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The references have been added at the end of the references list and here:

Gallardo B, zu Ermgassen PSE, Aldridge DC (2013) Invasion ratcheting in the zebra mussel (Dreissena polymorpha) and the ability of native and invaded ranges to predict its global distribution. Journal of Biogeography 40:2274-2284

Heiler KC, Bij de Vaate A, Ekschmitt K, et al. (2013) Reconstruction of the early invasion history of the quagga mussel (Dreissena rostriformis bugensis) in Western Europe. Aquatic Invasions 8:53-57

Karatayev AY, Burlakova LE, Padilla DK (2015) Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746:97-112

Papeş M, Havel JE, Vander Zanden MJ. Using maximum entropy to predict the potential distribution of an invasive freshwater snail. Freshwater Biology. 2016;61(4):457–71

Rose PM, Kennard MJ, Moffatt DB, et al. (2016) Testing Three Species Distribution Modelling Strategies to Define Fish Assemblage Reference Conditions for Stream Bioassessment and Related Applications. PLOS ONE 11:e0146728

Original Paper

# Boat ramps facilitate the dispersal of the highly invasive zebra mussel (*Dreissena polymorpha*)

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## Abstract

Invasive bivalves can cause widespread ecological damage, but eradication has proved difficult. Identifying the pathways of dispersal is crucial to implementing more effective biocontainment measures. We examined the distribution of the highly invasive zebra mussel (*Dreissena polymorpha*) in Great Britain through Species Distribution Modelling to determine the drivers of distribution and generated suitability maps to predict future dispersal. Distance to boat ramps was the most important predictor of zebra mussel establishment, accounting for 27% of variation in occurrence. Probability of occurrence was highest within 3 km upstream of boat ramps, probably due to boating activity and the impounded waters typically associated with boat ramps. Our results highlight the need for implementing stringent control measures around boat ramps, and demonstrate the value of spatially modelling species distribution to create risk maps for targeting monitoring efforts at those locations most vulnerable to invasion.

**AQ1**

## Keywords

Aquatic invasive species

Niche models
Introduction pathways
Biosecurity
Prevention

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s10530-020-02453-9.

## Introduction

Invasive bivalves are expanding their range and causing widespread ecological damage, as well as important economic losses, which call for better control measures (Sousa et al. 2014). The zebra mussel (*Dreissena polymorpha*) is one of the most damaging invasive bivalves due to its wide niche, rapid population growth and negative impacts on the economy (Lowe et al. 2000). For example, in Great Britain £5 million are lost each year due to pipe fouling and damage to water infrastructures, while in North America $800,000 are spent yearly in each power plant infested by zebra mussels (Oreska and Aldridge 2011) which poses a significant biosecurity risk and a safety hazard (Meyerson and Reaser 2003).

Zebra mussels tend to outcompete native freshwater pearl mussels (Ricciardi et al. 1998) and can also disrupt food webs and trigger changes in ecosystem functioning (Strayer 2010), with consequent economic losses (Mckindsey et al. 2007). Since its introduction in 1824, zebra mussels have expanded their range in Great Britain (Aldridge et al. 2004; Gallardo and Aldridge 2015), invading new localities each year (NBN Atlas 2018). Over the past decade, there have been 750 records of zebra mussel in Great Britain, peaking in 2012, the year with the highest number of new occurrences (151 new records, Figure S1).

The eradication of zebra mussel has been met with limited success (Aldridge et al. 2006) and management relies mainly on controlling its spread and preventing further range expansion (Havel et al. 2015), in common to other aquatic invasive species such as the quagga mussel (*Dreissena rostriformis bugensis)* (Heiler et al. 2013; Karatayev et al. 2015), various Asian clams and the killer shrimp (Anderson et al. 2014).

**AQ2**

Given that prevention offers the best course of action for controlling the spread of zebra mussel, it is important that the mechanisms of dispersal are well understood. Natural dispersal of aquatic bivalves is mainly determined by the structure and connectivity of waterways (Fagan 2002), but anthropogenic factors are also expected to shape their distribution (Hulme 2016), particularly for species that tolerate a wide range of environmental conditions, as is the case for the zebra mussel (Bielen et al. 2016). Zebra mussels are often found in fragmented water masses (Matthews et al. 2014), suggesting that colonization is largely deterministic and shaped by point introductions, rather than by passive dispersal (Bossenbroek et al. 2001). Overland movement of recreational boats is a strong vector of zebra mussel introductions (De Ventura et al. 2016) but there is still controversy about the relative importance of different pathways of dispersal (Kappes and Haase 2012).

Species Distribution Models (SDM) have proved useful at disentangling the species requirements that drive successful invasions (Gallardo et al. 2013~~2~~; Rose et al. 2016), and can be used to predict range expansions, including those of various freshwater species (Papeş et al. 2016). We used SDMs to examine the macroecological distribution of the zebra mussel in relation to environmental and anthropic variables to better understand the role that human activities might play in its introduction and establishment. We then applied our results at smaller spatial scales, and generated suitability maps based on the probability of occurrence that might be used to prevent the spread of zebra mussel and other invasive bivalves with similar dispersal vectors.

# Methods

## Macroecological-scale model

Our study area was Great Britain, an island of 242,495 Km$^2$ that is relatively isolated to natural colonisation by freshwater invaders and whose first record of zebra mussel was in 1824, when zebra mussel was introduced as live bait (Aldridge et al. 2004). To account for non-linear relationships, we used Generalised Additive Models (GAM) (Hastie, Tibshirani 1990) which are more flexible than Generalized Linear Models and use smoothing functions along the gradients of the variables (Guisan et al. 2002). To examine the distribution of zebra mussel in Great Britain, we fitted a GAM with a logit link function (binomial) using the *mgcv* R package (Wood and Wood 2016) followed by stepwise selection using the *step.gam* function in R (Hastie and Hastie 2015). We compared stepwise model selection with model selection based on REML and null space penalization (Marra and Wood 2011; Wood 2017) using the *mgcv* package in R (Wood and Wood 2016).

