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Predicting the risk of aquatic plant invasions in Europe: how climatic factors and anthropogenic activity influence potential species distributions

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ABSTRACT

Predicting where species invasions will occur is one of the greatest challenges in conservation. Freshwater ecosystems are very vulnerable to the introduction of non-native species for two reasons: (1) there are many routes of introduction by which non-natives can arrive in freshwater systems; and, (2) freshwater systems are heavily impacted by a wide variety of human activities. Non-native aquatic plants can have harmful effects if they change habitat conditions, alter ecosystem functioning, and/or become key primary producers in invaded ecosystems. In this study, we focused on the potential distribution of non-native aquatic plants in Europe. The main objectives were to (1) identify environmentally suitable areas into which focal species could potentially spread; (2) generate a combined risk map for all the focal species and for the ten most harmful species in Europe; and (3) identify the main physicochemical characteristics of the areas at greatest risk. The results revealed that the potential distributions of non-native species were best predicted by climatic factors, notably by temperature-related variables. Anthropogenic activity was also a major contributor to the distribution patterns of all the non-native species examined. Areas experiencing high levels of eutrophication, a phenomenon that is strongly associated with anthropogenic activity, were among those at greatest risk of invasions. The approach presented here was

intended to be broadly applicable. For example, it could be used to look at other taxonomic groups, regions, and/or systems. The overarching aim is to provide an effective basis for developing and implementing management and control strategies that can mitigate the effects of current invasions and prevent future ones.

Keywords: biological invasions; exotic species; invasion risk; MaxEnt; modelling techniques; species distribution models

1. Introduction

Freshwater ecosystems are considered to be major biodiversity hotspots (Strayer & Dudgeon, 2010). They are also one of the most threatened ecosystems in the world (Collen et al., 2014; Dudgeon et al., 2006). Biological invasions, together with habitat disturbance, are among the main causes of biodiversity decline in inland aquatic habitats (Sala et al., 2000; Simberloff et al., 2013). The arrival of non-native species has been facilitated by an increase in eutrophication worldwide, as well as by globalisation (Keller, Geist, Jeschke, & Kühn, 2011). Although substantial resources have been invested in biodiversity conservation, efforts in freshwater systems remain limited because information is lacking and it is challenging to predict invasion risks (Abell et al., 2010; Brundu, 2015).

Over the past 20 years, researchers have been describing the ecological problems associated with the arrival and spread of non-native aquatic plants in Europe (Brundu, 2015; Keller et al., 2011; Sheppard, Shaw, & Sforza, 2006; Willby, 2007). Non-native aquatic plants have reached the continent via different introduction pathways. Aquariums and garden ponds have played an important role (Keller et al., 2011), as have waterbirds and boats (i.e., transport of stowaways) (Hulme, 2009; Reynolds, Miranda, Cumming, & Keller, 2015). Unfortunately, introduction pathways are so numerous, and even ubiquitous, that there is little hope of eliminating them completely (Strayer, 2010). Propagule pressure appears to be key to introduction success (the propagule pressure hypothesis), and, consequently, anthropogenic activity is strongly correlated with the presence of non-native species (Hulme, 2009; Pysek & Richardson, 2010).

Non-native aquatic species are, in general, largely successful because they can tolerate a wide range of environmental conditions, and their establishment is facilitated when there is climatic similarity between the native and invaded ranges (the habitat filtering hypothesis; Gallien, Münkemüller, Albert, Boulangéat, & Thuiller, 2010; Melbourne et al., 2006). Other key contributing factors are their high degree of phenotypic plasticity and the absence of natural enemies in invaded areas (adaptation and enemy release hypotheses; Duncan & Williams, 2002; Ren & Zhang, 2009).

Non-native aquatic species have negative impacts on natural biodiversity (Ricciardi & Kipp, 2007). Because they can alter ecosystems by modifying habitat structure, substrate, and water composition (Strayer, 2010), non-native species represent a threat to ecosystems and native aquatic species (Havel, Kovalenko, Thomaz, Amalfitano, & Kats, 2015; Simberloff et al., 2013). One of the most relevant consequences of such processes is that native species are displaced (Stiers, Crohain, Josens, & Triest, 2011).

For these reasons, it is critical to predict where invasions are most likely to occur and when they will result in the successful establishment of non-native species. Such an early-warning system is important because ecologists know that eradication is usually effective only when efforts are implemented prior to the establishment of non-native species (Crafton, 2015): once non-natives are established in a new habitat, control efforts are expensive, and most species are essentially impossible to eradicate (Thouvenot, Haury, & Thiebaut, 2013).

Species distribution models (SDMs) are increasingly being used to identify landscapes that most resemble those in which a given species is currently found. SDMs are based on environmental layers and species occurrence data (Guisan & Thuiller, 2005); they can work with information on a set of species and predict areas at risk of invasion (O'Donnell et al., 2011; Thuiller et al., 2005). For example, climatic variables are widely known to limit the distribution of species (Woodward & Williams, 1987) and remain one of the best predictors of distribution patterns at large spatial scales (Kelly, Leach, Cameron, Maggs, & Reid, 2014). Although few variables exist to model the distribution of inland aquatic species, terrestrial climatic variables are useful when modelling species distributions in inland aquatic environments (Reshetnikov & Ficetola,

2011). Novel approaches to SDMs have demonstrated the importance of including variables that reflect anthropogenic activity (Gallardo, Zieritz, & Aldridge, 2015). The human footprint is an index that helps quantify the effects of humans on the environment (Sanderson et al., 2002) and is correlated with factors that may influence the introduction and distribution of non-native species (Gallardo et al., 2015). These factors may include propagule pressure—which is related to the number of introduction routes and population density—and changes in land use and habitat transformation, which can both impact native biodiversity by leaving ecosystem gaps that can be exploited by non-native species (empty niche and opportunity windows hypotheses; Champion, Clayton, & Hofstra, 2010; Compton, De Winton, Leathwick, & Wadhwa, 2012; Hierro, Maron, & Callaway, 2004; Shea & Chesson, 2002). When the occupation of empty niches by non-native species is combined with different disturbance events (disturbance hypothesis), the entry of other non-native species may be facilitated, producing a domino effect known as invasion meltdown (Hood & Naiman, 2000; Mack, 2003).

SDMs yield biogeographical and ecological data that allow the development and implementation of effective management strategies and that provide guidance on how to prioritise the deployment of limited resources (Gordon, Onderdonk, Fox, & Stocker, 2008; Havel et al., 2015; Vander Zanden & Olden, 2008). Although tools exist for establishing the areas in which the management and control of non-native species should be prioritised, no study has yet sought to analyse the broad spectrum of non-native aquatic plants present across all of Europe. Only region or species-specific studies have been carried out (Gallardo & Aldridge, 2013b; Gallardo et al., 2015; Kelly et al., 2014; Rodríguez-Merino, Fernández-Zamudio, & García-Murillo, 2017).

Here, we focused on the current distribution of non-native aquatic plants in Europe (in total 60 species). There were three main objectives: (1) to identify areas that could potentially be colonised by non-native aquatic plants using species-specific SDMs based on bioclimatic and socioeconomic variables; (2) to overlay these species-specific models to generate combined invasion risk maps, revealing the areas of Europe at greatest risk of multiple invasions—maps were created using all 60 species and using the ten most harmful species in Europe; and, (3) to identify the physicochemical characteristics of water bodies and sediments in these areas of greatest invasion risk.

2. Material and methods

2.1. Study area

The models developed in this study are global in scale, and Europe was selected as the focal region. Over the centuries, Europe has been a center for international trade by different civilisations and, as a consequence, a large number of non-native species have become established there (Keller et al., 2011). Europe is of particular interest because it is one of the most threatened regions of the world as a result of the species introductions that mainly took place during the late twentieth century (Early et al., 2016). Furthermore, part of Europe falls within the Mediterranean basin, an important biodiversity hotspot whose conservation is crucial (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Finally, both species invasions and habitat disturbance are major causes of biodiversity loss in this region (Sala et al., 2000).

2.2 Species occurrence data

Sixty non-native aquatic plants that are present in Europe were modelled (Table A.1). The list came from Hussner (2012) and was modified in the following way: (1) species considered native in any part of Europe were eliminated; (2) species with low sample sizes were excluded to avoid model performance issues ($n \geq 10$) (Papeş & Gaubert, 2007); and, (3) species with lower performance values in the SDMs (i.e., under 0.7) were eliminated (Elith & Leathwick, 2007).

