

## Europe's top 10 invasive species: relative importance of climatic, habitat and socio-economic factors

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Using a representative set of 10 of the worst invasive species in Europe, this study investigates the relative importance of climatic, habitat and socio-economic factors in driving the occurrence of invasive species. According to the regression models performed, these factors can be interpreted as multi-scale filters that determine the occurrence of invasive species, with human degradation potentially affecting the performance of the other two environmental filters. Amongst climate factors, minimum temperature of the coldest month was one of the most important drivers of the occurrence of Europe's worst freshwater and terrestrial invaders like the red swamp crayfish (*Procambarus clarkii*), Bermuda buttercup (*Oxalis pes-caprae*) and Sika deer (*Cervus nippon*). Water chemistry (alkalinity, pH, nitrate) determines the availability of habitat and resources for species at regional to local levels and was relevant to explain the occurrence of aquatic and semi-aquatic invaders such as the brook trout (*Salvelinus fontinalis*) and Canada goose (*Branta canadensis*). Likewise, nitrate and chlorophyll-*a* concentration were important determinants of marine invaders like the bay barnacle (*Balanus improvisus*) and green sea fingers (*Codium fragile*). Most relevant socio-economic predictors included the density of roads, country gross domestic product (GDP), distance to ports and the degree of human influence on ecosystems. These variables were particularly relevant to explain the occurrence of the zebra mussel (*Dreissena polymorpha*) and coypu (*Myocastor coypu*), species usually associated to disturbed environments. The Japanese kelp (*Undaria pinnatifida*) was generally distributed much closer to ports than the other two marine organisms, although insufficient information on human impacts prevented a correct assessment of the three marine species. In conclusion, this study shows how socio-economic development is associated with the presence of the top 10 worst European invasive species at a continental scale, and relates this fact to the provision and transport of propagules and the degradation of natural habitats that favour the establishment of invasive species.

KEY WORDS: cold tolerance, country GDP, Europe, human influence index, logistic model, port, road density.

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## INTRODUCTION

The pan-European project Delivering Alien Invasive Species Inventories for Europe (DAISIE, <http://www.europe-aliens.org>) reported that a total of 12,000 non-native species are currently present in Europe, which is probably an underestimation of the real figure (DAISIE 2009). Some of the most abundant groups include plants, fish and crustaceans that come predominantly from Asia and the Americas. Their mechanisms of introduction are variable depending on the species but they are all directly or indirectly related to global trade, transport and human presence. Moreover, in their invaded range, species tend to be associated with human-modified ecosystems – such as urban or agricultural lands – stressing the link between invasive species and socio-economic development (DAISIE 2009). Amongst the thousands of invasive species currently thriving in Europe, VILÀ et al. (2010) identified the top 10 worst organisms in terms of variety of ecological and economic impacts. The list included four terrestrial: the Canada goose (*Branta canadensis* Linnaeus 1758), Sika deer (*Cervus nippon* Temminck 1838), coypu (*Myocastor coypus* Molina 1782) and Bermuda buttercup (*Oxalis pes-caprae* Linnaeus 1753); three freshwater: the zebra mussel (*Dreissena polymorpha* Pallas 1771), red swamp crayfish (*Procambarus clarkii* Girard 1852) and brook trout (*Salvelinus fontinalis* Mitchell 1814); and three marine organisms: the bay barnacle (*Balanus improvisus* Darwin 1854), green sea fingers (*Codium fragile tomentosoides* P.C. Silva 1955) and Japanese kelp (*Undaria pinnatifida* (Harvey) Suringar 1873). These top 10 species have numerous multilevel impacts. By way of example, *P. clarkii* has decimated its European counterparts through competition and parasite transmission (HOLDICH & PÖCKL 2007); the costs associated to remove *D. polymorpha* from intake pipes and other water facilities are in the multimillions (ORESKA & ALDRIDGE 2011); both *C. nippon* and *B. canadensis* are known to hybridize with native species, posing a serious threat to the conservation of genetic diversity (CORBET & HARRIS 1991; REHFISCH et al. 2010). A complete discussion of the impacts on ecosystem services of these 10 representative species can be found in McLAUGHLAN et al. (2013). In spite of multiple calls from the research community to increase our understanding of biological invasions (most recently, SIMBERLOFF 2013), almost nothing is known about the large-scale factors driving the distribution of 90% of Europe's worst invasive species (VILÀ et al. 2010). This study makes use of this representative list of 10 species to investigate the relative importance of climatic, habitat and socio-economic factors in driving the large-scale occurrence of invasive species in Europe.

Temperature and precipitation are major climatic constraints to the global distribution of species that have traditionally been used to delineate the biogeographic regions available to certain species (HIJMANS & GRAHAM 2006). However, invasive species have often challenged the idea of a fixed environmental niche by expanding their areas of distribution towards new climates, exhibiting extraordinary adaptation capabilities (PEARMAN et al. 2008). Climate may thus be insufficient to accurately describe the potential distribution of invasive species. Habitat characteristics such as geomorphology, water chemistry and vegetation condition are also important regional-scale determinants of invasive species occurrence (LOO et al. 2009). However, drivers controlling the global-scale spread of invasive species fundamentally differ from those of native species in that their transport and introduction depend on socio-economic activities (PYSEK et al. 2010; ESSL et al. 2011). Transport, trade and tourism are directly associated with the pathways of introduction and eventually the establishment and spread of invasive species (HULME 2009). For instance, sea ports, a classic symbol of trade and economic development, are

important gateways for invasive species that arrive as imports (e.g. plants and animals), contaminants of products (e.g. timber pathogens) or stowaways (e.g. ship hull fouling or transport with ballast water) (HULME 2009). Roads, railways and canals represent potential corridors along which invasive species spread with and without human intervention (GOZLAN et al. 2009). As well as providing an entrance point, ports, roads, railways and canals are highly disturbed areas, providing an artificial environment where invasive species can establish and increase in abundance (BAX et al. 2003). Consequently, socio-economic factors can be related not only to transport and propagule pressure, but also to the vulnerability of ecosystems to invasion, since invasive species are tolerant of a wider range of environmental stress and are often able to capitalize on the excess of nutrients derived from human activities. For instance, population density and human wealth have been associated with increasing rates of invasion at both continental (e.g. TAYLOR & IRWIN 2004; PYSEK et al. 2010) and national (e.g. KELLER et al. 2009) scales, as they are associated with a more intense use of ecosystems and habitat degradation. Furthermore, recent investigations suggest that current spatio-temporal patterns of invasion are the result of economic activity and the following species invasions from decades ago (*sensu* invasion debt, ESSL et al. 2011). We should therefore expect that the probability of invasion be due jointly to factors related to climate, habitat and socio-economic development, all of which need to be integrated in risk assessments (PYSEK et al. 2010; GALLARDO & ALDRIDGE 2013).

While the relationship between invasive species and socio-economic factors has been explored before, studies have been mostly conducted at the local scale, and when using large continental scales, they have often relied on regional or country-level information (e.g. TAYLOR & IRWIN 2004; PYSEK et al. 2010). By using geographical information at a high resolution (1 km<sup>2</sup>), this study provides accurate insights into the geographic correlation between invasive species occurrence and several climate, habitat and socio-economic indicators at a continental scale.