We included 30 environmental and anthropic predictors from the invaded region, including climatic predictors relevant to the natural expansion of the species as well as indicators of river accessibility, as discussed in (Rodríguez-Rey et al. 2019) (Table 1). As calcium and pH may limit the distribution of zebra mussel (Ramcharan et al. 1992; Whittier et al. 2008), we used water quality data from the European Environment Agency (available at https://www.eea.europa.eu/data-and-maps/data/waterbase-water-quality) to test their effect on zebra mussel distribution. Only 10% of water quality stations had calcium concentration below 12 mg/l or pH values below 7.1, the limits below which zebra mussel do not occur (Claudi et al. 2012). We therefore assumed that calcium and pH conditions were appropriate for zebra mussel in most of Great Britain. Occurrence records, reported as xy coordinates, were extracted from 5 × 5 km$^2$ grid cells from the NBN Gateway database (http://www.nbn.org.uk/), excluding grid cells with more than 30% of coastal water. This resolution was chosen to cluster occurrences close together and remove spatial bias (Fourcade et al. 2014). Watercourse cartography for rivers was obtained from the Ordnance Survey (available in www.ordnancesurvey.co.uk) which included freshwater rivers, tidal estuaries and canals. We estimated land use predictors within a 50 m buffer strip from the river banks for each cell. We retained predictors with a Variance Inflation Factor smaller than 10 to reduce bias due to collinearity (Chatterjee and Hadi 2006).

**Table 1**

Environmental and anthropogenic predictors, data sources and reasons for inclusion in the m
mussel distribution

| Variable | Description | Reason for inclusion | Data source |
|---|---|---|---|
| *Environmental* | | | |
| ~~Slope~~**Slope** | ~~Mean slope in each grid obtained from a Digital Elevation Model~~**Mean slope in** | ~~Topographic predictor~~**Topographic predictor** | ~~http://www.sharegeo.ac /10672/7~~**http: //www.sharegeo.ac.uk /10672/7** |

Variables in bold with VIF scores smaller than 10 were the only ones retained for analysi

| Variable | Description | Reason for inclusion | Data source |
|---|---|---|---|
| | **each grid obtained from a Digital Elevation Model** | | |
| Bio1 | Annual Mean Temperature | Climatic variable | http://www.worldclim. |
| Bio2 | Mean Diurnal Range (Mean of monthly (max temp - min temp)) | Climatic variable | http://www.worldclim. |
| ~~Bio3~~**Bio3** | ~~Isothermality (Bio2/Bio7) x 100~~**Isothermality (Bio2/Bio7) x 100** | ~~Climatic variable~~**Climatic variable** | ~~http://www.worldclim. /bioclim~~**http://www.worldclim.org/** |
| ~~Bio4~~**Bio4** | ~~Temperature Seasonality (SD x 100)~~**Temperature Seasonality (SD x 100)** | Climatic variable | http://www.worldclim. |
| Bio5 | Max Temperature of Warmest Month | Climatic variable | http://www.worldclim. |
| ~~Bio6~~**Bio6** | ~~Min Temperature of Coldest Month~~**Min Temperature of Coldest Month** | ~~Climatic variable~~**Climatic variable** | ~~http://www.worldclim. /bioclim~~**http://www.worldclim.org/** |
| Bio7 | Temperature Annual Range (Bio5-Bio6) | Climatic variable | http://www.worldclim. |
| ~~Bio8~~**Bio8** | ~~Mean Temperature of Wettest Quarter~~**Mean Temperature of Wettest Quarter** | ~~Climatic variable~~**Climatic variable** | ~~http://www.worldclim. /bioclim~~**http://www.worldclim.org/** |
| ~~Bio9~~**Bio9** | ~~Mean Temperature of Driest Quarter~~**Mean Temperature of Driest Quarter** | ~~Climatic variable~~**Climatic variable** | ~~http://www.worldclim. /bioclim~~**http://www.worldclim.org/** |
| Bio10 | Mean Temperature of Warmest Quarter | Climatic variable | http://www.worldclim. |
| Bio11 | Mean Temperature of Coldest Quarter | Climatic variable | http://www.worldclim. |
| Bio12 | Annual Precipitation | Climatic variable | http://www.worldclim. |

Variables in bold with VIF scores smaller than 10 were the only ones retained for analysi

| Variable | Description | Reason for inclusion | Data source |
|---|---|---|---|
| Bio13 | Precipitation of Wettest Month | Climatic variable | http://www.worldclim. |
| Bio14 | Precipitation of Driest Month | Climatic variable | http://www.worldclim. |
| ~~Bio15~~**Bio15** | ~~Precipitation Seasonality (CV)~~**Precipitation Seasonality (CV)** | ~~Climatic variable~~**Climatic variable** | ~~http://www.worldclim. /bioclim~~**http: //www.worldclim.org/** |
| Bio16 | Precipitation of Wettest Quarter | Climatic variable | http://www.worldclim. |
| Bio17 | Precipitation of Driest Quarter | Climatic variable | http://www.worldclim. |
| ~~Bio18~~**Bio18** | ~~Precipitation of Warmest Quarter~~**Precipitation of Warmest Quarter** | ~~Climatic variable~~**Climatic variable** | ~~http://www.worldclim. /bioclim~~**http: //www.worldclim.org/** |
| Bio19 | Precipitation of Coldest Quarter | Climatic variable | http://www.worldclim. |
| ~~Land~~**Land** | ~~Percentage of grassland in a 100 m buffer along the river~~**Percentage of grassland in a 100 m buffer along the river** | ~~Indicator of conservation of riparian vegetation~~**Indicator of conservation of riparian vegetation** | ~~CORINE Land Cover~~**C Land Cover** ~~http://land.copernicus. european~~**http: //land.copernicus.eu/p european** |
| *Anthropogenic* | | | |
| ~~Pop~~**Pop** | ~~Population density~~**Population density** | ~~Indicator of human pressure~~**Indicator of human pressure** | ~~Diva-GIS~~**Diva-GIS** ~~http://www.diva-gis.or~~ **//www.diva-gis.org/Da** |
| ~~Road~~**Road** | ~~Kilometres of road~~**Kilometres of road** | ~~Indicator of human accessibility~~**Indicator of human accessibility** | ~~https://www.ordnances /~~**https: //www.ordnancesurve** |
| ~~d_intro~~**d_intro** | ~~Euclidean distance to location of first reported record~~**Euclidean distance to location of first reported record** | ~~To account for spatially-correlated patterns of dispersal~~**To account for spatially-correlated patterns of dispersal** | ~~https://data.nbn.org.uk~~ **//data.nbn.org.uk**/ an ~~http://www.nonnatives /factsheet/~~**http: //www.nonnativespeci /factsheet/** |