For each species, all available occurrence data in both the native and invasive ranges were included to avoid underestimating the fundamental niche (Jiménez-Valverde et al., 2011); this approach is the most common one (but see Bradley, Blumenthal, Wilcove, & Ziska 2010). These data were obtained from the Global Biodiversity Information Facility (GBIF, 2016). Only records from 1950 onwards were included in order to match the framework for current climate data (Gillard, Thiébaud, Deleu, & Leroy, 2017; Kelly et al., 2014). The data set was cleaned up by removing erroneous taxonomic occurrences, duplicates, and geographic outliers using R software (R Core Development Team, 2014). Additionally, spatial autocorrelation in the data was reduced to minimise problems with model overfitting (Boria, Olson, Goodman, & Anderson, 2014). The criterion was that the distance between data pairs should be less than 10 km; the same grid cell was used in the resolution of the predictor layers. By avoiding possible biases in data distributions, this filtering protocol allows occurrence

data from databases (e.g., the GBIF) to be effectively used to analyse macroecological patterns (García- Roselló et al., 2015).

2.3. Predictor layers

Nineteen different bioclimatic layers (Table A.2) were obtained from WorldClim-Global Climate Data (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Worldclim, 2015). The variables chosen focused on temperature and precipitation and represent annual trends, seasonality, and extremes that are relevant to species survival and distribution (Hijmans et al., 2005). Climatic variables can be used as filters to delimit the potential distributions of non-native species on a coarse scale (Gallardo et al., 2015; Kelly et al., 2014). The resolution chosen here was 5 arc minutes (~10 km at the equator).

The human footprint (HFP) was considered to be a suitable way of quantifying anthropogenic activity; it integrates different types of geographic data (Sanderson et al., 2002) and reflects land-use-related disturbances—such as urbanisation, communication routes, and farming—that could significantly influence the distribution of non-native aquatic plants (Gallardo & Aldridge, 2013b; Gallardo et al., 2015; Kelly et al., 2014). HFP data were obtained from the Socioeconomic Data and Applications Center (SEDAC, 2015). Since the resolution level was 30 arc seconds (~1 km), it was transformed to 5 arc minutes and projected using the World Geodetic System (WGS 1984) to achieve equivalence with the WorldClim layers.

Dimensionality among variables was reduced using Pearson's correlation coefficient analysis, which was performed with the raster package in R (Hijmans & van Etten, 2015). Variance inflation factors (VIFs) were used to assess collinearity among variables and to decide which ones to retain; the HH package in R was used (Heiberger, 2015). The number of variables was reduced to eight because the use of many layers, especially those associated with small sample sizes, could increase model overfitting (Heikkinen et al., 2006). The variables that remained in the model were annual mean temperature (Bio 1), temperature seasonality (Bio 4; standard deviation*100), minimum temperature in the coldest month (Bio 6), mean temperature in the warmest quarter (Bio 10), annual precipitation (Bio 12), precipitation seasonality (Bio 15; coefficient of variation), precipitation in the driest quarter (Bio 17), and HFP. Mean temperature and precipitation as well as their seasonal variation can influence species phenology (Forrest

& Miller-Rushing, 2010). The other variables represent different kinds of stress, such as cold stress (Bio 6), heat stress (Bio 10), and drought stress (Bio 17), which can place limits on species distributions (Godefroid, Cruaud, Rossi, & Rasplus, 2015).

2.4. *Species distribution modelling*

The maximum entropy algorithm, MaxEnt version 3.3.3k, was used to generate niche models (Phillips, Anderson, & Schapire, 2006). The MaxEnt algorithm is one of the most effective presence-only data algorithms available and has been shown to perform well even when sample sizes are low and there are moderate georeferencing errors (Elith et al., 2006; Mateo et al., 2013; Phillips et al., 2006; Wisz et al., 2008).

The SDMs developed in this study were global in scale, and Europe was selected as the focal region. The modelling parameters described in Phillips et al. (2006), Phillips and Dudík (2008), and Elith et al. (2011) were used. The maximum number of iterations was 1,000, and the number of background points was 10,000. To reduce the probability of model overfitting, the multiple regularisation parameter was changed to 2.5 from the default of 1 (Elith et al., 2010; Gallardo & Aldridge, 2013a; Rodríguez-Merino et al., 2017). The models were calibrated using 70% of the occurrence data, and the remaining 30% of the data was used to test the models obtained. In addition, for each model, a 10-fold cross-validation procedure was used to estimate the errors associated with the fitted functions and the predictive performance of the data that had been set aside (Elith et al., 2011). The output was the probability of presence for each species, which took on a value between zero and one (Phillips & Dudík, 2008).

Model performance was assessed using the area under the receiver operating characteristic (ROC) curve (Hosmer & Lemeshow, 2000), or the area under the curve (AUC) for short. Calculating the AUC is one of the most common methods for evaluating presence-only data models (Merow, Smith, & Silander, 2013). This metric reflects a model's ability to discriminate among suitable and unsuitable habitats (Phillips et al., 2006). The AUC was calculated for each model, and the mean AUC was then determined for a set of 10 replicates to obtain a more robust estimate of predictive performance (Barnes et al., 2014).

2.5. *Invasion risk maps*

The 10th percentile training presence threshold was used to transform continuous maps into presence/absence maps (Jiménez-Valverde & Lobo, 2007; Liu, Berry, Dawson, & Pearson, 2005). This threshold was chosen because it does well at correctly predicting the presence of non-native species and representing species distributions in suboptimal habitats (Kelly et al., 2014; Pearson, Raxworthy, Nakamura, & Peterson, 2007; Reshetnikov & Ficetola, 2011). The highly conservative estimate of this threshold yields more significant and ecologically relevant results (Jarnevich & Reynolds, 2011).

A first invasion risk map was created by overlaying the presence/absence maps for the 60 focal species to produce stacked SDMs (Crafton, 2015; Gallardo et al., 2015; Thuiller et al., 2005); ArcGIS was used (ESRI, 2008). This map revealed the cumulative risk of invasion, and also highlighted those areas where the presence of aquatic invasive species is expected to be higher and, as a consequence, the places where invasion risk is expected to be higher. A second invasion risk map was created that just focused on the ten invasive species considered to be most harmful to aquatic environments in Europe by the European Parliament and the European Council (Commission Implementing Regulations EU 2016/1141 and EU 2017/1263 [Table 1]).

Table 1 near here

The invasion risk maps were then filtered such that only cells containing water bodies were retained (Gillard et al., 2017). The layer containing lakes, reservoirs, and wetlands was obtained from Lehner and Döll (2004), and the layer containing main rivers and tributaries came from the European Environment Agency (European Environment Agency, 2018). Layers were converted to raster format; cells of 5 arc minutes (i.e., study resolution) that contained at least one water body were selected.

2.6. Generalised additive model analysis

The relationships between physicochemical variables and invasion risk in Europe were analysed for the 60 focal species using generalised additive models (GAMs). GAM fitting allows predictor variables to be combined using non-specific functions, which is a helpful feature that is not available in other regression techniques (Wood, 2008). This analysis allowed the detection of the factors that prevail in areas at higher risk of invasion, which helps identify the environmental features that are facilitating non-native aquatic plant invasions.

Levels of nitrate, sulphate, dissolved organic carbon (DOC), alkalinity, and electrical conductivity in surface water and of phosphorus in sediment were obtained from the Geochemical Atlas of Europe (Salminen, Plant, & Reeder, 2005). These variables were used to characterise the trophic state of water sources in areas considered to be at higher risk of invasion and were chosen based on their predictive power. They have previously been used as predictive variables in models of potential species distributions (Gallardo & Aldridge, 2013a; Vieira et al., 2018), but this is the first time (to our knowledge) that they have been used to help understand the risk of invasion by non-native aquatic plant species. In ArcGIS software (ESRI, 2008), inverse distance weighting, a multivariate interpolation method, was used to create continuous maps of Europe in raster format (resolution: 5 arc minutes). By using a radius of 12 and a power of 2, the influence of the closest points was reduced and a smoother final surface was produced.

To carry out the GAM analysis, 10,000 random points were generated: they were distributed throughout Europe and separated from each other by 10 km. At these points, values were extracted for water and sediment physicochemical variables (independent variables) and for invasion risk for the 60 focal species (dependent variable). GAMs (poisson distribution and logarithmic link function) were then performed (Alahuhta, Heino, & Luoto, 2011). First, single-variable models were run to evaluate variable explanatory ability. Second, based on this information, a forward-selection approach was used to sequentially add variables until a model was obtained that explained the greatest amount of deviance (Hastie & Tibshirani, 1990). Third, the Akaike Information Criterion (AIC) approach was used to guide the selection of the smoothing parameters and the variables to include in the model (Akaike, 1974). Finally, both adjusted R^2 values and AIC were used to assess the suitability of the final model. Models were run using the *mgcv* package in R (Wood, 2006)

3. Results

3.1 Species occurrences

In total, there were 19,576 records for the 60 focal species (Table A.1). The mean per species was 326.27 records. *Elodea nuttallii* had the most (1,741), and

Hygrophila polysperma had the fewest (15). The number of non-native aquatic plant species in Europe has increased over time. One large spike occurred during the 1960s (Fig. 1).

Fig. 1 near here

3.2. Species distribution modelling

Based on the AUC values (all above > 0.914 (mean = 0.953; SD = 0.022); see Table A.1), the models were good at predicting species presence/absence (i.e., significantly better than random chance). For the applied threshold, the omission rates for the binomial test were close to zero, and each of the 10 replicates yielded statistically significant results ($P < 0.001$), indicating model reliability.