## METHODS

### *Data gathering*

*Species occurrence.* Geo-referenced information on the top 10 worst invasive species occurrence in Europe (latitude and longitude coordinates) was obtained from internet data gates such as the Global Biodiversity Information Facility (GBIF, <http://data.gbif.org>), the Biological Collection Access Service for Europe (BioCase, <http://www.bioCase.org>), Discover Life (<http://www.discoverlife.org>), the Ocean Biogeographic Information System (OBIS, <http://www.iobis.org/>), the Census of Marine Life (COML, <http://www.coml.org/>) and the Botanical Society of the British Isles (BSBI, <http://www.bsbi.org.uk/>). The reliability of resulting occurrence maps was checked against distribution maps published by Delivering Alien Invasive Species Inventories for Europe (DAISIE, <http://www.europe-aliens.org>). As a result, a total of 19,075, 2390 and 5007 data points were extracted for freshwater, terrestrial and marine species respectively.

*Explanatory predictors.* Variables considered as potential relevant indicators of species occurrence were divided into three sets: climate, habitat and socio-economic. All continental maps were downloaded at the highest spatial resolution available: 30 arcseconds, which corresponds approximately to 1 km<sup>2</sup>. For the marine environment, only habitat and socio-economic variables could be retrieved at 5 arcminute (ca 100 km<sup>2</sup>) resolution.

*Climatic factors.* A set of eight climatic variables were obtained from WorldClim-Global Climate Data (WorldClim, <http://www.worldclim.com>): maximum temperature of the warmest month (Max T), minimum temperature of the coldest month (Min T) and temperature seasonality (T season), annual rainfall (Annual PP), and rainfall of the driest (Min PP) and wettest (Max PP) months. Selected climate variables showed relatively low levels of inter-correlation (Pearson product coefficient  $r < 0.7$ ) overall considering the close relationship that can be expected amongst them. Climatic factors are known to constrain species distribution at a global scale (MOKANY & FERRIER 2011), are pertinent to both terrestrial and aquatic taxa, and are thus reliable indicators to investigate invasive species occurrence at large continental scales.

*Habitat factors.* A layer containing altitude was also obtained from WorldClim. In addition, a number of habitat-related variables were used, including latitude and longitude, Normalized Difference Vegetation Index (NDVI) (NASA Goddard Earth Sciences and Information Services Center, <http://disc.gsfc.nasa.gov>), and water chemistry (pH, alkalinity and nitrate concentration, extracted from the Geochemical Atlas of Europe, GAE, <http://www.gtk.fi>). Several studies have found the abundance and diversity of invasive species to follow clear altitudinal and latitudinal gradients (e.g. ALCARAZ et al. 2005; LIU et al. 2005; PINO et al. 2005) because these geographic variables act as proxies of local environmental conditions – such as temperature and vegetation – that affect species survival (AUSTIN 1980). Geographic variables were thus included in analyses to account for the spatial variability and clustering of occurrence data due to regional gradients (PINO et al. 2005).

For the marine environment, a set of variables was extracted from NASA Ocean Color Web (NASA-OCW, <http://oceancolor.gsfc.nasa.gov/>), the Simple Ocean Data Assimilation (SODA, <http://www.atmos.umd.edu/~ocean/>) and the National Oceanographic Data Center (NODC-NOAA, <http://www.nodc.noaa.gov>) including: bathymetry (Bathym.), slope, photosynthetically available radiation (PAR), particulate organic carbon (POC), chlorophyll-*a*, turbidity, salinity, dissolved oxygen concentration (DO) and mean sea surface temperature (Temperature). Further details can be found in TYBERGHEIN et al. (2012). These variables set the fundamental habitat conditions for marine species and are expected to be closely linked to the distribution of the three marine invaders included in the top 10 list. Latitude and longitude were also included as variables reflecting the geographic distribution of marine species.

*Socio-economic factors.* Several socioeconomic layers were used to reflect the economic richness of countries, human impacts on natural ecosystems and propagule pressure. First, the human influence index (HII) was obtained from the Socio Economic Data and Application Centre (SEDAC, <http://sedac.ciesin.org>). This layer is a combination of factors presumed to exert an influence on ecosystems: urban extent, population density, land cover, night lights and distance to roads, railways, navigable rivers and coastlines. Each of these factors is assigned a degradation score that is later summed up to constitute the human influence layer (SANDERSON et al. 2002), which ranges from 0 = close to pristine locations, to 64 = much degraded areas. This map is expected to be relevant to explain the large-scale distribution of the top 10 invaders because human activities responsible for the introduction of invasive species are more frequent in densely populated areas, land-use pressure can decrease the capacity of natural environments to buffer human activities (including biological invasions) and transport routes provide pathways along which species can disperse (GALLARDO & ALDRIDGE 2013). Although partially accounted for within HII, the density of human population (Population, Oak Ridge National Laboratory, ORNL, <http://www.ornl.gov/>) was included as a separated layer because it has been successfully used before to assess the large-scale distribution of invasive species (e.g. PYSEK et al. 2010). In addition, Gross Domestic Product (GDP) was obtained for each European country from the International Monetary Fund (IMF, <http://www.imf.org>). Three distance layers were generated: closeness to the coastline, ports and reservoirs. To that end, a map delineating the European coastline was obtained from the official Environmental Systems Research Institute (ESRI) repository (<http://www.esri.com/>); a list of the most important commercial ports of the world (volume traded > 10 megatonnes) was extracted from the American Association of Port Authorities (AAPA, <http://www.aapa-ports.org/>); and a list of dams with a

capacity > 1 km<sup>3</sup> was extracted from the Global Water Systems Project (GWSP, <http://www.gwsp.org/>). Coastal landscapes, particularly in the vicinity of ports, are being transformed as a consequence of the increasing demand for infrastructures to sustain residential, commercial and tourist activities. Thus, intertidal and shallow marine habitats are largely being replaced by a variety of artificial substrata (e.g. breakwaters, seawalls, jetties) that are very susceptible to invasion (AIROLDI & BULLERI 2011). Likewise, reservoir construction is known to facilitate the introduction and establishment of freshwater invaders by providing easy public access to disturbed habitats (HAVEL et al. 2005; KELLER et al. 2009). The linear distance from any given pixel to the closest coastline, port or reservoir was calculated using the Spatial Analyst toolbox of ArcGIS 10.0 (©ESRI). Finally, the densities of roads and railways were calculated using the Spatial Analyst toolbox from linear maps obtained at the ArcGIS Resource Center (<http://resources.arcgis.com>).

For the marine environment, only two human-related factors could be incorporated into this study: the human impact to marine ecosystems and distance to commercial ports. The Global Map of Human Impacts to Marine Ecosystems (HIM, National Centre for Ecological Analysis and Synthesis, NCEAS, <http://www.nceas.ucsb.edu/globalmarine/>) is similar to the HII used for freshwater and terrestrial species. This map summarises information on 17 human activities that directly or indirectly have an impact on marine ecosystems such as fishing, shipping, pollution, location of benthic structures and population pressure. Additionally, the linear distance to the closest port in the marine environment was calculated as described above for the continental environment. In addition to HIM and port proximity, chlorophyll-*a* is commonly used as indicator of eutrophication resulting from coastal activities (i.e. agriculture, aquaculture, sewage) (FERREIRA et al. 2011), and was therefore used as indirect proxy for the socio-economic influence on marine habitats.