Variables in bold with VIF scores smaller than 10 were the only ones retained for analysi

| Variable | Description | Reason for inclusion | Data source |
|---|---|---|---|
| ~~d_city~~**d_city** | ~~Euclidean distance to cities with more than 50,000 habitants from 2011 census~~**Euclidean distance to cities with more than 50,000 habitants from 2011 census** | ~~Indicator of human pressure~~**Indicator of human pressure** | ~~Own creation based on Office of National Stat~~**creation based on dat Office of National Sta** |
| ~~d_aqua~~**d_aqua** | ~~Euclidean distance to closest aquaculture facility~~**Euclidean distance to closest aquaculture facility** | ~~Indicator of pressure from AIS~~**Indicator of pressure from AIS** | ~~Own creation~~**Own crea** |
| ~~d_boat~~**d_boat** | ~~Euclidean distance to closest boat ramp~~**Euclidean distance to closest boat ramp** | ~~Indicator of accessibility and propagule pressure~~**Indicator of accessibility and propagule pressure** | ~~http://www.boatlaunch. /#/map~~**http: //www.boatlaunch.co.** |
| ~~d_port~~**d_port** | ~~Euclidean distance to closest port~~**Euclidean distance to closest port** | ~~Indicator of accessibility and propagule pressure~~**Indicator of accessibility and propagule pressure** | ~~https://www.sharegeo.a /~~**https://www.sharegec** |

Variables in bold with VIF scores smaller than 10 were the only ones retained for analysi

Records of zebra mussel occurrences were collated from different sources, including detections by trained volunteers and records from government agencies as described in Roy et al. (2014). Most records were derived from monitoring centres which ensures a more frequent and reliable survey. For bivalves, a positive detection usually means full establishment because it is unusual to record single specimens.

We corrected for sampling bias (i.e. the error that occurs when more accessible or more conspicuous species are more likely to be detected (Araujo and Guisan 2006) by using the inverse p-weighted bias correction (Fourcade et al. 2014). This approach adjusts the model by weighting the sample points according to the inverse of the probability of inclusion in the sample. We used information on sampling effort to downweigh those sites that were more likely to have been sampled, based on the target group sampling method developed by Phillips et al. (2009). In this approach, occurrence data from a pool of species that are sampled with similar techniques are used to create a map of sampling effort in different areas. The species included in the pool were the freshwater pearl mussel (*Margaritifera margaritifera*), the Asian clam (*Corbicula fluminea*) and the quagga mussel (*Dreissena bugensis*).

We evaluated each model using a temporal independent validation (i.e. data from different time periods) (Dobrowski et al. 2011; Rodríguez-Rey et al. 2019; Svenning et al. 2011). For that purpose, we split the presence data into training and testing data sets based on the time period the species was first recorded. We selected the 70% oldest records for training and the 30% youngest records for testing, which is a more robust procedure than simply choosing training and testing data based on random splitting (Araújo et al. 2005; Jiménez-Valverde et al. 2011; Roberts et al. 2017). We selected ten times more absences than presences in the training database and the same number of absences and presences in the testing database. Therefore, the number of presences and absences in the training dataset were 376 and 3760 respectively, and 161 and 161 in the testing dataset. Our temporal database only included occurrences, so absences were not temporally split but randomly selected instead [called pseudoabsences, (Barbet-Massin et al. 2012)].

Spatial autocorrelation may pose a problem in SDMs as it tends to generate inflated model results (spatial sorting bias, (Hijmans 2012). We removed this bias by pairwise distance sampling on the evaluation data (testing). We paired the testing presences and absences that had the greatest distance to their nearest training presence using the *dismo* R package with a distance threshold of 0.1 (Hijmans et al. 2016) (Figure S2). Predictive ability was assessed using True Skills Statistic (TSS), with a threshold that maximizes both sensitivity and specificity, and the Area Under the Curve (AUC) for the final model, and this was compared to a null model based on 500 random permutations of the predictors (Börger and Nudds 2014). Variable importance was calculated accounting for the correlation structure between predictors with the *VarImp* function in the ‘caret’ R package (Williams et al. 2017) and assessed by inspection of partial plots of the predictors. To illustrate the application of our results, we generated suitability maps based on best model fits and predicted the probability of occurrence across the entire study area.

## Fine-scale model

To investigate the pattern of zebra mussel dispersal at a finer spatial scale, we examined four watersheds with high boating activity (Thames, Severn, Stour, and Avon). The aim was to test whether boat ramps affected zebra mussel dispersal at a local scale. For each watershed, we calculated the weighted distance ($\sum 1/d$) from each sampling site to the four nearest boat ramps (upstream and downstream) to obtain an index of propagule pressure (Consuegra et al. 2011). We then modelled the distribution of zebra mussel (as in the coarse-scale model) as a function of both propagule pressures (upstream and downstream), altitude and watershed identity, using a generalized additive model with a binomial logit link. We included altitude to account for longitudinal variation (i.e. stream order) as altitude is positively related to slope and to water velocity in streams (Vannote et al. 1980). We used the *step* function in R to derive a minimal adequate model based on AIC criteria and refitted with a quasi-binomial link to account for overdispersion and compared with the REML selection approach implemented in the *mgcv* package in R (Wood and Wood 2016) as for the model in the whole of Great Britain.

# Results

## Macroecological-scale model

A model containing 6 anthropogenic and 6 bioclimatic predictors explained the distribution of zebra mussel significantly better than chance (Table 2; TSS model = 0.2658, TSS null = 0.1709; AUC model = 0.6654, AUC null = 0.5830) across the whole study area (Fig. 1). Distance to boat ramps and to cities with more than 50,000 inhabitants were the most influential predictors, explaining 26.96% and 17.12% of variation in zebra mussel occurrence, respectively (Fig. 2).

