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Research Article

Modelling hot spot areas for the invasive alien plant *Elodea nuttallii* in the EU

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Abstract

Elodea nuttallii is an invasive plant widely distributed in many European freshwater habitats. The species has been recently added to the list of invasive alien species of Union concern (European Union (EU) Regulation 1143/2014). We aim to investigate the species' potential distribution across the EU to provide a scientific basis for preventing further spread. To this end, we generated a model-based habitat suitability map for *E. nuttallii* in the EU, showing areas where the plant is most likely to establish and persist over time. The MaxEnt algorithm was used for implementing the map, taking into account environmental information and the most updated geographically referenced data on the species' occurrence. The R package ENMeval and extraction of occurrence data at three spatial scales were used to compensate for sampling bias and model overfitting. Our results suggest that most of the EU suitable areas for the establishment of *E. nuttallii* are already occupied by the species. Still, there are many non-infested areas across the EU, and considering the rapid spread of *E. nuttallii* and the highly connected waterbodies in Europe, it is likely that these areas will be invaded in the near future. Among these, several areas fall within sites of the Natura 2000 protected network. We suggest that these areas should receive conservation priority, and early warning and rapid response mechanisms should be locally developed against new introductions of the species.

Key words: prevention early warning, environmental variables, distribution modelling, habitat suitability, freshwater, Natura 2000

Introduction

Invasive Alien Species (IAS) constitute one of the most important threats to biodiversity, causing severe ecological and socio-economic impacts (Sarukhán et al. 2005; Ricciardi et al. 2013; Jeschke et al. 2014). At a conservative estimate, IAS cost the European Union (EU) Member States €12 billion in damages on an annual basis (Kettunen et al. 2009). Recognizing the need for a coordinated set of actions to prevent, control and mitigate alien species invasions, the European Parliament and the Council have adopted EU Regulation no. 1143/2014 on the prevention and management of the introduction and spread of IAS (EU 2014; hereafter referred to as the IAS Regulation).

It is widely accepted that prevention is the best strategy to tackle IAS, since it is much more cost efficient than eradication or containment and control (Heink et al. 2016). Key elements for effective prevention are early warning coupled with rapid response, to be implemented before an IAS can establish and spread widely (Genovesi and Shine 2004). Early warning can benefit from risk modelling and mapping indicating areas of high suitability for the successful establishment, reproduction and spread of an IAS (Baker et al. 2005). This kind of information can be valuable to managers and stakeholders to enable them to choose and prioritize measures in decision-making processes against IAS (Venette 2015).

Species Distribution Modelling (SDM), particularly Maximum Entropy Modelling (MaxEnt), can evaluate environmental suitability for the establishment of a species and indicate the probability of presence at non-sampled locations (Phillips et al. 2004). As a result, MaxEnt has been frequently used to assess risks related to the potential distribution of IAS (e.g. Rodda et al. 2011; Crall et al. 2013; Elith 2017). In addition, it is a widely used tool to aid coordination of prevention activities related to IAS (Ward 2007; Roura-Pascual and Suarez 2008; Vaz et al. 2008). Studied species include mysids, amphipods, crayfishes, and terrestrial and aquatic plants (Gallardo and Aldridge 2013; Kelly et al. 2014).

The perennial freshwater plant *Elodea nuttallii* (Planch.) John is an IAS in Europe. It can grow in lakes, reservoirs, ponds, rivers, streams, canals and ditches. It is most suited to meso- to eutrophic slow-flowing or static waters, but can even thrive in clear oligo-mesotrophic waters (Thiébaut et al. 1997; Greulich and Trémolières 2006). The species prospers in disturbed areas, particularly where large quantities of reduced iron are found (Thiébaut and Di Nino 2009). It tolerates salinity of up to 14 ppm (Josefsson 2011), its optimal pH is between 7 and 9, and it prefers calcium rich waters (Jones et al. 1993). The species grows best in shallow waters, occurring most frequently in less than 3 m depth (Simpson 1990; Xu et al. 2016), although it has been reported up to 5 m depth (Ikusima 1984).