Information on the conditions currently tolerated by Europe's top 10 invasive species at each of their known locations was extracted from the above described maps using the Spatial Analyst toolbox at ArcGIS 10.0. As a result, a data matrix of species occurrence and explanatory variables was obtained that was later analysed through uni- and multivariate statistical techniques. It should be noted that the data extracted from invasive species occurrence points in Europe represent the conditions of the invaded range in this continent, and not the native range or invaded range of the species elsewhere (with the exception of the zebra mussel, *D. polymorpha*, whose native range comprises several eastern European countries included in the calculations).

### *Statistical analyses*

*Major drivers of Europe's top 10 invasive species collectively.* A principal component analysis (PCA) was used to identify the main environmental and socioeconomic gradients driving the occurrence of the 10 species investigated collectively. PCA-axes' scores were further used to analyse differences in the environmental range of the 10 species. Two PCAs were developed: one for the continental (freshwater and terrestrial species) and another for the marine environment. Because of the high number of data points used for calibrating PCAs (19,074 and 5807 for terrestrial and marine species respectively), boxplots were used to illustrate the position of each of the 10 species along the PCA's first axis of variation.

*Major drivers of Europe's top 10 invasive species individually.* Logistic regression models were used to identify the main factors explaining the presence in Europe of each of the 10 invasive species evaluated. Dealing with presence-only data constituted one of the main challenges of this study. Presence-only data is being increasingly used in the literature to investigate the habitat preference of invasive species, because there is often little or no information on species absence available from systematic surveys (ELITH & LEATHWICK 2007). A common approach is to first create 'pseudo-absences', usually achieved by randomly choosing point locations in the region of interest and treating them as absences. Then the presence/pseudo-absence dataset is analysed using standard analysis methods for presence/absence data (PEARCE & BOYCE 2006; ELITH &

LEATHWICK 2007). In this study, 5000 random pseudo-absences were generated across Europe (i.e. the European continent excluding Russia and Turkey). This figure was chosen because the species investigated showed on average 4800 occurrence points per species. Pseudo-absences represent the variation in climate, habitat and socio-economic covariates available to the species across Europe.

First, individual logistic models were fitted using the presence-absence of species as response variable, and each of the climatic, habitat and socio-economic variables as predictors. Plots were used to further investigate the shape of the relationship.

Afterwards, multiple regression models were calculated using all climatic, habitat and socio-economic factors together as explanatory variables. Variables were sequentially removed and the model with the lowest Akaike Information Criterion (AIC) was selected until reaching a 'minimum adequate model' (CRAWLEY 2005). Although this stepwise procedure of variable selection does not test for every possible combination of explanatory variables, it helps to remove variables that are not relevant to explain the species occurrence, or that are redundant. Because explanatory variables were expressed in different units, standard coefficients (i.e. scaled to 0–1 so coefficients are not affected by differences in units) were used to allow comparison of the relative importance of each of the variables in the model. The frequency with which each factor was included in uni- and multivariate regression models was finally used as an indicator of its importance to explain the large-scale distribution of Europe's top 10 invasive species. All statistical analyses were performed with MiniTab® 16 (Minitab Inc., State College PA).

## RESULTS

### *General characteristics of invasive species locations*

Data on the climate, habitat and socio-economic conditions of locations inhabited by Europe's top 10 invaders is summarized in Table 1. Amongst species, *O. pes-caprae* illustrated a preference for warm and dry climates at the southwesternmost locations; whereas *M. coypu* showed the lowest temperature and highest precipitation values across species. *Dreissena polymorpha* showed a strong association with high levels of human influence, proximity to commercial ports, intensely populated areas and high road/railway density. In contrast, the brook trout *S. fontinalis* was associated with low human influence scores, population and road density. Marine species showed very variable human influence scores, with average values in general much lower than those of terrestrial species. Amongst them, *U. pinnatifida* was generally distributed much closer to ports than the other two marine organisms.

### *Major drivers of Europe's top 10 invasive species jointly*

The continental PCA relating all variables with the occurrence of the seven targeted freshwater and terrestrial species was significant and explained a total of 43.5% of the initial variance in its first and second axes. The first axis was positively related with minimum annual temperature and several socio-economic indicators such as the density of roads and the country GDP, together with water chemistry variables indirectly related to high levels of human disturbance such as alkalinity and nitrate (Fig. 1A). We interpret this gradient as reflecting propagule pressure, with increasing economic development at positive coordinates discriminating species frequently found in urban and suburban environments such as *D. polymorpha*, *M. coypu* and *C. nippon* (Fig. 2A).

Table 1.

Climatic, habitat and socio-economic conditions of sites inhabited by Europe's top 10 worst invasive species. Values correspond to means of all the locations where the species is present in Europe  $\pm$  standard deviation. T: temperature, PP: precipitation, NDVI: Normalized Vegetation Index, POC: particulate organic carbon, PAR: photosynthetically available radiation, HIM: human influence on marine ecosystems, GDP: gross domestic product (in PPP, purchasing power parity, to allow comparison). Empty cells: not applicable.