**Table 2**

Parameter estimates for the minimal adequate generalized additive model (GAM) fitted with a binomial link to assess the relationship between zebra mussel occurrence (presence/absence) and various environmental and anthropogenic predictors

| | Estimate | Std. Error | z value | p-value |
|---|---|---|---|---|

Discrepancies between stepwise selection and REML from mgcv package are reported with (*) when the methods differ in the inclusion of the smooth term or by (#) if the methods differ in the inclusion of the term

| | **Estimate** | **Std. Error** | **z value** | **p-value** |
|---|---|---|---|---|
| (Intercept) | -20.17 | 4.96 | -4.066 | < 0.0001 |
| bio6* | 0.1198 | 0.0283 | 4.237 | < 0.0001 |
| bio18* | 0.0276 | 0.0051 | 5.380 | < 0.0001 |
| d_city* | 0.0001 | 0.000001 | -10.372 | < 0.0001 |
| d_aqua | 4.533 | 1.472 | 3.080 | 0.0021 |
| **Terms** | **Edf** | **Ref.df** | **Chi.sq** | **p-value** |
| s(d_intro) | 5.332 | 9 | 52.52 | < 0.0001 |
| s(slope) | 4.819 | 9 | 33.18 | < 0.0001 |
| s(bio4) | 5.068 | 9 | 40.61 | < 0.0001 |
| s(bio8) | 5.919 | 9 | 34.25 | < 0.0001 |
| s(bio15) | 6.614 | 9 | 47.72 | < 0.0001 |
| s(pop) | 6.095 | 9 | 46.21 | < 0.0001 |
| s(d_boat) | 2.945 | 9 | 172.28 | < 0.0001 |
| s(d_port) | 7.555 | 9 | 87.20 | < 0.0001 |

Discrepancies between stepwise selection and REML from mgcv package are reported with (*) when the methods differ in the inclusion of the smooth term or by (#) if the methods differ in the inclusion of the term

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**Fig. 1**

GAM model predictions of the probability of occurrence of zebra mussel for a model including all the predictors

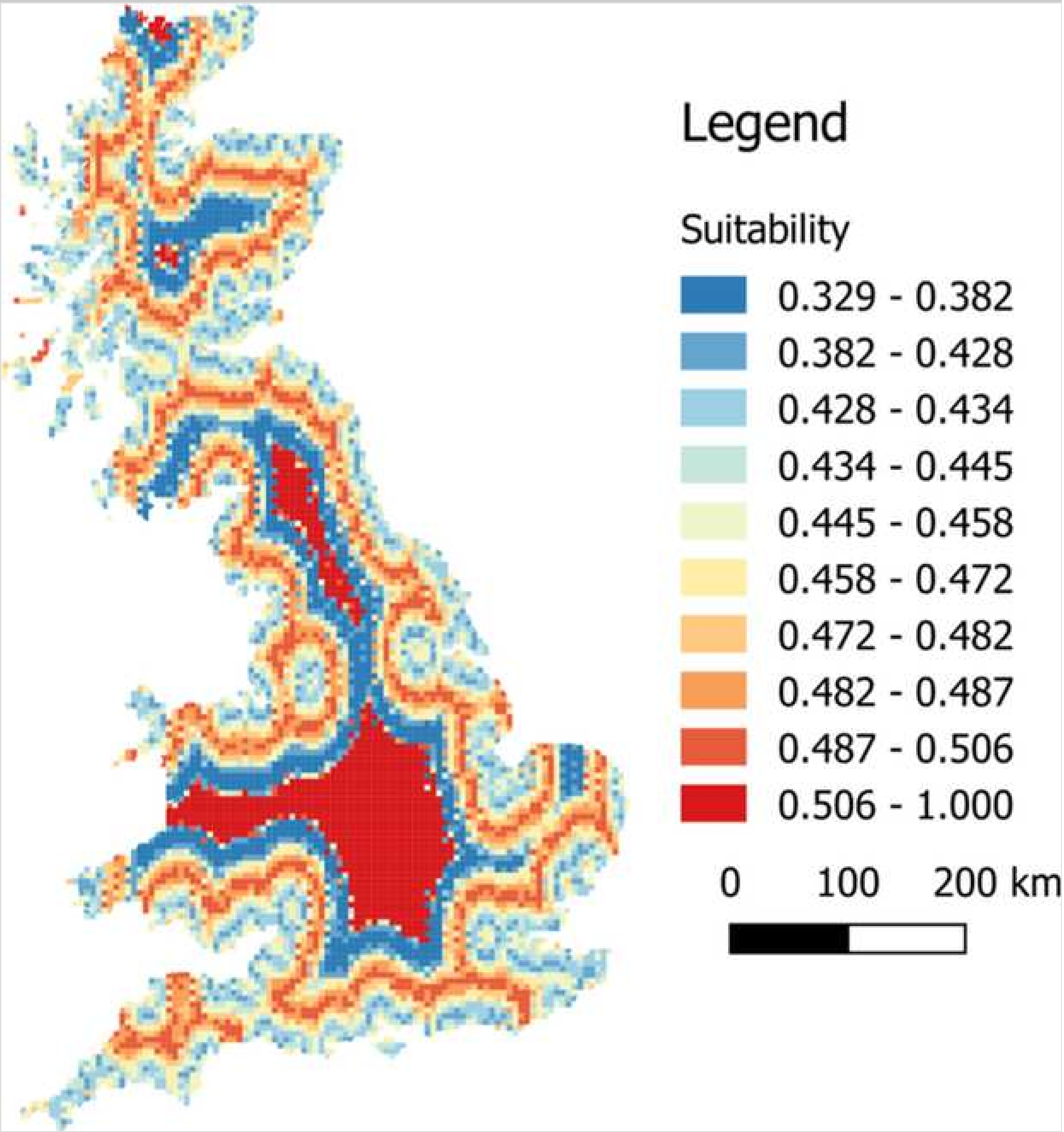
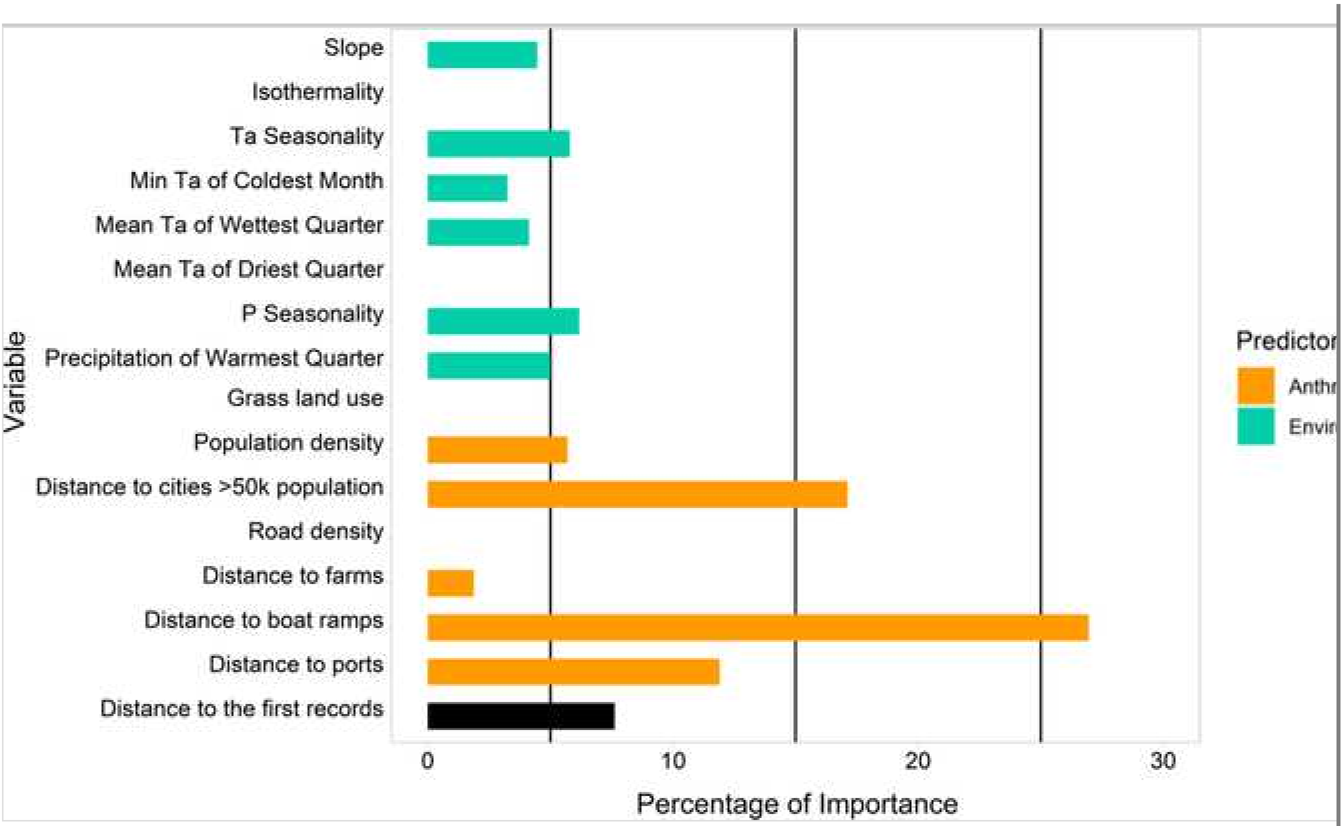


