently present in the Netherlands (Year NTL). Ninety-five percentage confidence intervals (CI) around the mean value are provided. Year reported GB: actual year in which four Ponto–Caspian species (at the bottom of the list) were reported in Great Britain

	Year NTL	Year predicted GB (95% CI)	Year reported GB
<i>E. ischnus</i>	1991	1992–2005	
<i>J. istrì</i>	1997	1996–2011	
<i>L. benedeni</i>	1998	1997–2012	
<i>D. bispinosus</i>	1998	1997–2012	
<i>E. trichiatus</i>	2001	1999–2014	
<i>P. marmoratus</i>	2002	2000–2015	
<i>C. robustum</i>	2003	2001–2016	
<i>N. melanostomus</i>	2004	2001–2017	
<i>D. bugensis</i>	2006	2003–2019	
<i>P. semilunaris</i>	2008	2014–2021	
<i>D. villosus</i>	1994	1994–2008	2010
<i>H. invalida</i>	1995	1995–2009	2008
<i>H. anomala</i>	1997	1996–2011	2004
<i>D. haemobaphes</i>	2000	1998–2013	2012

Among environmental variables, minimum temperature of the coldest month was an important driver for the distribution of all species investigated, which showed a peak in suitability between -5 and 0°C minimum (air) temperature. Among human-related predictors, models revealed the human influence index (HII) as one of the most important drivers of Ponto–Caspian species distribution, able to explain more than 25% of the distribution of *C. curvispinum*, *C. sowinskyi*, *D. haemobaphes*, *D. villosus* and *O. obesus* (Table S5, Supporting information). The influence of other *a priori* relevant indicators, such as port

closeness or population density, was lower than expected, quite likely because the HII already accounts for these factors.

Suitability scores for Ponto–Caspian invaders were generally highest towards the south-east of England. The only species showing relatively low suitability scores across Great Britain were *C. pengoi*, *E. ischnus*, *C. warpaczowski*, *C. sowinskyi* and *O. crassus* (Fig. S2, Supporting information). The 23 individual species maps were combined to generate a ‘heat map’ that reflects spatially the cumulative total number of species predicted present (Fig. 2, Supporting information). The heat map highlighted the lower reaches of the Great Ouse, Broadland, Thames and Severn rivers as the most prone to invasion, with up to 20 Ponto–Caspian species predicted to be or become present. Most of England was under threat of multiple invasions while the risk in Wales was considerably lower, and concentrated along a strip of the south coast.

Discussion

In accordance with the invasional meltdown hypothesis, the relative dominance of positive interspecific interactions, primarily through the provision of habitat and resources, suggests Ponto–Caspian invaders typically facilitate each other’s establishment. Negative interactions were rarely reported, except for predatory gobies, with

most species able to partition their habitat to allow coexistence. Accordingly, experience on mainland Europe suggests that Ponto–Caspian species can sometimes be so dominant that benthic samples comprise entirely species of Ponto–Caspian origin (Bij de Vaate *et al.* 2002). Moreover, our evaluation is likely an underestimation of the potential breadth of interactions among species for two reasons: data incorporated in the data base include only cases that are supported by empirical evidence, and community-level interactions are not considered. As discussed by Simberloff & Von Holle (1999), mutualistic interactions are less frequently reported in the literature than competitive ones, and the effects of invasive upon native species are reported more frequently than the interaction between invaders. Furthermore, community patterns of interaction are complex and may result in the indirect facilitation of species, thus playing a largely unknown role in the invasional meltdown. In a meta-analysis, Parker, Burkepile & Hay (2006) revealed native plants are more vulnerable to predation by invasive herbivores than invasive plants because of the lack of specific resistance strategies. The replacement of native by invasive predators can thus eliminate the biotic resistance offered by native predators, thereby triggering invasional meltdown (Parker, Burkepile & Hay 2006). Likewise, the effect of Ponto–Caspian predators (e.g. gobies) upon invasive prey (e.g. amphipods) can be net positive instead of negative when the predatory pressure is higher upon native competitors. In this case, we should expect exacerbated impacts of invasive species on native communities. In our case, Ponto–Caspian species were frequently reported to simply co-occur along a river stretch or lake with no further information on their relationship, hence the high number of interactions being assigned as neutral. Remarkably, no cases of mutualism were specifically reported, although the progressive increase in the number and coverage of Ponto–Caspian invasions and the high sympatry of Ponto–Caspian species within their invader ranges (Bij de Vaate *et al.* 2002), altogether suggests they may possess mechanisms that facilitate their coexistence through processes in addition to habitat partitioning, such as community-level interactions.