	<i>B. canadensis</i>	<i>C. rippon</i>	<i>D. polyomorpha</i>	<i>M. coypus</i>	<i>P. clarkii</i>	<i>S. fontinalis</i>	<i>O. pes-caprae</i>	<i>B. improvisus</i>	<i>C. fragile</i>	<i>U. pinnatifida</i>
<b>I. Climatic</b>										
Maximum T (°C)	20.8 $\pm$ 1.1	17.9 $\pm$ 1.9	21.6 $\pm$ 2.3	23.1 $\pm$ 2.7	28.2 $\pm$ 3.5	19.9 $\pm$ 2.4	29.8 $\pm$ 2.9			
Minimum T (°C)	-7.4 $\pm$ 4.4	-13.0 $\pm$ 1.6	-0.9 $\pm$ 2.5	-0.2 $\pm$ 2.1	2.1 $\pm$ 2.7	-8.8 $\pm$ 4.4	5.7 $\pm$ 2.4			
T Season	7.2 $\pm$ 1.1	4.5 $\pm$ 0.6	5.6 $\pm$ 1.2	5.4 $\pm$ 0.8	5.7 $\pm$ 0.6	7.2 $\pm$ 1.2	5.2 $\pm$ 0.7			
Annual PP (mm)	652 $\pm$ 135	1183 $\pm$ 358	752 $\pm$ 148	727 $\pm$ 166	659 $\pm$ 216	760 $\pm$ 227	544 $\pm$ 185			
Min PP (mm)	34.4 $\pm$ 17.3	66.3 $\pm$ 17.3	43.4 $\pm$ 9.6	43.2 $\pm$ 10.5	25.4 $\pm$ 10.9	40.6 $\pm$ 17.7	6.1 $\pm$ 10.9			
Max PP (mm)	77.1 $\pm$ 14.4	134.2 $\pm$ 48.2	80.3 $\pm$ 17.6	79.2 $\pm$ 22.9	83.6 $\pm$ 27.3	91.6 $\pm$ 17.7	83.0 $\pm$ 10.9			
<b>II. Habitat</b>										
Altitude (m)	95.0 $\pm$ 97.8	266.5 $\pm$ 184.9	47.6 $\pm$ 134.3	144.1 $\pm$ 235.8	319.6 $\pm$ 310.9	456.5 $\pm$ 492.3	235.1 $\pm$ 274.0			
Latitude	15.3 $\pm$ 6.2	-3.2 $\pm$ 3.6	6.2 $\pm$ 9.2	3.2 $\pm$ 5.9	0.4 $\pm$ 5.6	11.7 $\pm$ 5.9	38.2 $\pm$ 3.1	53.7 $\pm$ 2.8	54.6 $\pm$ 3.9	48.9 $\pm$ 3.4
Longitude	59.0 $\pm$ 3.2	55.7 $\pm$ 2.5	51.9 $\pm$ 3.26	48.9 $\pm$ 3.6	42.2 $\pm$ 3.4	57.6 $\pm$ 6.5	-2.7 $\pm$ 6.31	9.1 $\pm$ 8.87	-2.2 $\pm$ 7.1	-1.0 $\pm$ 4.6
Water nitrate (mg/L)	2.8 $\pm$ 6.2	9.4 $\pm$ 9.5	10.7 $\pm$ 8.7	22.5 $\pm$ 12.9	11.1 $\pm$ 8.8	2.5 $\pm$ 6.2	10.5 $\pm$ 6.1			
Water pH	6.7 $\pm$ 0.5	7.6 $\pm$ 0.3	7.5 $\pm$ 0.4	7.8 $\pm$ 0.4	7.8 $\pm$ 0.8	6.7 $\pm$ 0.8	8.1 $\pm$ 0.3			
Water alkalinity (mg/L)	47.4 $\pm$ 53.5	76.9 $\pm$ 70.8	237.1 $\pm$ 92.6	202.5 $\pm$ 80.9	205.9 $\pm$ 92.2	50.9 $\pm$ 70.5	234.4 $\pm$ 66.5			
NDVI	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.05 $\pm$ 0.02			
Sea bathymetry (m)								-9.3 $\pm$ 13.7	-12.0 $\pm$ 21.3	-5.8 $\pm$ 10.5
Sea PAR (Einstein/m <sup>2</sup> . day)								30.4 $\pm$ 2.4	27.9 $\pm$ 1.9	28.7 $\pm$ 1.3

Sea POC (mol/m <sup>3</sup> )	737 ± 462	529 ± 262	530 ± 244							
Sea chlorophyll- <i>a</i> (mg/m <sup>3</sup> )	16.1 ± 10.9	5.7 ± 5.4	5.1 ± 4.2							
Sea dissolved oxygen (ml/L)	7.3 ± 0.8	6.4 ± 0.4	6.1 ± 0.3							
Sea water current (m/sec)	0.004 ± 0.6	0.5 ± 1.4	0.01 ± 0.6							
Sea slope	4.9 ± 12.4	10.5 ± 13.8	7.8 ± 10.9							
Sea turbidity (mg/L)	9.2 ± 3.1	10.6 ± 2.4	12.6 ± 2.8							
Sea salinity (PSS)	18.7 ± 12.5	33.4 ± 3.1	34.9 ± 1.2							
Sea mean T (°C)	9.7 ± 1.6	10.8 ± 1.8	12.8 ± 1.8							
<b>III. Socio-economic</b>										
Port (km)	276.0 ± 1.4	140.7 ± 3.1	122.6 ± 3.4	173.0 ± 3.6	204.8 ± 8.2	339.9 ± 6.7	204.8 ± 8.2	170.1 ± 124.2	200.1 ± 129.8	111.6 ± 132.7
Human influence (HII and HIM)	30.6 ± 0.1	22.5 ± 0.2	34.5 ± 0.3	30.8 ± 0.3	30.6 ± 0.8	19.0 ± 0.4	35.9 ± 0.6	10.15 ± 14.73	10.14 ± 14.32	7.8 ± 14.96
Reservoir (km)	226.2 ± 1.2	53.5 ± 2.1	105.9 ± 1.9	90.1 ± 2.1	56.2 ± 3.2	122.4 ± 3.8	76.9 ± 4.3			
Population density (Num./km <sup>2</sup> )	119.3 ± 4.1	34.2 ± 7.3	367.5 ± 25.3	124.0 ± 12.1	207.1 ± 90.5	20.4 ± 7.0	244.7 ± 42.6			
GDP × 1000	387 ± 3.3	1548 ± 8.7	755 ± 12.9	1619 ± 14.3	1309 ± 33.5	642 ± 25.6	990 ± 13.2			
Road density	2.4 ± 0.1	2.5 ± 0.1	4.5 ± 0.1	3.5 ± 0.04	2.9 ± 0.1	2.1 ± 0.1	1.9 ± 0.1			
Railways density	0.9 ± 0.1	1.1 ± 0.1	1.2 ± 0.1	0.9 ± 0.1	1.1 ± 0.1	0.6 ± 0.1	0.4 ± 0.1			



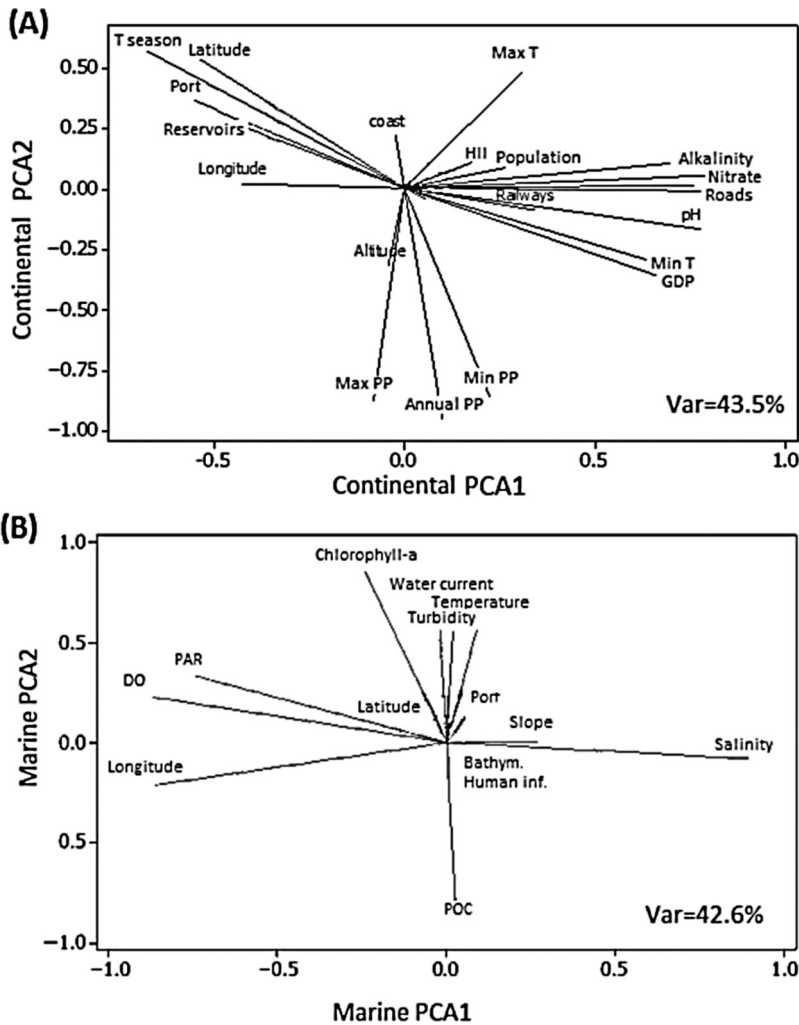


Fig. 1. — Principal component analysis (PCA) showing the importance of climatic, habitat and socio-economic variables to explain the European distribution of (A) seven continental (freshwater and terrestrial) and (B) three marine invasive species. The two first principal components are plotted with the proportion of variance explained in the bottom right corner of the plot. T: temperature, PP: precipitation, HII: Human Influence Index, GDP: Gross Domestic Product, DO: dissolved oxygen, PAR: photosynthetic active radiation, Bathym: bathymetry, Human inf.: human influence on marine ecosystems.