**Fig. 2**

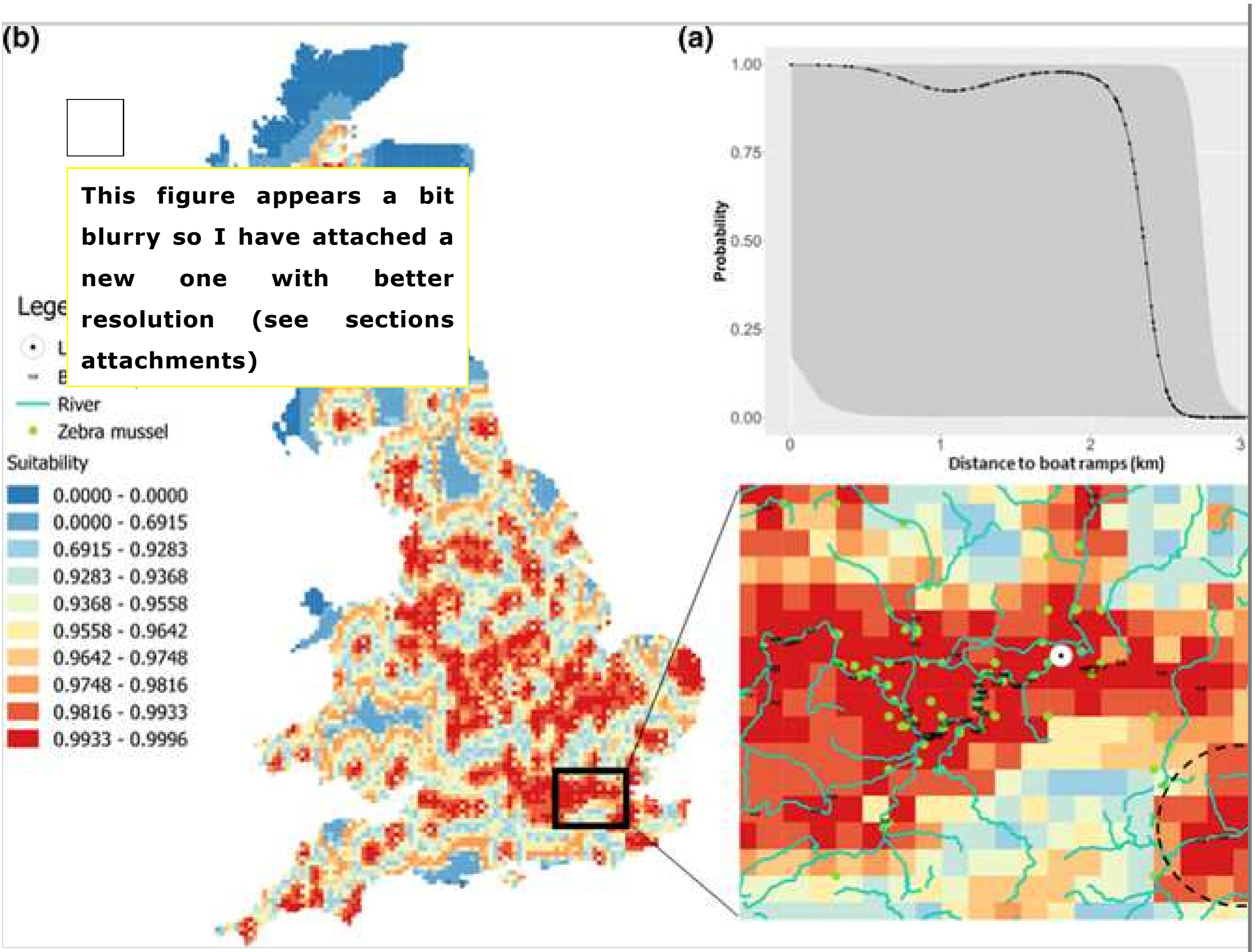
Relative importance of environmental and anthropic predictors of zebra mussel distribution in Great Britain based on Generalized Additive Model (GAM)



The probability of finding zebra mussel was highest within 3 km from the location of boat ramps, once the effects of other confounding factors were statistically controlled for (Fig. 3a). A suitability map, generated using the location of boat ramps while controlling for other significant predictors, identified locations currently without zebra mussel that have a high risk of becoming invaded (Fig. 3b). Such high risk or suitable areas are areas where prevention can be prioritised (the dashed area in inset Fig. 3b) and serve to illustrate the application of our findings for management.