After collecting data on the spatiotemporal patterns of freshwater invasions into Great Britain, we identified a higher concentration of invasive species in coastal catchments towards the south-east of England, which can be related to the location of major ports in the London area (e.g. London and Medway), the East of England (e.g. Ipswich, Lowestoft, Felixstowe), the south of Wales (e.g. Bristol, Cardiff, Port Talbot) and North West England (Liverpool, Manchester). These ports receive between 2.9 and 5.1 MMT ballast water annually, predominantly from north Europe, thus exacerbating the risk of Ponto–Caspian species being inadvertently transported (Enshaei & Mesbahi 2009). Our study also confirms the findings of Jackson & Grey (2013) who recently highlighted the River Thames as a ‘focal hot spot’ of freshwater invasion.

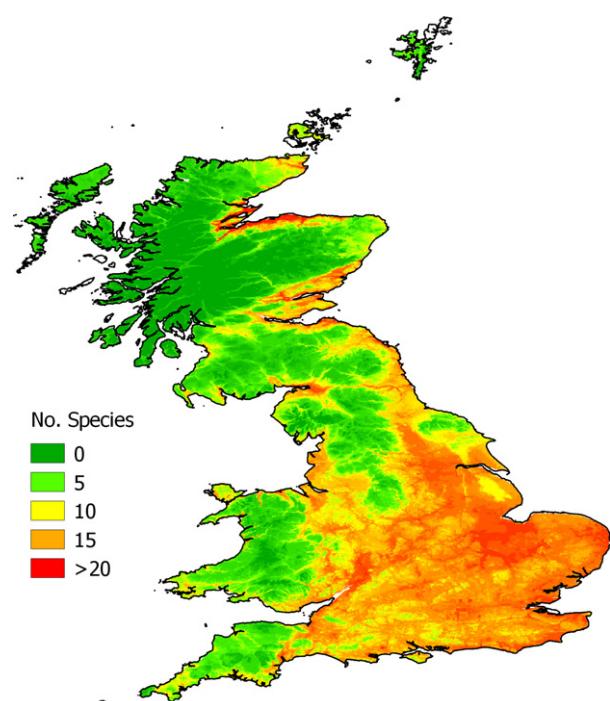


Fig. 2. Heat map showing the cumulative probability of presence of 23 Ponto–Caspian species. The estuaries and lower reaches of the Rivers Thames, Great Ouse, Severn and Broadlands are prone to the invasion of up to 20 different invasive Ponto–Caspian species and for this reason are considered potential hot spots of invasion.

Upon analysis of introduction dates, a change in spatio-temporal invasion patterns between the Netherlands and Great Britain emerged. The time-lag between a given species report in the Netherlands and Great Britain has notably decreased over the last century from an average 30 years at the beginning of the 20th century to merely 5 years in the last decade. Likewise, Jackson & Grey (2013) revealed a sixfold increase in the rate of invasion of the Thames estuary in the last century (from 1950 to 1989).

Linear regression models predicted four Ponto–Caspian species may have arrived into Great Britain between 2005 and 2011 (Table 2). Two alternative explanations can be suggested to explain this result. First, species might have been already established in Great Britain but not yet reported. This scenario is supported by experience with the killer shrimp (*D. villosus*), which was located in Great Britain 2 years later than Table 2 predicted. Nonetheless, experts suggested it may have established in the wild years before being noticed, based on its abundance, size spectra and reproductive stage of individuals (MacNeil *et al.* 2010), which would rather support our prediction. Considering the difficulty of identifying some Ponto–Caspian species, and the lack of appropriate monitoring plans for their early detection, this option cannot be disregarded. Alternatively, the species abundance and geographic spread in the Netherlands might be too limited to trigger the species expansion, which highlights the role of propagule pressure (Lockwood, Cassey & Blackburn 2005). Information about the likely time frame of introduction should be thus analysed jointly with information on the species abundance and spread in donor areas in order to provide more realistic predictions. Nonetheless, since the longer a species is present in the Netherlands, the higher the probabilities are of unwanted introduction into Great Britain, species in Table 2 are considered to be of high concern. Special attention should be paid to the quagga mussel *D. r. bugensis*, since regression models predict its likelihood of introduction to be very high (Table 2), and a number of reviews believe there is a high risk of introduction and establishment of this species into Great Britain (Gallardo & Aldridge 2013a; Roy *et al.* 2014).