Similarly, the two first axis of the marine PCA explained 42.6% of the initial variability in the occurrence of marine invaders. The first axis was positively related to water salinity and negatively to dissolved oxygen and PAR (Fig. 1B). Chlorophyll-*a*, an indirect indicator of eutrophication, was positively related to the second axis. These two axes separated *C. fragile* and *U. pinnatifida* at higher coordinates from *B. improvisus* (Fig. 2B). The other human-related variables included in this PCA – human influence and closeness to port – showed very low scores in the first and second PCA axes.

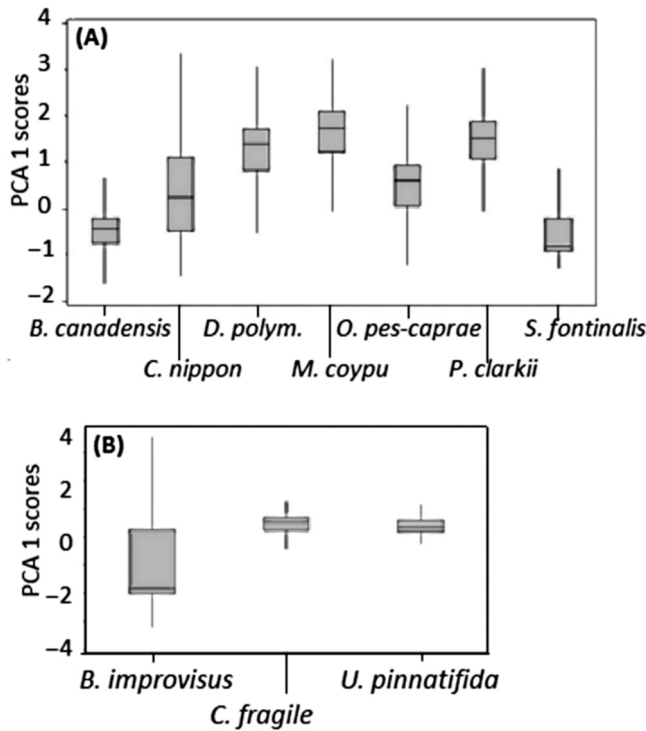


Fig. 2. — Boxplots representing the position of (A) seven continental (freshwater and terrestrial) and (B) three marine invasive species, along the first principal component analysis (PCA) axis of variation. PCA plots of variable importance can be consulted in Fig. 1.

#### *Major drivers of each of Europe's top 10 invasive species independently*

Univariate logistic models identified minimum and maximum annual temperature, latitude and longitude, alkalinity and human influence as the variables most significantly related to the occurrence of the seven freshwater and terrestrial species investigated. Fig. 3 illustrates the response of *D. polymorpha*'s probability of presence to varying levels of these factors, used as a representative example. Graphs corresponding to the other nine species can be consulted in Appendices 1–6 (available online). Invasive species consistently showed an increased probability of occurrence with increasing minimum temperature (Fig. 3B, with the exception of *B. canadensis*) and decreasing maximum temperature (Fig. 3C, except *O. pes-caprae* typical of warm southern climates as shown in Table 1). Alkalinity favoured aquatic species such as *D. polymorpha* (Fig. 3E) and *M. coypu*, but not *S. fontinalis* or *P. clarkii* (Appendix 5, available online). All species showed a consistent positive logistic response to increasing levels of human influence (Fig. 3F and Appendices 1–5, available online). Regarding marine species, both *B. improvisus* and *C. fragile* showed a significant positive response to the concentration of chlorophyll-*a* and POC (Appendix 6, available online). The probability of *C. fragile* occurrence was also highest in shallow areas close to commercial ports (Appendix 6, available online). No significant univariate logistic model was found for

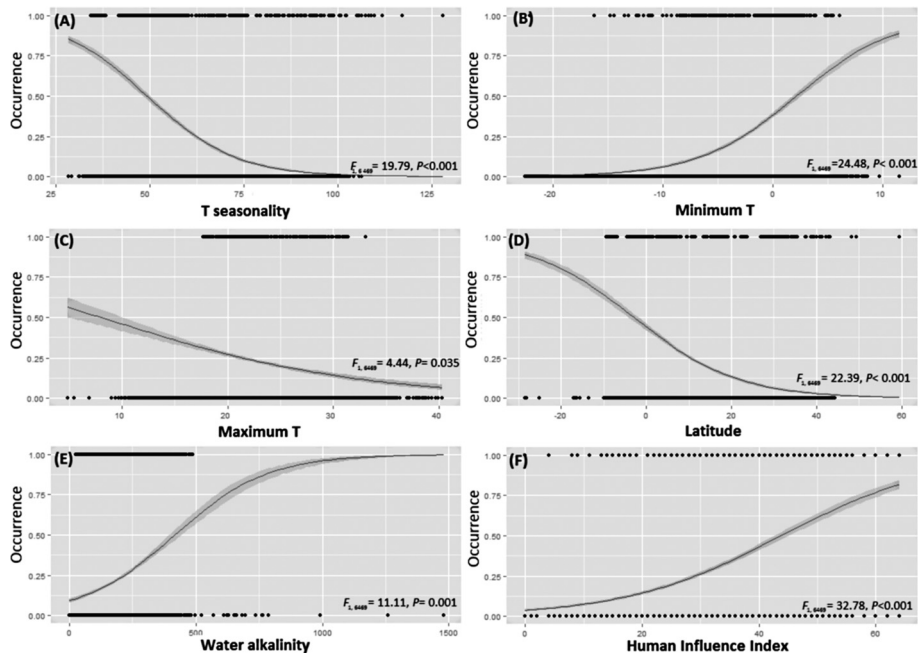


Fig. 3. — Results from univariate logistic models performed between the presence-absence of *Dreissena polymorpha* in Europe and (A) temperature seasonality, (B) minimum temperature, (C) maximum temperature, (D) geographic latitude, (E) water alkalinity concentration and (F) the human influence index. The F-ratio and P-value of each model is indicated in the bottom right corner of each plot. The shaded area around the regression line represents the SE of the model.

*U. pinnatifida*, even though occurrence locations were predominantly located in shallow areas close to ports, at low levels of human influence, and high concentrations of chlorophyll-*a* and organic carbon (Table 1).