**Fig. 3**

Generalized Additive Model predictions (± 95 CI envelope) of the effect of distance to boat ramps on probability of occurrence of zebra mussel (**a**), and **b** suitability map of zebra mussel vulnerability. Inset shows close-up of the Thames River as an example of a high risk area that has not yet been invaded (dashed line), and should be targeted for monitoring and prevention



This figure appears a bit blurry so I have attached a new one with better resolution (see sections attachments)

## Fine-scale model

The most plausible model of zebra mussel occurrence at fine spatial scale according to both methods of variable selection included upstream propagule pressure (edf = 1.71, SE = 0.743, $t = 2.30$, $P = 0.023$) and altitude (edf = − 0.015, SE = 0.005, $t = -2.93$, $P = 0.004$) as predictors. The number of $5 \times 5\ \text{km}^2$ grid cells between sampling sites and boat ramp localities ranged between 0 and 32 along the watershed.

# Discussion

The zebra mussel is one of the most damaging and difficult to control freshwater invaders (Strayer 2009), making the identification of areas at risk of invasion of paramount importance for management (Kappes and Haase 2012; Strayer 2009). We have shown how this can be achieved by considering only a few predictors, of which the location of boat ramps is by far the most important. Other modelling approaches, like spatially explicit gravity models, have also forecasted the dispersal of invasive species by assuming that movement is based on human transportation (Hui and Richardson 2017). For example, overland boat movements or boat traffic predict the spread of zebra mussel (Bossenbroek et al. 2007; Bossenbroek et al. 2001; Padilla et al. 1996) highlighting the potential role of boat ramps (Leung et al. 2006).

Boating is a main vector for the spread of many other aquatic invasive species, including the spiny water flea (MacIsaac et al. 2004), the macrophyte *Cabomba caroliniana* (Jacobs, Macisaac 2009), the Eurasian watermilfoil (Buchan, Padilla 2000), and zooplankton discharged from ballast water (Kelly et al. 2013). Our study highlights the fact that although environmental variables explain almost half of the variation in zebra mussel occurrence, consideration of anthropic drivers holds the key for preventing further spread (Sousa et al. 2014).

Ports can be important vectors for the introduction of zebra mussel (Minchin et al. 2005), but in our study they were less relevant than boat ramps, possibly because zebra mussel cannot survive in places with high salinity (Sylvester et al. 2013). Proximity to large cities also affected the distribution of zebra mussel in our study, suggesting that water bodies around urban areas may be more prone to be invaded. However, road density was not a significant predictor of zebra mussel presence and population density only explained 5.7% of the variation, highlighting the role that water sports—and not merely human pressure - play in the distribution of zebra mussel (Bossenbroek et al. 2007; Kappes and Haase 2012). This also suggests that sampling bias in our data must have been low, as road and population density are usually good proxies of sampling effort (Block et al. 2016).

Zebra mussel can disperse during all life stages, and passive drift as well as other dispersal and gravity models have been used to predic its downstream dispersal (Bossenbroek et al. 2001). However, the species can also survive in damp conditions outside the water for at least 5–7 days (Ricciardi et al. 1998; Ricciardi et al. 1995) and can be readily transported upstream between waterways by anglers, canoeists, motorboats and occasionally, birds (Carlton 1993; Matthews et al. 2014). Anglers and canoeists in Great Britain typically visit 2–3 different catchments more than once a week and only few clean or dry their equipment (Anderson et al. 2014). This probably makes overland transport one of the main routes of dispersal of zebra musel, as noted in other study areas (Bossenbroek et al. 2007; De Ventura et al. 2016; Johnson et al. 2001), along with recreational boats (Bacela-Spychalska et al. 2013; De Ventura et al. 2016). Great Britain has more than 3000 miles of canals and navigable rivers, and more than 340 registered river boats (Zhou et al. 2003), making boating a very popular activity. Our fine scale study of four catchments indicates that distance upstream of boat ramps was a significant predictor of zebra mussel occurrence. This may reflect the uptake by anglers and canoeists, as well as the impoundment associated with barriers and barrages, where boat ramps are typically located, and which provide ideal conditions for the establishment of zebra mussel (Aldridge 2010; Strayer 2009).

Our modelling approach has made it possible to identify several factors responsible for the spread of zebra mussel, and through the use of suitability maps, identify areas at high risk of invasion where biosecurity measures are most needed. Such measures could range from the installation of cleaning facilities to the closure of particular boat ramps or limitations on boating at vulnerable locations, where invasion by zebra mussel could pose risks to sensitive infrastructures, such as power or water treatment plants. Hot pressure washing seems to be the only efficient method of disinfecting zebra mussel from equipment (Anderson et al. 2014; Morse 2009), and our risk mapping approach could be used to inform the location of cleaning stations at localities with a high risk of invasion. For example, suitability mapping might particularly be useful for deploying mobile decontamination stations in response to boat traffic, like those being deployed in the US (United States Department of Interior 2019), or in the case of many European countries which lag behind in preventive measures regarding bivalves invasions (De Ventura et al. 2016).

Management of zebra mussel rests heavily on the identification of uninfected locations and on managing and reducing risks (Invasive Mussel Collaborative 2018), (United States Department of Interior 2019). Although our study reflects the application of suitability maps to the spread of zebra mussel in Great Britain alone, the generation of risk maps that consider boat ramps might also prove useful for other species and contexts, given the widespread influence that water sports have on the dispersal of invasive bivalves with similar vectors of introduction (e.g. the quagga mussel or the Asian clam) (Anderson et al. 2014; Bidwell et al. 2010).