The potential distributions of the focal species were better explained by temperature-related variables (46.44%) than by precipitation-related variables (31.64 %) (Table 2). The variable with the greatest explanatory ability for most of the species was HFP (21.92%) (Table 2): some of the highest percentages were obtained for *Egeria densa* (50.11%), *H. polysperma* (50.50%), and *Nymphaea mexicana* (62.61%) (Table A.1). HFP explained more than 10% of total variance for 80% of the focal species. Temperature seasonality and annual mean temperature were the main variables explaining species distributions (16.70% and 16.04%, respectively). Precipitation in the driest quarter was the precipitation-related variable that made the greatest contribution (14.19%) (Table 2).

Table2 near here

The potential distributions of the ten most harmful species in Europe are depicted in Figure 2. The general and water-body-filtered maps of presence and absence are in the appendix (Fig. A.1 and Fig. A.2, respectively).

Fig. 2 near here

3.3. Invasion risk maps

The invasion risk map for the 60 focal species revealed the areas that are at risk of a large number of aquatic species invasions (general map: Fig. 3A; water-body-filtered map: 3C). In these areas, environmental conditions may promote the colonisation and spread of focal species. They include major river basins and locations with intense anthropogenic activity, like urban centres, major seaports, coastlines, and agricultural regions (or other regions with high levels of land-use transformation). One of the most at-risk areas is the British Channel and southern North Sea. Others are the littoral region in Italian Peninsula, the Atlantic zone of the Iberian Peninsula and the area fringing the Mediterranean Sea for Iberian Peninsula and France (Fig. 3A). The invasion risk map for the ten most harmful species in Europe shows a similar pattern (general map: Fig. 3B; water-body-filtered map: 3D). However, it is clear that their distribution is limited in northeastern Europe.

Fig. 3 near here

3.4. Generalised additive model analysis

The final model included all the variables and explained 48.6% of the total deviance (Table 3). Indeed, the risk of invasion was higher in areas with higher levels of nitrate (deviance explained: 39.5%), electrical conductivity (deviance explained: 32.6%), and alkalinity (deviance explained: 31.9%). In contrast, invasion risk was lower in areas where DOC was higher (Fig. 4).

Table 3 near here

Fig. 4 near here

4. Discussion

Our study is the first to biogeographically assess the invasion risks associated with a large number of non-native aquatic plants within Europe as a whole. This goal was accomplished using modelling techniques commonly exploited in species distribution studies (Thuiller et al., 2005). Our results highlight that the most at-risk

areas may face intense invasion pressure because their environmental and anthropogenic conditions favour the establishment of non-native aquatic plant species.

The number of non-native aquatic plant species in Europe has increased over recent decades (Keller et al., 2011). Humans are vectors for these species in a highly globalised world; the lack of barriers allows their numbers to ever increase (Havel et al., 2015; Strayer, 2010). Furthermore, there was a peak in establishment events in the 1960s, a possible effect of the Green Revolution. During this period, traditional agricultural systems were replaced by intensive agricultural systems, a process that helped establish a multitude of non-native aquatic species. Intensive agriculture transforms ecosystems and has a strong negative effect on biodiversity (Verhoeven & Setter, 2010). High levels of fertilisers and pesticides were used to improve crop productivity (Horlings & Marsden, 2011; Tilman, Cassman, Matson, Naylor, & Polasky, 2002). Freshwater systems act as reservoirs for nutrients and pollutants flowing in from adjacent crop fields. The resulting habitat alterations can create invasion opportunities, which could transform natural habitats and thus create new niches, a process that would facilitate the establishment of various non-native aquatic species (Zedler & Kercher, 2004).

Our results indicate that invasion risks are highest in southern and western Europe, particularly around the British Channel (in northwestern France, Belgium, the Netherlands, northern Germany, and southern Great Britain). Other high-risk areas include the northwestern Iberian Peninsula, the Italian Peninsula, and the western Balkan Peninsula. In these areas, conditions would seem to promote the establishment of a greater number of non-native aquatic plant species. Bellard et al. (2016), Gallardo et al. (2015) and Liu, Guo, Ke, Wang, and Li (2011) have suggested that these areas could be more readily colonised by different groups of non-native species, an assessment that is supported by our results.

Temperature-related variables had the strongest link to invasion risk, like in other studies (Gillard et al., 2017). Temperature seasonality was the best at explaining the distributions of non-native aquatic plants (Bellard et al., 2016; Root et al., 2003), followed by annual mean temperature, which is considered one of the best predictors for the distribution of freshwater aquatic species (Gallardo et al., 2015). Variables reflecting

cold or heat stress are more useful in delimiting the distributions of different species (Araújo et al., 2013). With regards to the precipitation-related variables, the most relevant was precipitation in the driest quarter, followed by annual precipitation. This finding underscores the importance of water availability in the maintenance of the aquatic communities in ephemeral systems, shallow-water systems, and isolated water bodies (Reshetnikov & Ficetola, 2011). Our results support the hypothesis that invasion success depends on climatic variables (Ficetola, Thuiller, & Miaud, 2007; Gallien et al., 2010; Thuiller et al., 2005). Like Theoharides and Dukes (2007), we found that decreased temperatures can act as barriers in species distributions. They cause areas to be more inhospitable to the colonisation and spread of non-native species, which mostly originate from warm and temperate environments (Hussner, 2012; Hussner, Van de Weyer, Gross, & Hilt, 2010). Nonetheless, aquatic plants are known to be extremely plastic in their traits (Ren & Zhang, 2009; Santamaría, 2002), which allows them to compete across broad environmental conditions. One interesting case of study is the invasion of *Azolla filiculoides* in Britain, where the species was found to be highly tolerant of extremely cold temperatures; it only died off when winters were very severe and temperatures dropped to -10°C (Janes, 1998). The ability of *A. filiculoides* to tolerate a wide range of environmental conditions and to reproduce under unfavourable conditions (i.e., via vegetative reproduction) makes it one of the most harmful invasive species found in aquatic ecosystems (Fernández-Zamudio, Cirujano, Sánchez-Carrillo, Meco, & García-Murillo, 2013; Janes, 1998).

Estimates of anthropogenic activity have been shown to be extremely useful in predictive models involving non-native species (Bellard et al., 2016; Gallardo et al., 2015; Rodríguez-Merino et al., 2017). Here, HFP had good explanatory power in most of the species distribution models. This pattern is likely due to the strong relationship between HFP and introduction pathways, dispersal mechanisms, and propagule pressure (Compton et al., 2012; Kelly et al., 2014). Although most of the focal species cannot naturally disperse over long distances, anthropogenic transport networks allow for efficient facilitated dispersal (Havel et al., 2015; Strayer, 2010). For example, transport networks and large river basins act as corridors for the introduction of non-native species (Gallardo et al., 2015).

Like those of Pyšek and Richardson (2010), our results support the hypothesis that non-native species are more common in anthropogenic environments than are native species. Indeed, such environments can result in the formation of unoccupied niches that can be filled by non-native species (Catford & Downes, 2010; Quinn, Schooler, & Van Klinken, 2010). The invasion risk maps revealed that the areas at greatest risk are those experiencing greater anthropogenic pressure (e.g., river floodplains, transport networks, agricultural zones, and urban areas), a relationship that has been highlighted by other researchers as well (Bellard et al., 2016; Gallardo et al., 2015; Rodríguez-Merino et al., 2017). *Eichhornia crassipes* is a clear example of a non-native species that does well in anthropogenic environments; it takes advantage of the increased nutrient levels that result from intensive agricultural activity in adjacent floodplains, and also disperses along irrigation channels (Ruiz et al., 2008). These factors, combined with the species' reproductive capacity, make it one of the most devastating aquatic invaders in the world (Kriticos & Brunel, 2016; Lowe, Browne, Boudjelas, & De Pooter, 2004).