Multivariate regression models showed that, for freshwater and terrestrial species, the amount of variability that can be explained by all the factors included in this study ranged from 21% for *S. fontinalis* to 98% for *O. pes-caprae* (Table 2). In agreement with the univariate models described before, minimum temperature and geographic location (altitude, latitude and longitude) were important factors explaining the occurrence of Europe's top freshwater and terrestrial invaders. Amongst socio-economic indicators, port closeness and GDP were also relevant predictors. Surprisingly, the HII and human population were only considered significant in four and three models respectively (Table 2).

Marine multivariate regression models explained a lower fraction (11–50%) of the species occurrence variability. Latitude and turbidity were negatively related to the probability of occurrence of *U. pinnatifida* and *B. improvisus*, whereas *C. fragile* was positively related to shallowness, and the concentration of chlorophyll-*a* and POC. Surprisingly, port closeness was not included in any multivariate marine model, despite species being generally located in the vicinity of ports. Human influence contributed significantly to *U. pinnatifida* and *C. fragile* models.

The frequency with which each variable was included in uni- and multivariate regression models was used as an indicator of its importance (Figs 4–5). Climatic

Table 2.

Results of stepwise regression models performed with the species occurrence as response variable (species real occurrences and 5000 pseudo-absences random points) and three sets of climatic, habitat and human related predictors.  $R^2(\text{adj})$  = percentage of variance explained by the model, adjusted for the number of predictors included. T: temperature, PP: precipitation, NDVI: Normalized Difference Vegetation Index, POC: Particulate Organic Carbon, PAR: Photosynthetic Active Radiation, DO: Dissolved Oxygen, TSS: Total Suspended Solids, HIM: Human Influence Index, HIMI: Human Influence on Marine ecosystems, GDP: Gross Domestic Product.

	<i>B. canadensis</i>	<i>C. nippon</i>	<i>D. polymorpha</i>	<i>M. coypus</i>	<i>P. clarkii</i>	<i>S. fontinalis</i>	<i>O. pes-caprae</i>	<i>B. improvisus</i>	<i>C. fragile</i>	<i>U. pinnatifida</i>
<b>I. Climatic</b>										
Constant	6.6	1.5	2.9	1.5	0.5	2.0	0.2	1.3	2.7	0.4
Tseason	-1.0	-1.9		-1.9	-1.3	0.3				
MaxT		0.2	-0.8	0.9	0.8		0.02			
MinT	-1.0	-1.5	1.0	-1.8	-1.07	0.5	-0.03			
Annual PP		0.5	0.9			-0.8				
Min PP	-0.5		-1.2	-0.3	-0.1		-0.1			
Max PP			-0.2	0.5		0.6				
<b>II. Habitat</b>										
Altitude	-0.7	-0.5	-0.3	-0.3	-0.2	0.3	-0.1			
Alkalinity	-1.7	-0.3	0.4				-0.02			
Water nitrate		0.1	-0.4	0.7	-0.2	0.3	0.02			
pH		0.8		0.2	-0.1	-0.5	-0.01			
Latitude	0.3	-0.6	-0.2	-0.7	-0.4	-0.2	0.02	-1.8	-0.6	-0.6
Longitude	2.6	0.6	0.3	-0.2	-0.5	0.9	-0.1	-0.2	-0.9	
NDVI	-0.1	-0.2	-0.5		-0.2	0.3	-0.1			
Chlorophyll-a								0.6	1.6	0.2
POC								0.7	1.4	0.2
PAR								-0.4	-1.3	-0.3
DO								0.3	0.3	

(Continued)

Table 2.  
(Continued)

	<i>B. canadensis</i>	<i>C. nippon</i>	<i>D. polymorpha</i>	<i>M. coypus</i>	<i>P. clarkii</i>	<i>S. fontinalis</i>	<i>O. pes-caprae</i>	<i>B. improvisus</i>	<i>C. fragile</i>	<i>U. pinnatifida</i>
Water temp.										
Salinity								-0.2	0.7	0.1
TSS								-1.5	-0.9	-0.7
Bathymetry								0.6	1.3	0.2
Water current								0.1	-0.3	
<b>III. Socio-economic</b>										
Ports	-0.9	-0.4	-0.6	-0.3	0.1	-0.3	0.03			-0.05
Coast										
Reservoirs	0.4	-0.2	0.1			-0.1	0.02			
Population	0.1		0.18		0.1					
HII/HIM	0.5		0.3	0.2		0.1			-0.4	-0.2
GDP	-0.3	0.3	-0.5	0.5	0.2	0.1				
Roads	0.5	-0.6	1.2			0.2	0.02			
Railways		0.4	-0.4	-0.3		-0.4	-0.01			
<b>R<sup>2</sup> (adj)</b>	0.68	0.64	0.55	0.46	0.23	0.21	0.98	0.34	0.55	0.12

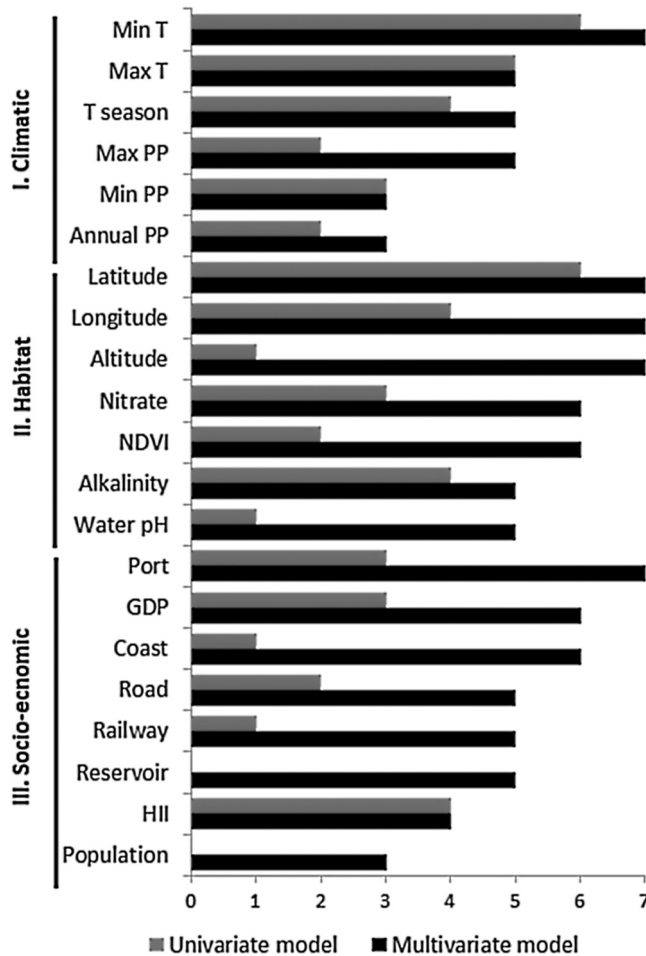


Fig. 4. — Relative importance of climatic, habitat and socio-economic variables to explain the occurrence of seven of the worst freshwater and terrestrial invasive species in Europe. Grey bars represent the number of species showing a significant response to each variable in univariate logistic models, whereas black bars refer to multivariate logistic models. T: temperature, PP: precipitation, NDVI: Normalized Difference Vegetation Index, GDP: Gross Domestic Product, HII: Human Influence Index.