In conclusion, we have shown that boat ramps favour the dispersal of the highly invasive zebra mussel and illustrate how suitability maps could be used by managers for prevention purposes, the preferred management strategy for invasive species (Simberloff et al. 2013). Explicit consideration of risk factors should improve the efficacy of control measures, by targetting those locations most vulnerable to invasions.

### Publisher’s note

### Author contributions

M.R-R., C.G.L and S.C. conceived the idea. M.R-R. compiled and curated the data and M.R-R., C.G.L. and L.B analysed the data. S.C. obtained the funding. All authors interpreted the outputs, contributed to manuscript writing, gave approval for publication and agree to be accountable for any question related to this work.

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### Availability of data and material and Code availability

The data used is derived from public domain resources and available in Online Supplementary Material.

### Compilance with ethical standards

*Conflict of Interest*   The authors have no conflict of interest.

## Electronic supplementary material

Below is the link to the electronic supplementary material.

Supplementary Material 1

# References

Aldridge DC (2010) *Dreissena polymorpha* in Great Britain: history of spread, impacts and control. In: van der Velde G, Rajagopal S and bij de Vaate A (eds) The Zebra Mussel in Europe. Backhuys Publishers, Leiden, pp. 79–91

Aldridge DC, Elliott P, Moggridge GD (2004) The recent and rapid spread of the zebra mussel (*Dreissena polymorpha*) in Great Britain. Biol Cons 119:253–261

Aldridge DC, Elliott P, Moggridge GD (2006) Microencapsulated BioBullets for the control of biofouling zebra mussels. Environmental Science Technology 40:975–979

Anderson LG, White PCL, Stebbing PD et al (2014) Biosecurity and vector behaviour: evaluating the potential threat posed by anglers and canoeists as pathways for the spread of invasive non-native species and pathogens. Plos One 9:e92788

Araujo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. J Biogeogr 33:1677–1688

Araújo MB, Pearson RG, Thuiller W et al (2005) Validation of species–climate impact models under climate change. Glob Change Biol 11:1504–1513

Bacela-Spychalska K, Grabowski M, Rewicz T et al (2013) The ‘killer shrimp’*Dikerogammarus villosus* (Crustacea, Amphipoda) invading Alpine lakes: overland transport by recreational boats and scuba-diving gear as potential entry vectors? Aquatic Conservation: Marine and Freshwater Ecosystems 23:606–618

Barbet-Massin M, Jiguet F, Albert CH et al (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 3:327–338

Bidwell J, Van der Velde G, Rajagopal S et al (2010) Range expansion of

Dreissena polymorpha: a review of major dispersal vectors in Europe and North America. The zebra mussel in Europe. Backhuys Publishers, Leiden, pp 69–78

Bielen A, Bošnjak I, Sepčić K et al (2016) Differences in tolerance to anthropogenic stress between invasive and native bivalves. Science of The Total Environment 543:449–459

Block S, Saltré F, Rodríguez-Rey M et al (2016) Where to dig for fossils: Combining climate-envelope, taphonomy and discovery models. PloS one 11:e0151090

Börger L, Nudds TD (2014) Fire, humans, and climate: modeling distribution dynamics of boreal forest waterbirds. Ecol Appl 24:121–141

Bossenbroek JM, Johnson LE, Peters B et al (2007) Forecasting the expansion of zebra mussels in the United States. Conserv Biol 21:800–810

Bossenbroek JM, Kraft CE, Nekola JC (2001) Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. Ecol Appl 11:1778–1788

Buchan LAJ, Padilla DK (2000) Predicting the likelihood of Eurasian Watermilfoil presence in lakes, a macrophyte monitoring tool. Ecol Appl 10:1442–1455

Carlton JT (1993) Dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*). In: Nalepa TF, Schloesser DW (eds) Zebra Mussels: Biology, Impacts, and Control. Lewis Publisher, Chelsea, pp 677–697

Chatterjee S, Hadi AS (2006) Regression analysis by example. John Wiley & Sons

Claudi R, Graves A, Taraborelli AC et al (2012) Impact of pH on survival and settlement of dreissenid mussels. Aquatic Invasions 7

Consuegra S, Phillips N, Gajardo G et al (2011) Winning the invasion roulette: Escapes from fish farms increase admixture and facilitate establishment of non-native rainbow trout. Evol Appl 4:660–671

De Ventura L, Weissert N, Tobias R et al (2016) Overland transport of recreational boats as a spreading vector of zebra mussel *Dreissena polymorpha*. Biol Invasions 18:1451–1466

Dobrowski SZ, Thorne JH, Greenberg JA et al (2011) Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. Ecol Monogr 81:241–257

Fagan WF (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83:3243–3249

Fourcade Y, Engler JO, Rödder D et al (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. Plos One 9:e97122

Gallardo B, Aldridge DC (2015) Is Great Britain heading for a Ponto–Caspian invasional meltdown? J Appl Ecol 52:41–49

Guisan A, Edwards TC Jr, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Model 157:89–100

Hastie T, Hastie MT (2015) Package ‘gam’. GAM Package CRAN, cran. r-project. http://www.org/web/packages/gam/gam.pdf

Hastie T, Tibshirani R (1990) Exploring the nature of covariate effects in the proportional hazards model. Biometrics:1005–1016

Havel JE, Kovalenko KE, Thomaz SM et al (2015) Aquatic invasive species: challenges for the future. Hydrobiologia 750:147–170

Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93:679–688

Hijmans RJ, Phillips S, Leathwick J et al (2016) Package ‘dismo’. Circles 9:1

Hui C, Richardson DM (2017) Invasion dynamics. Oxford University Press

Hulme PE (2016) Climate change and biological invasions: evidence, expectations, and response options. Biol Rev 92:1297–1313

Invasive Mussel Collaborative (2018) Strategy to Advance Management of Invasive Zebra and Quagga Mussels

Jacobs MJ, Macisaac HJ (2009) Modelling spread of the invasive macrophyte *Cabomba caroliniana*. Freshw Biol 54:296–305

Jiménez-Valverde A, Peterson AT, Soberón J et al (2011) Use of niche models in invasive species risk assessments. Biol Invasions 13:2785–2797

Johnson LE, Ricciardi A, Carlton JT (2001) Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. Ecol Appl 11:1789–1799