Species distribution models allowed the investigation of the combined influence of environmental and human drivers on the current distribution of each species. From here, areas most vulnerable to multiple invasions were identified. Amongst climatic factors, minimum temperature was the most important driver of the investigated species' distributions, and this is in accordance with previous studies in the area (Gallardo, Errea & Aldridge 2012; Gallardo & Aldridge 2013a,b). Notwithstanding the important effect of temperature, human-related factors also significantly affected the spatial distribution of Ponto–Caspian species. Higher suitability scores could be observed in densely populated areas, regions close to the coast and in zones with relatively dense transport links (Fig. S1, Supporting information). Previous studies have similarly shown that

the incorporation of human factors into SDM resulted in 20% amplification of risk scores for freshwater invaders in highly developed areas of Great Britain and Ireland (Gallardo & Aldridge 2013a).

While individual prediction maps can be useful to address the risk posed by individual species, the heat map featured in Fig. 2 synthesizes information regarding the risk associated with Ponto–Caspian species collectively. The heat map suggests there is room for expansion of current invaders while at the same time the arrival of newcomers poses a tremendous challenge in terms of prevention and management. This is because many Ponto–Caspian species are able to change the abiotic conditions of the habitat they invade, facilitating not only their own survival but also the successful colonization of additional Ponto–Caspian invaders, as shown in Table S1 (Supporting information).

Conclusions and management recommendations

We have gathered enough information to make the case that Great Britain is on the brink of invasional meltdown, and as a consequence, confronting the problem of Ponto–Caspian invasive species is a vital element for national biosecurity. Predictive models and maps developed in this study can be used in decision-making to set priorities for the best use of time and funds and to help determine whether and what kind of strategy should be adopted in Great Britain.

A number of biosecurity recommendations can be drawn from this study. First, prevention strategies based on pathways rather than on individual species provide the most efficient way to concentrate efforts at sites where species are most likely to enter national boundaries and to intercept several potential invaders linked to a single pathway (Wittenberg & Cock 2001). In the case of Great Britain, the ornamental trade was highlighted by Keller, Ermgassen & Aldridge (2009) as the dominant vector of introduction of invasive freshwater species into Great Britain over the last two centuries. Special attention should be paid to areas under risk of multiple invasions and subject to a high frequency of first reports of invasive species, such as the lower reaches of the Rivers Great Ouse, Thames, Severn and the Broadlands, which are projected to be affected by up to 20 Ponto–Caspian species.

The rate of colonization of invasive species into Great Britain coming from the Netherlands has accelerated in recent decades. This can be attributed to both increasing globalization, and thus travel and freight transport (Jackson & Grey 2013), and also from an increasing propagule pressure, with the richness and abundance of Ponto–Caspian species increasing in potential donor countries (Bij de Vaate *et al.* 2002). This is worrying, as the number of Ponto–Caspian species in the Netherlands but not yet present in Great Britain stands as ten and thus poses a serious threat to the conservation of British aquatic

ecosystems. For this reason, cross-country sharing and updating of information on the status and impacts of invasive species is fundamental, so that the presence of known invasive species is detected early, and the risks they pose are rapidly assessed (GB-NNSS 2008). Finally, a continuing process for evaluating invasive species and detecting new introductions should be established, since invasive species problems are increasing dramatically and the vectors for introduction of potential invasive can change over time.

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Data accessibility

Species interaction: uploaded as online supporting information. Data on first occurrence of species: uploaded as online supporting information. Species location data and R scripts: deposited in the Figshare repository doi: 10.6084/m9.figshare.1157479 (Gallardo & Aldridge 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Residual plots from Generalized Additive Models (GAM).

Fig. S2. Prediction maps resulting from Species Distribution Models (SDM).

Table S1. Reported interactions between Ponto-Caspian invasive species.

Table S2. Tabulated table of interactions between Ponto-Caspian invaders.

Table S3. Dates of introduction and time lags for aquatic invasive species.

Table S4. Pearson correlation between layers used for Species Distribution Model (SDM) calibration.

Table S5. Statistics from species distribution models.