High levels of nitrate, phosphorus, and sulphate are associated with eutrophication in aquatic systems; availability of these nutrients is tied to the intensification of industrial and agricultural activities (Salminen et al., 2005; Santamaría, 2002; Smith & Schindler, 2009). Most non-native species can easily exploit higher levels of nutrient availability (Davis, Grime, & Thompson, 2001), such as those found in southern Great Britain, northern inland Europe, and certain parts of the Mediterranean Basin. High nitrogen levels seem to be a component of environmental suitability for non-native aquatic plants. It is known that nitrogen helps limit the distribution of aquatic plant species (Hutchinson, 1975). However, because non-native aquatic plants display greater plasticity and tolerance than native aquatic plants, the former may make more effective use of nitrogen, which would allow them to colonise and spread in high-nitrogen environments (Lukács et al., 2017). Areas with higher alkalinity and electrical conductivity occur in southern Great Britain, northern and central inland Europe, and the Mediterranean Basin, all of which display higher invasion risks (Fig. 3A). These results support the hypothesis that, as compared to native aquatic plants, non-native aquatic plants have a greater affinity for more alkaline water bodies (Capers, Selsky, Bugbee, & White, 2009). While high levels of alkalinity

are usually the result of geological conditions (Frick & Norvell, 1984), industrial and household waste may also contribute (Salminen et al., 2005). DOC levels are highest in regions with humic environments, which are not suitable for most of the focal species (Salminen et al., 2005). These regions are mostly located in northern Europe (northern Great Britain, northern Ireland, and Scandinavia), where invasion risk is lower. They are also high in areas where agricultural waste, organic fertilisers, and manure are abundant—the resulting carbon makes its way into nearby water bodies, increasing DOC concentrations (Molinero & Burke, 2009). High DOC levels can have various ecological consequences; for example, they can increase water turbidity or reduce rates of photosynthesis and respiration (Steinberg et al., 2006), limiting the occurrence of aquatic plants. Of particular importance is the use of carbon for photosynthesis, which is a limiting factor in the growth of aquatic plants, because it is generally found in low concentrations in freshwater ecosystems. For this reason aquatic plants are forced to acquire a series of changes to maximise growth rates. Among these mechanisms of carbon acquisition are the development of aerial or floating leaves (morphological changes), or the use of crassulacean acid metabolism, or the C₄ metabolism found in the genus *Hydrilla* or *Egeria* (physiological and biochemical changes) (Maberly & Madsen, 2002). For example, the use of HCO₃⁻ as a carbon acquisition mechanism is the most widespread strategy in aquatic systems of high alkalinity, this fact could explain the affinity of certain species for alkaline rich freshwaters and the difference in the geographic distribution of certain invaders (Maberly & Madsen, 2002).

Taken together, our results suggest that the most at-risk areas are those with increased levels of eutrophication, as well as those in which propagule pressure is high due to the greater number of introduction pathways. The high degree of disturbance at such locations provides a colonisation opportunity for non-native species (Nilsson & Berggren, 2000) because they are more likely to invade modified or degraded aquatic habitats than more natural habitats (Bunn & Arthington, 2002; Dudgeon et al., 2006).

Although SDMs are a common tool for determining the potential distributions of non-native species, they should still be used with care. It is important to note that areas at low risk of invasion on the map could be considered by some authors to be "coldspots" (e.g., Kelly et al., 2014). This interpretation should be made with caution because species distribution models assume niche conservatism over time and space

(Peterson, 2011). Indeed, species' complete niches are frequently underestimated (Fletcher, Gillingham, Britton, Blanchet, & Gozlan, 2016; Tingley, Vallinoto, Sequeira, & Kearney, 2014) because assessments of habitat suitability are based exclusively on the variables included in the models. The accessibility of other, less favourable areas when more suitable areas are not available is not taken into account. This caveat is important because, given climate change, more areas may become suitable for non-native species in the not-too-distant future (Gillard et al., 2017; Havel et al., 2015; Hussner et al., 2010; Sheppard et al., 2006). Due to invasive species are typically generalists and have the capacity to tolerate broad climatic conditions (Walther et al., 2009), the effect of climate change is one of the factors that could affect the geographic distribution of invasive species in the future (Hellmann, Byers, Bierwagen, & Dukes, 2008). Increasing temperatures and alterations in flow regimes—caused by precipitation-based changes to surface water quality (Whitehead, Wilby, Battarbee, Kernan, & Wade, 2009)—are expected to alter the potential distributions of different species (Bellard et al., 2013), creating a northward trend (Gillard et al., 2017). These changes could also be one of the main drivers of future biological invasions (Bellard et al., 2013).

In the case of aquatic plant species, distribution patterns can be limited by factors such as dispersal barriers, historical biogeography, or biotic relationships (Pont, Hugueny, & Oberdorff, 2005). However, when humans act as vectors, such constraints may become irrelevant (Gallardo & Aldridge, 2013b). In any case, in the type of research undertaken in this study, it is preferable to overestimate potential species distributions (Jiménez-Valverde et al., 2011).

Record number is another important element to consider when modelling the potential distributions of non-native species since it could affect the ability to characterise habitat suitability. Past studies have estimated the minimum number of records needed and have found that a greater number of records will lead to more precise models (Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008). The number of records used in this study allowed a good level of precision.

Increasingly, models of potential species distributions are employing water-body filtering (Gillard et al., 2017). We decided to show both general maps and filtered maps

because layers containing information on water body surfaces remain incomplete. This fact means that valuable information related to habitat suitability is unavailable. For example, Mediterranean temporary ponds, small streams, and artificial water bodies such as irrigation channels and irrigation pools do not currently appear on continental-scale maps; they do, however, potentially provide suitable habitat for invasive species. Such species include *E. crassipes* and *Gymnocoronis spilanthoides*, which have both been detected in irrigation channels in Italy (Ardenghi, Barcheri, Ballerini, Cauzzi, & Guzzon, 2016; Brundu et al., 2013) or *Pistia stratiotes* in the South of Iberian Peninsula (García-Murillo, Dana, & Rodríguez, 2005).

Although the data used in the GAMs are reliable, they must be used with caution. First, these data were obtained via interpolation from measurements made at sampling stations distributed throughout Europe. However, they represent annual means (Salminen et al., 2005) and do not reflect any interannual variation or seasonality in the variables of interest. It is also important to recognise that interpolation precision will depend on variable range, which could lead to unrealistic results (Gallardo & Aldridge, 2013a). That said, we feel that these data suffice for a preliminary assessment of the physicochemical characteristics that prevail in the areas facing the greatest invasion risk. In contrast, we do not think it would be appropriate to use these data in the SDMs because data are not available for the species' entire distribution ranges (native and invasive); indeed, it is recommended that information on the native range be used when modelling of potential distributions (Jiménez-Valverde et al., 2011).

5. Conclusions

Our findings have helped identify areas in Europe that are at higher risk of invasion by non-native aquatic plants; we mapped the potential invasion risk by examining the influence of anthropogenic activity and climatic variables on non-native aquatic species colonisation and spread. In general, we wish to highlight the importance of paying attention to areas with mild winters and/or high levels of anthropogenic activity, such as southwestern Europe or the British Channel. These results can guide decision making, both by those managing non-native aquatic plant species and by those responsible for preserving biodiversity in aquatic systems (Strayer, 2010). Indeed,

studies like ours should make it possible to evaluate invasion risks even in remote and poorly studied areas (Hespanhol, Cezón, Felicísimo, Muñoz, & Mateo, 2015). Using modelling techniques to predict the early stages of colonisation and, more importantly, to anticipate the spread of non-native species could be key to efforts aimed at managing and preserving the natural environment (Liu et al., 2011; Thuiller et al., 2005).

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Figure legends

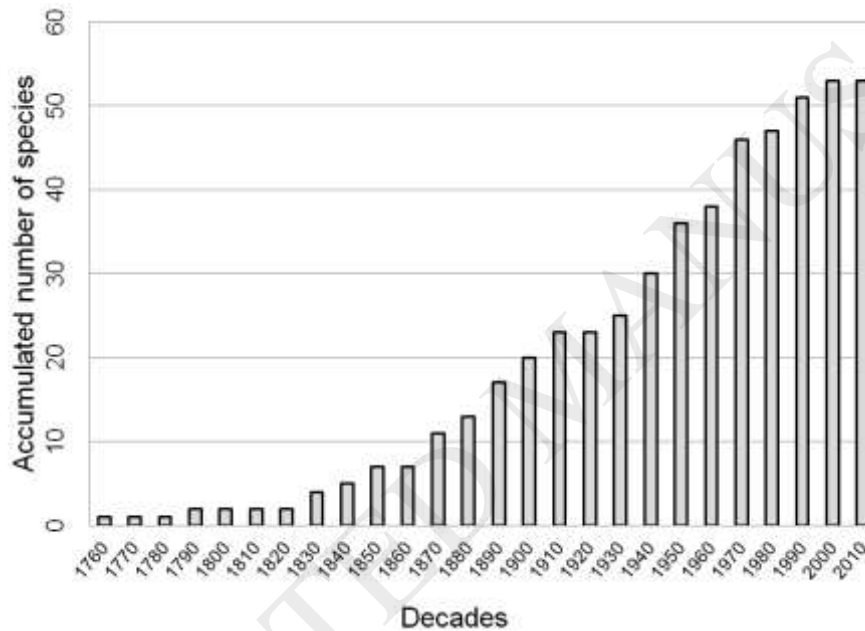
Fig. 1 Cumulative number of reported non-native aquatic plant species in Europe across time (from the 1760s to the 2010s) based on GBIF database records.