Kappes H, Haase P (2012) Slow, but steady: dispersal of freshwater molluscs. Aquat Sci 74:1–14

Kelly NE, Wantola K, Weisz E et al (2013) Recreational boats as a vector of secondary spread for aquatic invasive species and native crustacean zooplankton. Biol Invasions 15:509–519

Leung B, Bossenbroek JM, Lodge DM (2006) Boats, pathways, and aquatic biological invasions: estimating dispersal potential with gravity models. Biol Invasions 8:241–254

Lowe S, Browne M, Boudjelas S et al (2000) 100 of the world’s worst invasive alien species: a selection from the global invasive species database

MacIsaac HJ, Borbely JV, Muirhead JR et al (2004) Backcasting and forecasting biological invasions of inland lakes. Ecol Appl 14:773–783

Marra G, Wood SN (2011) Practical variable selection for generalized additive models. Comput Stat Data Anal 55:2372–2387

Matthews J, Van der Velde G, Bij de Vaate A et al (2014) Rapid range expansion of the invasive quagga mussel in relation to zebra mussel presence in The Netherlands and Western Europe. Biol Invasions 16:23–42

Mckindsey CW, Landry T, O'Beirn FX et al (2007) Bivalve aquaculture and exotic species: a review of ecological considerations and management issues. Journal of Shellfish Research 26:281–294

Meyerson LA, Reaser JK (2003) Bioinvasions, bioterrorism, and biosecurity. Front Ecol Environ 1:307–314

Minchin D, Lucy F, Sullivan M (2005) Ireland: a new frontier for the zebra mussel *Dreissena polymorpha* (Pallas). Oceanological hydrobiological studies 34:19–30

Morse JT (2009) Assessing the effects of application time and temperature on the efficacy of hot-water sprays to mitigate fouling by *Dreissena polymorpha* (zebra mussels Pallas). Biofouling 25:605–610

NBN Atlas (2018) National Biodiversity Network. NBN Atlas website at http://www.nbnatlas.org

Oreska MP, Aldridge DC (2011) Estimating the financial costs of freshwater invasive species in Great Britain: a standardized approach to invasive species costing. Biol Invasions 13:305–319

Padilla DK, Chotkowski MA, Buchan LA (1996) Predicting the spread of zebra mussels (*Dreissena polymorpha*) to inland waters using boater movement patterns. Global Ecology and Biogeography Letters:353–359

Phillips SJ, Dudík M, Elith J et al (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol Appl 19:181–197

Ramcharan CW, Padilla DK, Dodson SI (1992) Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Can J Fish Aquat Sci 49:2611–2620

Ricciardi A, Neves RJ, Rasmussen JB (1998) Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. J Anim Ecol 67:613–619

Ricciardi A, Serrouya R, Whoriskey FG (1995) Aerial exposure tolerance off zebra and quagga mussels (Bivalvia: Dreissenidae): implications for overland dispersal. Can J Fish Aquat Sci 52:470–477

Roberts DR, Bahn V, Ciuti S et al (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929

Rodríguez-Rey M, Consuegra S, Börger L et al (2019) Improving Species Distribution Modelling of freshwater invasive species for management applications. Plos One 14:e0217896

Roy HE, Preston CD, Harrower CA et al (2014) GB Non-native Species Information Portal: documenting the arrival of non-native species in Britain. Biol Invasions 16:2495–2505

Simberloff D, Martin J-L, Genovesi P et al (2013) Impacts of biological invasions: what’s what and the way forward. Trends Ecol Evol 28:58–66

Sousa R, Novais A, Costa R et al (2014) Invasive bivalves in fresh waters: impacts from individuals to ecosystems and possible control strategies. Hydrobiologia 735:233–251

Strayer DL (2009) Twenty years of zebra mussels: lessons from the mollusk that made headlines. Front Ecol Environ 7:135–141

Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshw Biol 55:152–174

Svenning J-C, Fløjgaard C, Marske KA et al (2011) Applications of species distribution modeling to paleobiology. Quatern Sci Rev 30:2930–2947

Sylvester F, Cataldo DH, Notaro C et al (2013) Fluctuating salinity improves survival of the invasive freshwater golden mussel at high salinity: implications for the introduction of aquatic species through estuarine ports. Biol Invasions 15:1355–1366

United States Department of Interior (2019) Safeguarding the West from Invasive Species. United States Department of Interior

Vannote RL, Minshall GW, Cummins KW et al (1980) The river continuum concept. Can J Fish Aquat Sci 37:130–137

Whittier TR, Ringold PL, Herlihy AT et al (2008) A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena spp*). Front Ecol Environ 6:180–184

Williams CK, Engelhardt A, Cooper T et al (2017) Package ‘caret’

Wood S, Wood MS (2016) Package ‘mgcv’. R package version:1.7–29

Wood SN (2017) Generalized additive models: an introduction with R. CRC press

Zhou P, Fet A, Michelsen O et al (2003) A feasibility study of the use of biodiesel in recreational boats in the United Kingdom. Proceedings of the Institution of Mechanical Engineers, Part M: Journal of Engineering for the Maritime Environment 217:149–158

Katharina Heiler, Abraham bij de Vaate, Klemens Ekschmitt, Parm von Oheimb, Christian Albrecht, Thomas Wilke, (2013) Reconstruction of the early invasion history of the quagga mussel (Dreissena rostriformis bugensis) in Western Europe. Aquatic Invasions 8 (1):53-57

Belinda Gallardo, Philine S. E. zu Ermgassen, David C. Aldridge, Joseph Veech, (2013) Invasion ratcheting in the zebra mussel ( ) and the ability of native and invaded ranges to predict its global distribution . Journal of Biogeography 40 (12):2274-2284

Alexander Y. Karatayev, Lyubov E. Burlakova, Dianna K. Padilla, (2015) Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746 (1):97-112

Peter M. Rose, Mark J. Kennard, David B. Moffatt, Fran Sheldon, Gavin L. Butler, Vincent Laudet, (2016) Testing Three Species Distribution Modelling Strategies to Define Fish Assemblage Reference Conditions for Stream Bioassessment and Related Applications. PLOS ONE 11 (1):e0146728

Monica Papeş, John E. Havel, M. Jake Vander Zanden, (2016) Using maximum entropy to predict the potential distribution of an invasive freshwater snail. Freshwater Biology 61 (4):457-471