variables, mostly minimum and maximum annual temperatures, were most important to discriminate invaded from uninvaded continental regions and were therefore included in a similar number of uni- and multivariate models (Fig. 4). Something similar could be observed with latitude, longitude and alkalinity. However, socio-economic variables were more frequently included in multivariate than univariate models. For instance, closeness to reservoirs and population density were not significantly related to any of the seven freshwater and terrestrial species individually, and yet these variables were significantly kept in five and three multivariate models respectively. Likewise, the relevance of human influence was better appreciated when used in combination with other variables in multivariate marine models, not being able to

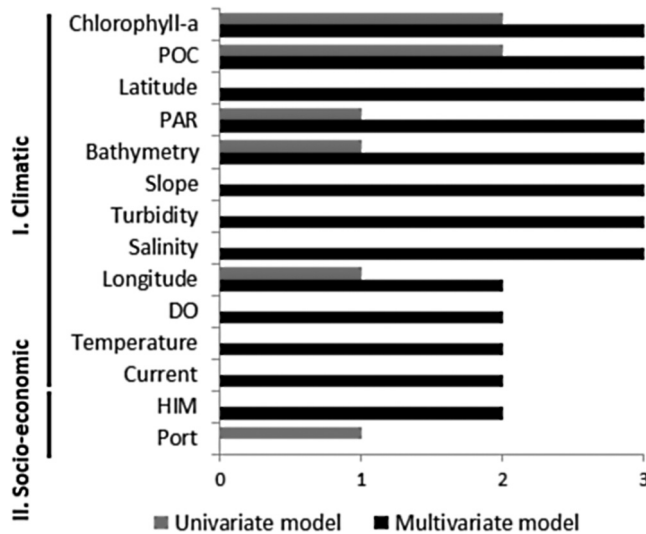


Fig. 5. — Relative importance of habitat and socio-economic variables explaining the occurrence of three of the worst marine invasive species in Europe. Grey bars represent the number of species showing a significant response to each variable in univariate logistic models, whereas black bars refer to multivariate logistic models. POC: Particulate Organic Carbon, PAR: Photosynthetic Active Radiation, DO: dissolved oxygen, HIM: human influence on marine ecosystems.

significantly explain species occurrence by itself. Primary productivity was clearly the most important determinant of marine bioinvasions according to both uni- and multivariate models (Fig. 5).

## DISCUSSION

### *The influence of climate and habitat factors*

This study investigated the relative contribution of climatic, habitat and socio-economic factors to explain the occurrence of Europe's worst invaders. Moreover, this was done for a range of organisms from different habitats including terrestrial, freshwater and marine species. Amongst climate factors, minimum temperature of the coldest month was one of the most important drivers of the occurrence of Europe's worst freshwater and terrestrial invaders. Minimum temperature showed a high loading on PCA's first axis (Fig. 1A), and it was included in six out of seven univariate and all seven multivariate regression models (Fig. 4). In particular, minimum temperature above 0 °C increased over 50% the probability of occurrence of invaders (Fig. 3B). The role of cold temperature in shaping the distribution of species has been recently highlighted by ARAÚJO et al. (2013), who after reviewing a large set of endotherms, ectotherms and plants concluded that the upper tolerance of species to temperature is relatively similar, with differences in the global distribution of species largely driven by their cold tolerance level. Temperature certainly affects the body size, reproduction, growth, ecological role and survival of species (GILLOOLY et al. 2001), and is a key

factor in determining success in the colonization and establishment stages of invasion (THEOHARIDES & DUKES 2007). Differences in thermal tolerance of marine organisms have been also investigated by ZEREBECKI & SORTE (2011), who observed that marine invaders tended to inhabit broader habitat temperature ranges and higher maximum temperatures than natives. Nevertheless, seawater temperature was only included in multivariate regression models for *C. fragile* and *U. pinnatifida*.

Amongst habitat indicators, models for freshwater and terrestrial species highlighted the importance of geographic factors such as latitude, longitude and also altitude, which achieved high loadings on PCA first axis (Fig. 1) and were included in all seven multivariate regression models (Fig. 4). Geographic factors are indirect determinants of local environmental conditions – such as temperature and vegetation – that affect species survival (AUSTIN 1980), and are thus commonly found to influence species distribution. For instance, ALCARAZ et al. (2005) found a significant effect of latitude on the distribution of several species of fish in the Iberian peninsula; plant invasions also showed clear geographic gradients in China (LIU et al. 2005) as well as in Catalonia (PINO et al. 2005). Geographic factors partially account for the spatial variability of occurrence data, thus suggesting an important clustering of the 10 investigated species in Europe that is probably driven by environmental preferences, dispersal limitations, or a combination of both. Regarding marine invaders, bathymetry was a prominent driver of the distribution of marine invaders, which showed preference for shallow coastal areas (< 30 m deep, Table 1).

Apart from geographic location, water chemistry factors such as pH, alkalinity and the concentration of nitrate were also important predictors for both aquatic invaders (*D. polymorpha*, *P. clarkii* and *S. fontinalis*) and semi-aquatic vertebrates (*B. canadensis* and *M. coypu*) that are commonly found in salt/brackish marshes. Water chemistry determines the availability of habitat and resources for species at regional to local levels and it was therefore expected to significantly contribute to the occurrence of invasive species. Results from univariate regression models performed with data from the Europe-wide distribution of species largely confirmed the relationship of invasive species to water chemistry reported by other authors at the local scale. For instance, an alkalinity threshold of 17 mg calcium carbonate ( $\text{CaCO}_3$ )  $\text{L}^{-1}$  has been identified to affect the reproduction and growth of *D. polymorpha* (MCMAHON 1996); *S. fontinalis* actively avoided low pH sites (pH < 4.5) for spawning (JOHNSON & WEBSTER 1977); pollution caused by high alkalinity and nitrate concentration has been related to the occurrence of successful aquatic invaders, which benefit from the increased ionic concentration and impoverished native communities (ARBAČIAUSKAS et al. 2008). Likewise, nitrate and chlorophyll-*a* concentration were important determinants of marine bioinvasions in this study, which might be explained by their direct relationship to the availability of food resources, and indirectly to their correlation with pollution in highly populated coastal areas.

#### *The influence of socio-economic factors*

According to the statistical models performed, the density of roads, country GDP, distance to ports and human influence were some of the most relevant predictors of invasion. The density of roads can be interpreted both as a vector of species spread and an indicator of economic development. In other words, the higher the road density in a particular region, the higher the propagule pressure, direct (road transport, frequency of visits) and indirect (human degradation, presence of other infrastructure and economic development). Many authors have described the role of roads as facilitators of



invasions for plants (FLORY & CLAY 2009; MORTENSEN et al. 2009; BARBOSA et al. 2010; JOLY et al. 2011), but rarely for other types of organisms (CAMERON & BAYNE 2009). Road density showed a particularly high  $R^2$  in *D. polymorpha*'s univariate model (not shown), and a high standard coefficient in the multivariate model (Table 2). The overland spread of this species is mostly related to the movement of boats and fishing gear between lakes (CARLTON 1993; ALDRIDGE et al. 2004; BOSSENBROEK et al. 2007), which may explain the particular importance of road connectivity in this species model.