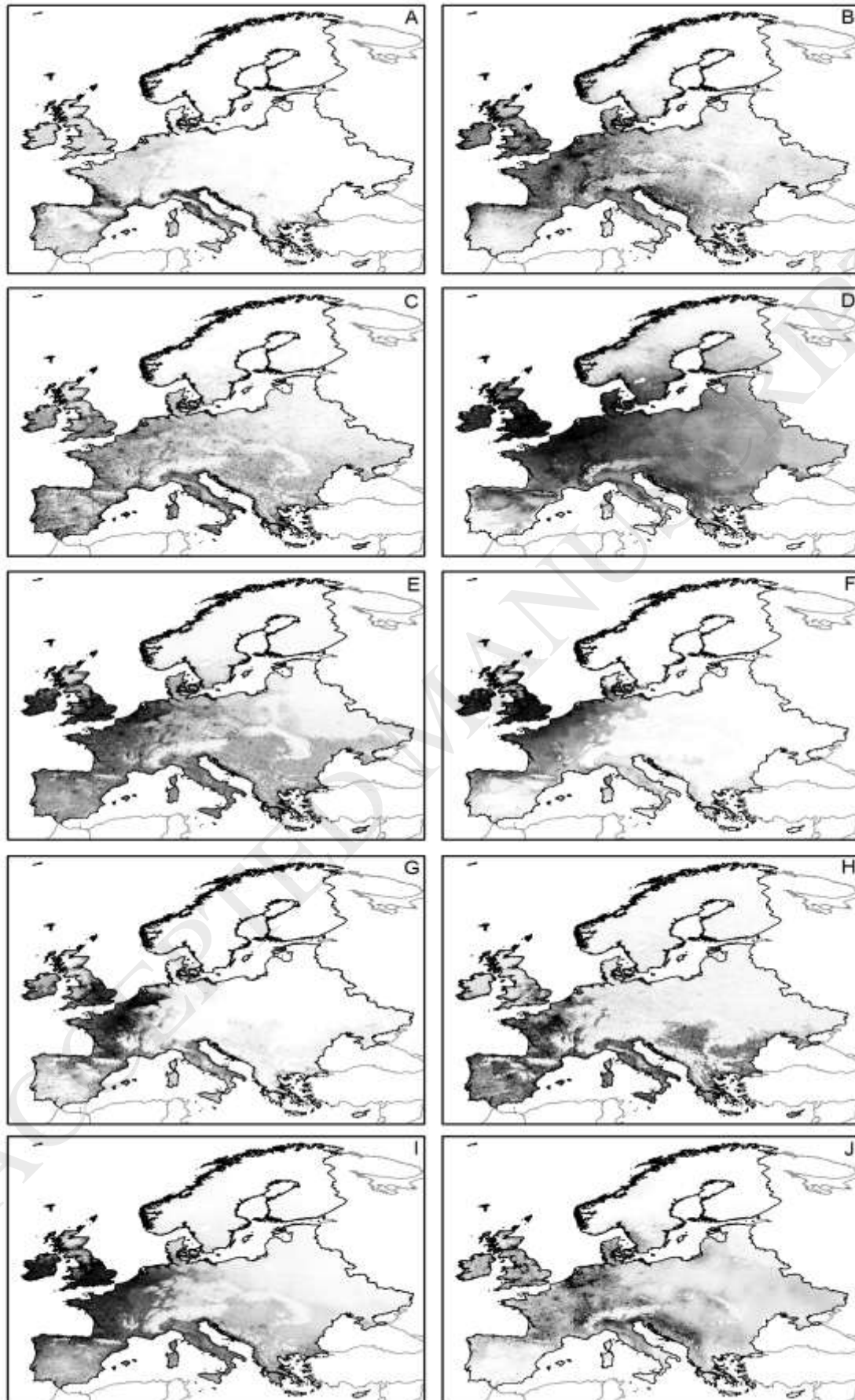
Fig. 2 SDMs for the ten most harmful species in Europe. MaxEnt logistic output. Darker colours indicate higher environmental suitability. **A.** *Alternanthera philoxeroides*. **B.** *Cabomba caroliniana*. **C.** *Eichhornia crassipes*. **D.** *Elodea nuttallii*. **E.** *Hydrocotyle ranunculoides*. **F.** *Lagarosiphon major*. **G.** *Ludwigia grandiflora*. **H.** *Ludwigia peploides*. **I.** *Myriophyllum aquaticum*. **J.** *Myriophyllum heterophyllum*.

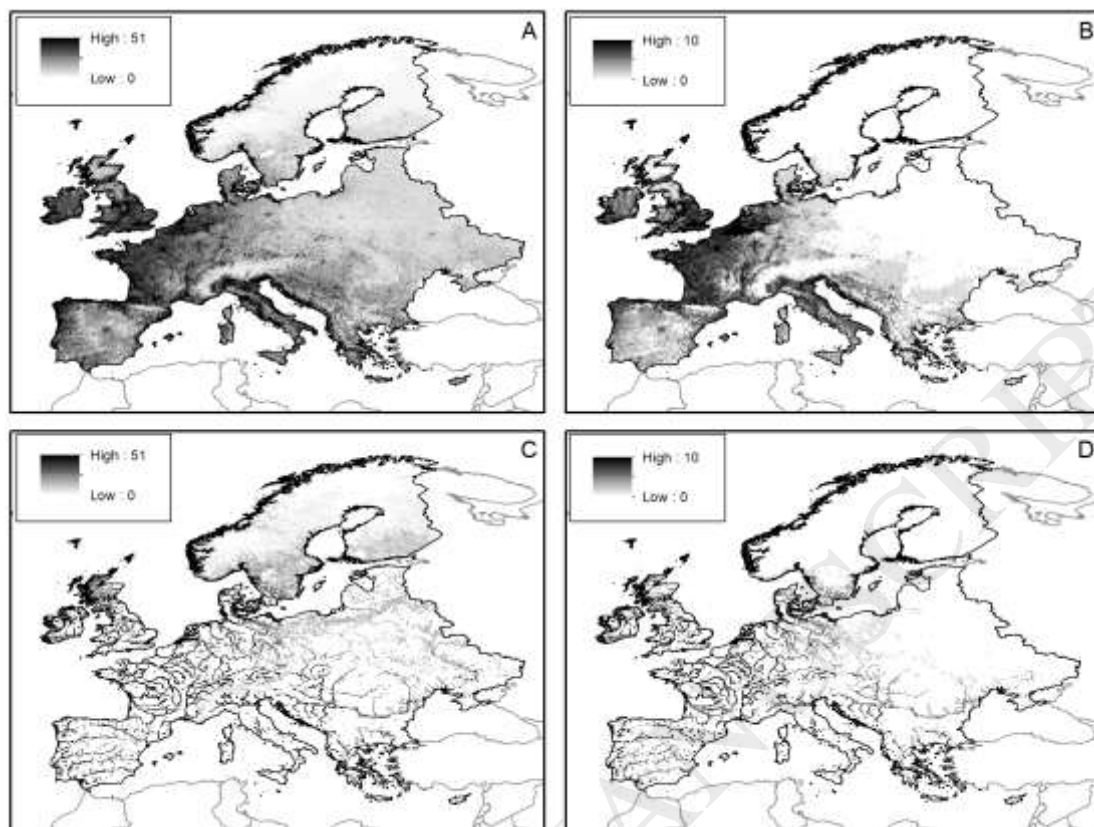
Fig. 3 Invasion risk maps illustrating the cumulative number of reported species in Europe. **A.** General map for the 60 focal species. **B.** General map for the ten most harmful species. **C.** Water-body-filtered map for the 60 focal species. **D.** Water-body-

filtered map for the ten most harmful species. The areas with highest cumulative risk scores are represented in dark grey.

Fig. 4 Results of GAMs performed to analyse the relationships between six physicochemical variables and invasion risk for the 60 focal species. The main-effects plot shows that when physicochemical variables had values of greater than zero, there was an effect on invasion risk. The shaded area depicts the 95% confidence interval. **A.** Nitrate. **B.** Phosphorus. **C.** Sulphate. **D.** Dissolved organic carbon. **E.** Electrical conductivity. **F.** Alkalinity.







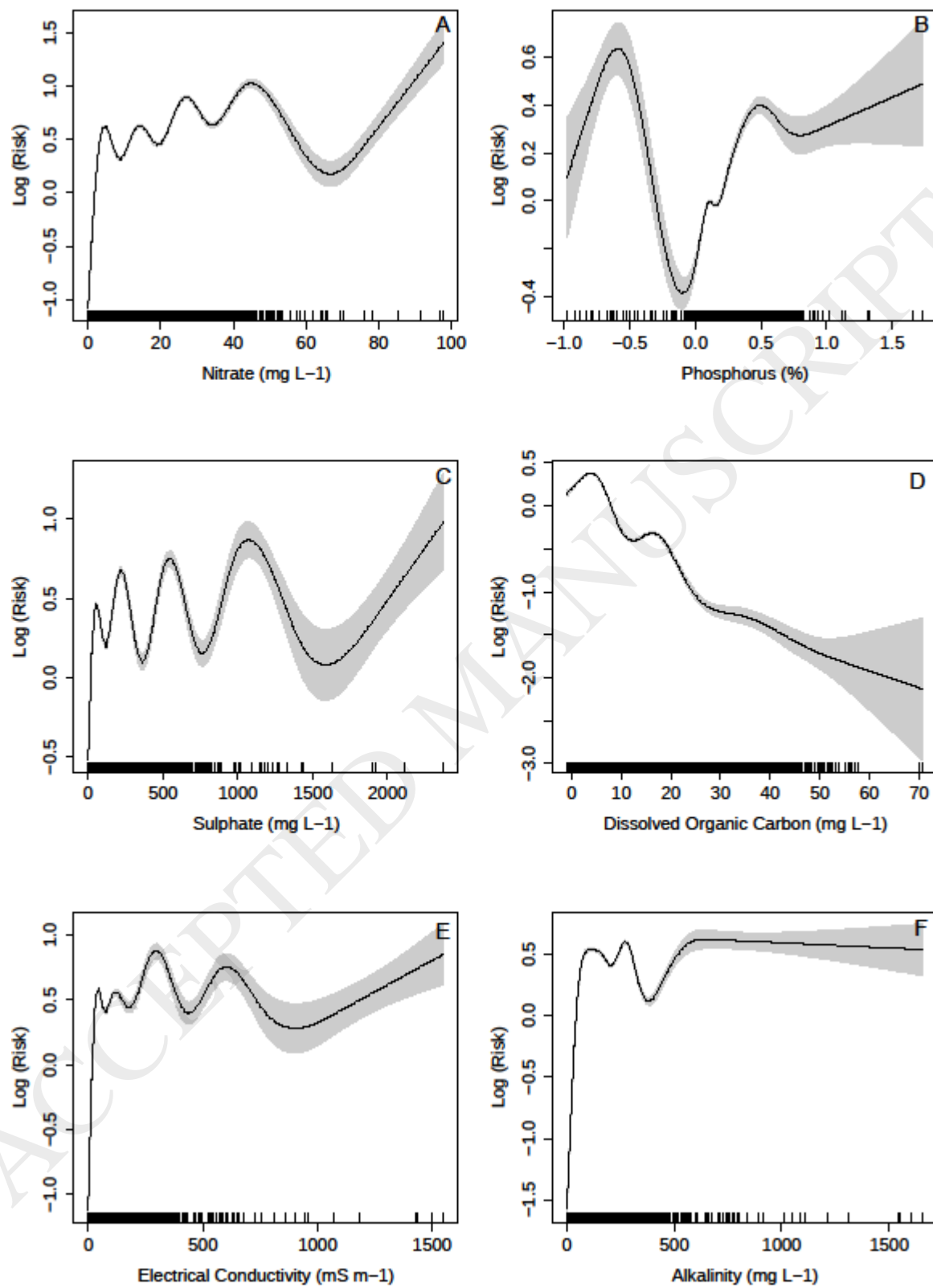


Table 1

The ten most harmful non-native aquatic plants in Europe according to the European Parliament and the European Council and conveyed by the following Commission Implementing Regulations (**CIRs**): **(1)** EU CIR 2016/1141 of 13 July 2016 adopting a list of invasive alien species of Union concern pursuant to EU Regulation No. 1143/2014 of the European Parliament and of the Council and **(2)** EU CIR 2017/1263 of 12 July 2017 updating the list of invasive alien species of Union concern established by EU CIR 2016/1141 pursuant to EU Regulation No. 1143/2014 of the European Parliament and of the Council.

Species	CIR
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	2
<i>Cabomba caroliniana</i> A. Gray	1
<i>Eichhornia crassipes</i> (Mart.) Solms	1
<i>Elodea nuttallii</i> (Planch.) H. St. John	2
<i>Hydrocotyle ranunculoides</i> L. f.	1
<i>Lagarosiphon major</i> (Ridl.) Moss	1
<i>Ludwigia grandiflora</i> (Michx.) Greuter & Burdet	1
<i>Ludwigia peploides</i> (Kunth) P. H. Raven	1
<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	1
<i>Myriophyllum heterophyllum</i> Michx.	2

Table 2

Contribution of different variables when building the SDMs. The table shows the percent contribution of variable groups (temperature, precipitation, and HFP = human footprint) and the percent contribution of individual variables (Bio 1 = annual mean temperature; Bio 4 = temperature seasonality [standard deviation * 100]; Bio 6 = minimum temperature in the coldest month; Bio 10 = mean temperature in the warmest quarter; Bio 12 = annual precipitation; Bio 15 = precipitation seasonality [coefficient of variation], and Bio 17 = precipitation in the driest quarter).

Variable groups	Variable	Percent contribution (%)	Standard deviation
Temperature		46.44	16.51
	Bio 1	16.04	13.33
	Bio 4	16.70	14.57
	Bio 6	8.89	8.83
	Bio 10	4.81	5.28
Precipitation		31.64	16.34
	Bio 12	11.94	12.32
	Bio 15	5.51	6.51
	Bio 17	14.19	14.07
HFP		21.92	13.52

Table 3

Estimates from the GAMs analysing the relationships between six physicochemical variables and invasion risk for the 60 focal species. DOC = dissolved organic carbon. R^2 (adj) = measure of model fit. Deviance (%) = percentage of variance in the data explained by the model. AIC = Akaike Information Criterion. Significance = ***; $p \leq 0.001$.

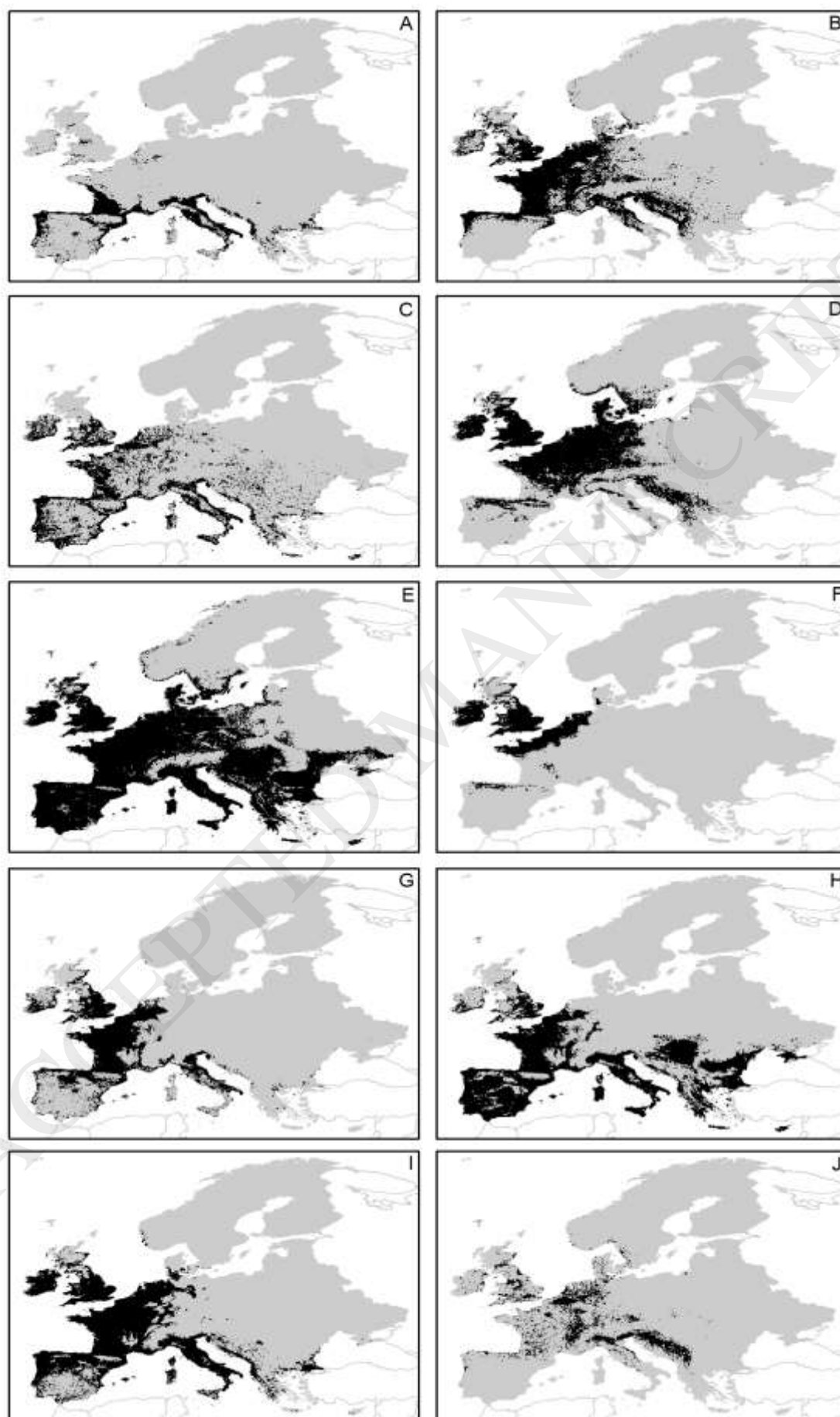
Model	Variables	p-value	R^2 (adj)	Deviance (%)	AIC
Nitrate		***	0.337	39.5	126906.1
Phosphorus		***	0.015	1.37	17629.4
Sulphate		***	0.134	15.7	157721.2
DOC		***	0.145	15.3	158236.0
Conductivity		***	0.281	32.6	135873.4
Alkalinity		***	0.294	31.9	136778.2
Full model		***	0.429	48.6	115150.1
	Nitrate	***			
	Phosphorus	***			
	Sulphate	***			
	DOC	***			
	Conductivity	***			
	Alkalinity	***			