Country GDP and population density have been identified before as main predictors of invasive species richness both at national (e.g. in the UK, KELLER et al. 2009) and continental (e.g. Europe, PYSEK et al. 2010) scales. Our study further confirms the critical effect of economic wealth and population density on species invasions regardless of the taxonomic group and habitat invaded. GDP was included in six out of seven multivariate models and was an important contributor to *D. polymorpha* and *M. coypus* univariate models. In contrast, population density had a lower impact than expected: it was only included in the *B. canadensis*, *D. polymorpha* and *P. clarkii* multivariate models, and even then showed low standard coefficients. This might reflect low population density in the locations where species are present, which are nonetheless in proximity to highly populated areas. It would make more sense therefore to use an alternative indicator reflecting the population density in a particular distance to an occurrence point or the distance to the closest urban area, rather than the real point value.

Finally, the human influence index proved to be a very promising indicator combining several degradation-related factors such as urban development, night lights, population density, and distance to roads, railways and navigable rivers. In a recent risk assessment, invasive species showed a consistent positive logistic response to human influence, suggesting that they display especially high invasion success in disturbed environments that are characterized by simplified communities, little competition or predation and abundant organic matter (GALLARDO & ALDRIDGE 2013). However, because it is a combined layer, it is difficult to disentangle how the different factors accounted for by the human influence index affect invasive species separately.

The effect of human-related factors on marine species was more difficult to address because only two indicators could be incorporated – distance to ports and human degradation – neither of which proved to be of much relevance. While marine invasive species are usually related to ports (BAX et al. 2003; SEEBENS et al. 2013), the variable reflecting distance to ports was only included in *U. pinnatifida*'s model, and even then with a relatively low coefficient. The combination of multiple factors potentially affecting the presence of invaders in the marine human influence layer (such as shipping, pollution and the location of benthic structures) makes it difficult to discern their specific effect, and might have an overall confounding effect. Other marine factors highlighted in the literature that could account for the unexplained variance include the density of shipping routes (KALUZA et al. 2010), distance between origin and recipient ports (SEEBENS et al. 2013), presence of fisheries (COPP et al. 2007), anthropogenic artificial structures that change disturbance regimes (AIROLDI & BULLERI 2011), and wave exposure (STEFFANI & BRANCH 2003).

### *Study conclusions*

Our analyses suggest that the occurrence of Europe's worst invaders is primarily limited by basic climate (temperature tolerance) and habitat (geographic location) constraints, while human activities related to transport (roads, ports) and the degree

of human impact (GDP, HII) seem to play a secondary though decisive role in their final distribution. Thus, climate, habitat and socio-economic development can be interpreted as multi-scale filters that determine the occurrence of invasive species, as already suggested by COLAUTTI et al. (2006). Under classic landscape filter theory, the species present at a particular site are the result of environmental filters acting at different scales (from continental to microhabitat) on the global pool of species (POFF 1997). Invasive species differ from native species in two main aspects. First, invasive species have usually a broad native range, phenotypic plasticity, wide abiotic tolerance, fast growth, early maturity, high fecundity and effective dispersal mechanisms, and are generalists in their use of habitat and resources, which altogether increase the success of invasive species passing through environmental filters (e.g. THEOHARIDES & DUKES 2007; DAVIDSON et al. 2011). Second, propagule pressure associated to socio-economic activities acts as a complementary filter that affects the transport, colonization, establishment and spread of invasive species at multiple scales (THEOHARIDES & DUKES 2007). While temperature still dominates the distribution of invasive species, socio-economic activities are revealed in this study as important complementary determinants of species invasion. Furthermore, socio-economic factors were only relevant when considered jointly with other climate and habitat factors, as illustrated in Figs 4–5. For instance, in a recent study, the inclusion of socio-economic factors to bioclimatic models resulted in a 20% increase in the probability of invasion in general and, in particular, a six-fold increase in the area predicted suitable for the quagga mussel (*D. r. bugensis*, a species closely related to *D. polymorpha*) (GALLARDO & ALDRIDGE 2013). The importance of socio-economic factors is likely to be because they reflect possible routes of introduction, such as ports, roads, railways and the ornamental trade. Thus climate and habitat filters are complemented with a socio-economic filter intimately related to propagule pressure, all of which are fundamental to understanding the large-scale distribution of invasive species. Yet socio-economic activities are often omitted in risk assessments because they are difficult to quantify, resulting in serious underestimation of the area at risk (GALLARDO & ALDRIDGE 2013). This study therefore advocates for the use of available global information on the country richness, population density, transport networks and human disturbance of ecosystems, as means to provide more accurate assessments of invasion risk.

### *Study limitations*

A number of factors may affect the accuracy of regression models, some of which are related to (i) the uneven number and spatial bias of occurrence points, (ii) the use of pseudo-absences instead of real absence points to calibrate regression models, (iii) high inter-correlation of explanatory variables, (iv) lack of additional relevant predictors and (v) limited number of species investigated per major habitat.

The number of occurrence points used to calibrate regression models varied widely from 72 for *U. pinnatifida* to over 13,000 for *B. canadensis*. Both the number and distribution of occurrences are important in models, since the ratio between presence and absence data and spatial bias of observations affects the ability of the model to discriminate between invaded and uninvaded areas. Spatial clustering of a large amount of data around particular geographic regions may actually explain the high importance of geographic factors (latitude and longitude) in this study, most conspicuously in the case of *O. pes-caprae* and *B. canadensis*. Although techniques exist to reduce the spatial clustering of species data, recent investigations recommend

using all available spatial information on invasive species to avoid underestimating their potential distribution (GALLARDO et al. 2013b). On the other hand, models should be greatly affected by the use of randomly selected pseudo-absence instead of real absence data (LOBO et al. 2010). Such information is usually not available for invasive species, and even when it is, it is usually not reliable as uninvaded locations can be invaded in the future, or might be already affected by invasive species that remain so far unnoticed. The generation of pseudo-absences is nevertheless commonly accepted when using other correlational approaches such as species distribution models (BARBET-MASSIN et al. 2012), and is considered to provide the best available approximation to investigate major differences in climate, habitat and socio-economic conditions between invaded and uninvaded sites.

Multicollinearity among predictors may affect the reliability of multivariate methods by artificially changing variable coefficients and increasing the percentage of variance explained by the model ( $R^2$ ). For this reason, variables included in this study were carefully chosen to exhibit low levels of inter-correlation (Pearson  $r < 0.70$ ,  $P > 0.05$ ), and  $R^2$  values adjusted for the number of predictors in the model were reported. On the other hand, while backward elimination of variables helped to remove irrelevant or redundant predictors, not all possible combinations of variables could be tested, which may have resulted in the over-representation of certain variables. Although the factors evaluated in this study provide valuable information on the effect of socio-economic development on invasive species, the inclusion of other predictors more directly related to propagule pressure and species dispersal may further improve the predictability of models. Finally, it has to be noted the very limited number of invasive species investigated per major habitat, which undoubtedly limits the generality of conclusions. Future studies using larger subsets of species will provide more robust insights into the preliminary patterns suggested here.

Despite these various caveats, this study provides a comprehensive overview of the relative importance of climate, habitat and socio-economic factors to explain the continental-scale occurrence of some of Europe's worst invaders. A range of statistical analyses were used to illustrate how socio-economic development is associated with the presence of the top 10 worst European invasive species at a continental scale, and this fact was related to the provision and transport of propagules and the degradation of natural habitats that favour the establishment of invasive species.

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