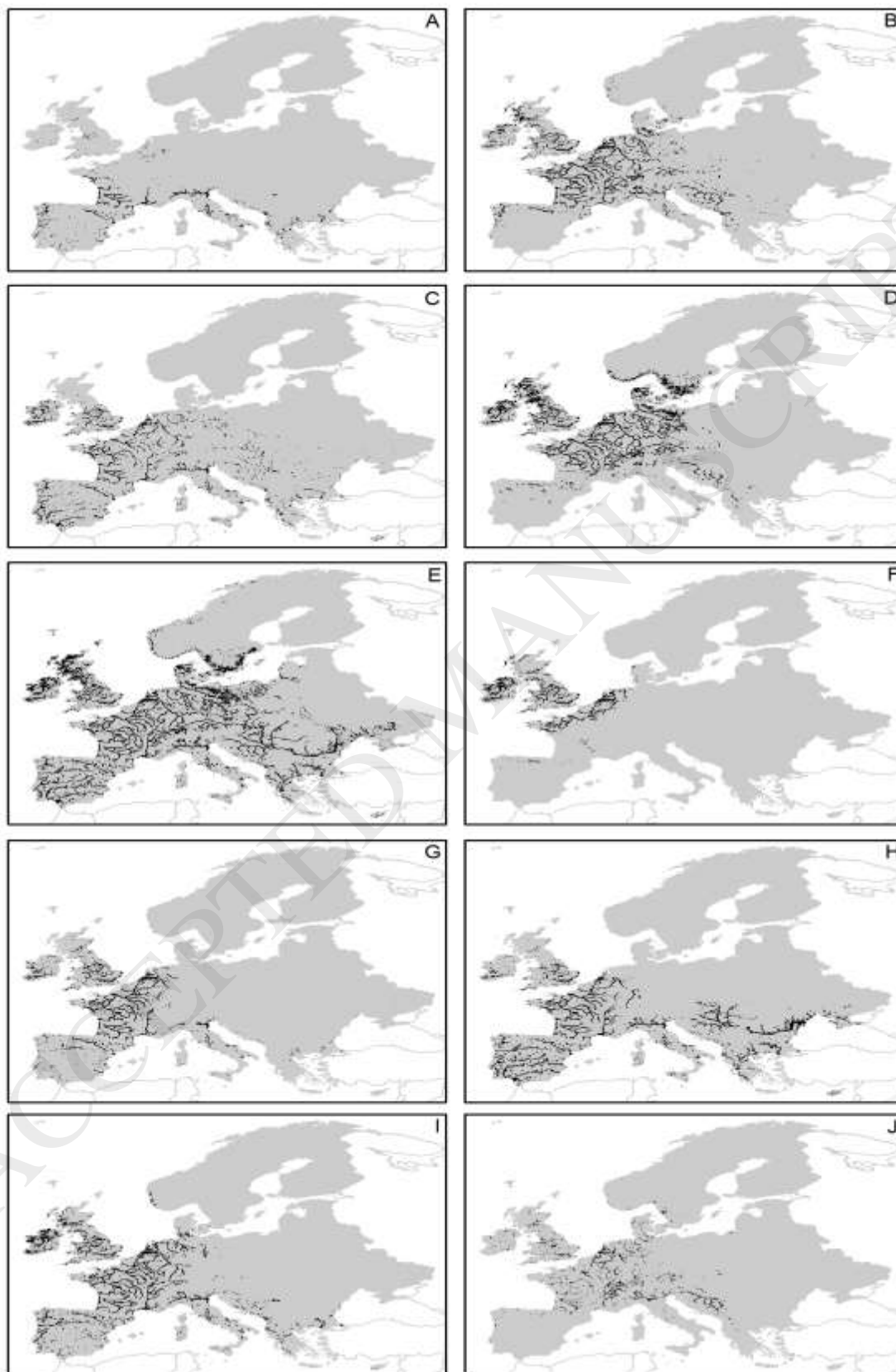
Appendix A

Fig. A.1 Presence/absence maps for the ten most harmful species in Europe. In black are the areas in which the species is present, based on the suitability threshold. **A.**

Alternanthea philoxeroides. **B.** *Cabomba caroliniana*. **C.** *Eichhornia crassipes*. **D.** *Elodea nuttallii*. **E.** *Hydrocotyle ranunculoides*. **F.** *Lagarosiphon major*. **G.** *Ludwigia grandiflora*. **H.** *Ludwigia peploides*. **I.** *Myriophyllum aquaticum*. **J.** *Myriophyllum heterophyllum*.

Fig. A.2 Presence/absence maps for ten most harmful species in Europe in which cells have been filtered by water-body presence. In black are the areas in which the species is present, based on the suitability threshold. **A.** *Alternanthea philoxeroides*. **B.** *Cabomba caroliniana*. **C.** *Eichhornia crassipes*. **D.** *Elodea nuttallii*. **E.** *Hydrocotyle ranunculoides*. **F.** *Lagarosiphon major*. **G.** *Ludwigia grandiflora*. **H.** *Ludwigia peploides*. **I.** *Myriophyllum aquaticum*. **J.** *Myriophyllum heterophyllum*.





ACCEPTED MANUSCRIPT

Table A.1

List of focal species. The table shows the number of records (N) used to build the individual models, the AUC values (mean \pm standard deviation) for MaxEnt model performance, and the percent contribution of variables to species-specific models. Bio 1 = annual mean temperature; Bio 4 = temperature seasonality [standard deviation * 100]; Bio 6 = minimum temperature in the coldest month; Bio 10 = mean temperature in the warmest quarter; Bio 12 = annual precipitation; Bio 15 = precipitation seasonality [coefficient of variation], Bio 17 = precipitation in the driest quarter; Human Footprint = HFP. The most important variable for each species is in bold.

Species	N	AUC \pm SD	Bio01	Bio04	Bio06	Bio10	Bio12	Bio15	Bio17	HFP
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	220	0.963 \pm 0.008	18.996	9.434	10.905	1.778	4.130	1.011	29.500	24.246
<i>Aponogeton distachyos</i> L.f.	122	0.987 \pm 0.004	13.224	34.765	13.894	9.394	0.788	12.136	5.963	9.837
<i>Azolla caroliniana</i> Willd.	152	0.932 \pm 0.010	8.649	5.968	17.431	5.567	6.215	2.546	25.209	28.415
<i>Azolla filiculoides</i> Lam.	1,497	0.929 \pm 0.003	23.238	31.333	14.534	0.878	1.180	7.577	1.020	20.241
<i>Bacopa monnieri</i> (L.) Wettst.	480	0.933 \pm 0.004	8.181	14.887	38.362	3.829	0.940	1.802	3.430	28.570
<i>Cabomba caroliniana</i> A. Gray	160	0.959 \pm 0.010	11.909	12.564	0.152	0.486	9.642	3.821	35.663	25.765
<i>Callitriche deflexa</i> A. Braun ex. Hegelm.	25	0.965 \pm 0.018	10.498	52.658	1.926	0.000	0.345	0.029	5.167	29.377
<i>Ceratopteris thalictroides</i> (L.) Brongn.	322	0.946 \pm 0.008	18.103	1.852	4.202	30.270	27.611	4.238	5.893	7.831
<i>Crassula helmsii</i> (Kirk) Cockayne	966	0.961 \pm 0.002	23.330	31.293	10.736	0.443	0.156	23.568	8.908	1.566
<i>Egeria densa</i> Planch.	278	0.954 \pm 0.005	8.394	8.483	13.851	3.396	1.602	1.001	13.163	50.111
<i>Eichhornia crassipes</i> (Mart.) Solms	704	0.914 \pm 0.005	18.483	2.569	21.979	3.192	14.841	1.447	4.008	33.481
<i>Elodea callitrichoides</i> (Rich.) Casp.	28	0.996 \pm 0.002	1.215	1.931	12.543	7.741	0.198	12.718	14.735	48.920
<i>Elodea canadensis</i> Michx.	928	0.932 \pm 0.002	37.405	7.395	1.728	11.101	2.251	3.405	18.391	18.323
<i>Elodea nuttallii</i> (Planch.) H. St. John	1,741	0.932 \pm 0.004	18.278	7.971	5.277	0.775	0.387	21.675	18.988	26.647
<i>Gymnocoronis spilanthoides</i> (D. Don ex. Hook. & Arn) DC.	70	0.985 \pm 0.004	19.762	11.707	3.964	0.595	15.337	2.629	36.070	9.936
<i>Heteranthera limosa</i> (Sw.) Willd.	260	0.950 \pm 0.009	31.217	5.596	1.310	6.763	13.160	8.605	11.037	22.312
<i>Heteranthera reniformis</i> Ruiz & Pav.	345	0.953 \pm 0.004	4.499	16.681	14.272	5.671	20.204	1.935	3.701	33.038

<i>Heteranthera rotundifolia</i> (Kunth.) Griseb.	164	0.960 ± 0.007	31.363	3.856	1.622	7.130	21.461	11.862	9.445	13.262
<i>Heteranthera zosterifolia</i> Mart.	21	0.921 ± 0.033	0.545	30.401	0.833	0.000	50.316	1.861	1.732	14.312
<i>Hydrilla verticillata</i> (L. f.) Royle	421	0.930 ± 0.008	33.646	13.333	1.393	4.907	22.433	2.230	9.675	12.384
<i>Hydrocotyle bonariensis</i> Lam.	346	0.959 ± 0.009	2.645	36.965	15.401	1.487	2.826	0.620	14.059	25.999
<i>Hydrocotyle moschata</i> G. Forst	91	0.994 ± 0.001	15.439	39.021	1.769	3.023	0.017	0.537	37.538	2.656
<i>Hydrocotyle ranunculoides</i> L.f.	380	0.939 ± 0.012	7.438	3.908	30.075	14.641	5.713	1.037	0.296	36.893
<i>Hydrocotyle sibthorpioides</i> Lam.	863	0.954 ± 0.004	21.962	4.587	33.256	0.068	4.221	0.352	34.811	0.742
<i>Hydrocotyle verticillata</i> Thunb.	297	0.937 ± 0.011	36.030	14.506	22.693	1.816	1.211	3.536	4.978	15.231
<i>Hygrophila polysperma</i> (Roxb.) T. Anderson	15	0.927 ± 0.033	5.927	31.155	11.659	0.305	0.218	0.110	0.123	50.503
<i>Lagarosiphon major</i> (Ridl.) Moss	572	0.975 ± 0.002	3.147	16.634	17.706	14.656	1.418	17.270	8.579	20.590
<i>Landoltia punctata</i> (G. Mey) Les & D. J. Crawford	80	0.944 ± 0.017	12.126	14.551	28.894	0.311	4.501	4.904	5.065	29.649
<i>Lemna aequinoctialis</i> Welw.	362	0.915 ± 0.011	55.542	11.274	0.909	4.752	18.286	1.501	2.858	4.879
<i>Lemna minuta</i> Kunth.	1,125	0.950 ± 0.004	17.372	17.085	4.350	4.128	0.654	23.790	6.701	25.921
<i>Lemna perpusilla</i> Torr.	55	0.927 ± 0.047	13.904	18.065	4.618	8.610	30.488	1.585	1.272	21.459
<i>Lemna turionifera</i> Landolt	286	0.959 ± 0.005	61.085	5.077	0.770	2.288	6.329	5.161	6.469	12.821
<i>Ludwigia grandiflora</i> (Michx.) Greuter & Burdet	170	0.980 ± 0.004	5.632	12.277	13.212	0.851	0.495	16.679	15.084	35.771
<i>Ludwigia peploides</i> (Kunth) P. H. Raven	374	0.932 ± 0.009	31.855	8.350	5.107	7.166	2.535	1.806	3.619	39.563
<i>Murdannia keisak</i> (Hassk.) Hand. Mazz.	96	0.979 ± 0.017	1.383	10.827	1.346	1.467	29.181	1.041	20.584	34.170
<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	711	0.953 ± 0.005	16.862	7.206	20.472	1.778	2.384	0.260	17.916	33.123
<i>Myriophyllum heterophyllum</i> Michx.	138	0.974 ± 0.002	11.712	9.465	11.159	1.472	20.186	9.561	22.431	14.015
<i>Myriophyllum verrucosum</i> Lindl.	625	0.952 ± 0.003	8.458	57.887	7.303	0.095	6.859	3.799	14.274	1.325
<i>Najas gracillima</i> (A. Braun ex. Engelmann) Magnus	77	0.955 ± 0.013	2.109	18.850	0.701	2.440	23.842	26.752	1.579	23.727
<i>Najas graminea</i> Delile	98	0.932 ± 0.014	20.151	9.149	2.173	8.722	34.314	12.630	4.097	8.764
<i>Najas guadalupensis</i> (Spreng.) Magnus	484	0.925 ± 0.006	25.681	7.450	3.113	8.356	9.828	4.635	9.686	31.251
<i>Nelumbo nucifera</i> Gaertn.	126	0.957 ± 0.006	19.968	6.633	2.877	6.550	29.853	3.467	6.501	24.152
<i>Nuphar advena</i> (Aiton) W.T. Aiton	43	0.962 ± 0.017	1.757	7.713	3.129	0.026	0.295	3.336	50.175	33.567
<i>Nymphaea lotus</i> L.	14	0.932 ± 0.020	9.035	68.751	2.145	2.743	2.332	0.836	0.761	13.397
<i>Nymphaea mexicana</i> Zucc.	46	0.967 ± 0.025	9.651	23.999	2.236	0.060	0.648	0.272	0.525	62.609

<i>Orontium aquaticum</i> L.	50	0.983 ± 0.010	0.901	12.316	4.257	7.670	0.386	0.175	59.591	14.703
<i>Ottellia alismoides</i> (L.) Pers.	85	0.944 ± 0.015	41.594	13.152	0.638	1.829	34.315	0.291	5.494	2.687
<i>Pistia stratiotes</i> L.	527	0.916 ± 0.008	10.760	21.425	13.064	6.719	26.232	0.672	1.806	19.322
<i>Pontederia cordata</i> L.	407	0.955 ± 0.005	8.048	11.500	0.302	5.109	16.626	4.555	41.369	12.492
<i>Potamogeton epihydrus</i> Raf.	262	0.943 ± 0.010	24.334	3.716	10.094	11.268	15.592	8.940	23.273	2.783
<i>Rotala indica</i> (Willd.) Koehne	92	0.984 ± 0.004	1.721	19.052	5.594	0.286	35.720	11.550	3.344	22.733
<i>Rotala ramosior</i> Koehne	245	0.931 ± 0.008	19.340	5.990	10.398	13.355	15.657	1.420	7.319	26.521
<i>Rotala rotundifolia</i> (Buch. Ham ex. Roxb.) Koehne	109	0.978 ± 0.011	9.705	15.133	13.302	0.059	38.222	5.187	0.923	17.470
<i>Sagittaria graminea</i> Michx.	149	0.967 ± 0.015	2.580	16.454	1.846	3.069	7.407	2.294	45.633	20.718
<i>Sagittaria latifolia</i> Willd.	495	0.918 ± 0.013	10.715	8.314	4.312	10.455	15.378	6.477	14.221	30.130
<i>Sagittaria platyphylla</i> (Engelm.) J. G. Sm.	137	0.982 ± 0.006	36.522	8.285	7.820	0.228	0.225	3.942	24.267	18.711
<i>Sagittaria rigida</i> Pursh	53	0.951 ± 0.009	25.133	0.717	3.163	1.132	20.701	1.919	7.484	39.752
<i>Salvinia auriculata</i> Aubl.	181	0.963 ± 0.010	3.729	37.350	10.730	6.012	16.370	0.993	14.173	10.643
<i>Saururus cernuus</i> L.	129	0.982 ± 0.006	0.408	13.450	1.966	11.829	14.418	7.393	38.381	12.156
<i>Vallisneria nana</i> R. Br.	151	0.972 ± 0.004	9.301	48.917	7.863	7.989	7.472	2.964	12.678	2.816

Table A.2

WorldClim-Global Climate Data variables and description.

Variables	Description
Bio 1	Annual mean temperature
Bio 2	Mean diurnal range (mean of monthly (max temperature – min temperature))
Bio 3	Isothermality (Bio 2/ Bio 7) * 100
Bio 4	Temperature seasonality (standard deviation * 100)
Bio 5	Maximum temperature of warmest month
Bio 6	Minimum temperature of coldest month
Bio 7	Temperature annual range (Bio 5- Bio 6)
Bio 8	Mean temperature of wettest quarter
Bio 9	Mean temperature of driest quarter
Bio 10	Mean temperature of warmest quarter
Bio 11	Mean temperature of coldest quarter
Bio 12	Annual precipitation
Bio 13	Precipitation of wettest month
Bio 14	Precipitation of driest month
Bio 15	Precipitation seasonality (coefficient of variation)
Bio 16	Precipitation of wettest quarter
Bio 17	Precipitation of driest quarter
Bio 18	Precipitation of warmest quarter
Bio 19	Precipitation of coldest quarter