Elodea nuttallii is native to the temperate regions of North America and was introduced into Europe through the ornamental and aquarium trade (EASIN 2018). The species is used as a pond oxygenator or for aesthetic purposes; in Ireland it can be found for sale in garden centers and pet shops (Wyse-Jackson 2014). Secondary spread is achieved through vegetative reproduction, which allows plant fragments to drift with currents (Cook 1987; Escobar et al. 2011). In Europe the species was first found in the wild in the United Kingdom (1914), and then in other European countries: Belgium (1939), the Netherlands (1941), France (1950s), Germany (1953), Austria (1970), Denmark (1974), Luxemburg (1980), Ireland (1984), Czech Republic (1988), Switzerland (1980s), Hungary and Sweden (1991), Italy (1994), Romania (1998), Slovakia

(2001), Bulgaria (2002), Serbia (2005), Croatia (2006), Norway (2006), Slovenia (2012), and Poland (2010) (Josefsson 2011; CABI 2018; EASIN 2018).

Elodea nuttallii can have major environmental and economic impacts. It can rapidly develop dense monospecific stands, which may fill entire lakes and watercourses, causing the reduction of native biodiversity and changing the balance of the entire ecosystem (Muller 2004; Barrat-Segretain 2005; Thiébaut and Di Nino 2009). *Elodea nuttallii* infestations can also hamper boating and angling, reduce water storage capacity and block intakes to hydro-electric systems (Larson 2003). Once established, the species is very difficult and extremely costly to control (Di Nino et al. 2005; Millane et al. 2016). It is therefore crucial to prevent its establishment in new areas. To this end, early detection is of paramount importance to prevent introductions in non-infested areas. Species Distribution Modelling has already been used for *E. nuttallii* (Luizza et al. 2016), although a model at the EU scale, indicating high-priority (alert) areas, has not been implemented so far.

In the current paper we produce a model-based potential distribution map of *E. nuttallii* within the EU, identifying areas currently free from the invasive plant, where the species is most likely to establish and persist over time. Uninfested areas included in the Natura 2000 network (European Environmental Agency 2015) should be prioritized due to their biodiversity value.

Materials and methods

MaxEnt requires good knowledge of the species biology and ecology, and is based on the relation of known occurrences to relevant environmental variables, such as climate data, water velocity and nutrients (Jarvenish and Young 2015). In the present study we have used MaxEnt software version 3.3.3k (Phillips et al. 2004) for producing the potential distribution map for *E. nuttallii* across the EU. MaxEnt requires two types of input data: raster grids containing environmental information and geographically referenced occurrence data of the species.

Environmental data

The environmental data chosen for this study fall in two broad categories: bioclimatic variables from http://www.worldclim.org (Hijmans et al. 2005), and environmental variables for Europe's river systems. The second set of data originated from two projects managed by the Joint Research Centre of the European Commission: data on nutrients generated by the Geospatial Regression Equation for European Nutrient losses (GREEN model) and data on hydromorphology and flow regime collected in the Water Pressure Indicators (WPI) project (Pistocchi et al. 2015).

The GREEN model output is generated through a statistical regression analysis based on geo-referenced input data for two different pathways (point and diffuse) of nutrient transfer from sources to the catchment outlet. The model estimates nutrient loads, nutrient diffuse emission and nutrient source apportionment at river basin scale (Grizzetti 2006). The model output is split into polygons of irregular size and shape, each one pertaining to a geographic identity that represents a unit of freshwater, i.e. river sub-basins (Bouraoui et al. 2011; Grizzetti et al. 2012).

Preparing environmental data for MaxEnt

The environmental data were mapped and processed using ArcGIS version 10.3 (ESRI 2011). As a first step, we selected the EU geographic area based on the corresponding coverage of all datasets. This included the whole EU territory with the exception of the EU overseas areas, Greece, Cyprus, Croatia and Malta. The EU's coastal regions, which are too saline for *E. nuttallii* persistence, were excluded. Subsequently, all raster layers were scaled to a grid cell size of 1 km^2, i.e. the resolution of the water velocity layer and the smallest unit.

The GREEN model polygons were scaled down to 1 km^2 grid size by slicing them into 1 km^2 squares. This represents a reasonable approximation of the polygon shape. These squares were then given the value of the GREEN polygon that contained more than 50% of the grid cell's surface area. No minimum overlap was set. Thus, the value of grid cells within a certain polygon did not differ for any of the GREEN model data layers. Moreover, some of the variables were discontinuous, e.g. the water velocity layer. For any discontinuous variables, the conversion to gridded datasets with grid cell sizes of 1 km^2 was done by calculating the average, minimum and maximum value of this variable for every GREEN polygon and attributing these values to each 1 km^2 grid cell which had its center inside the corresponding polygon. Thus, separate raster layers of the minimum, maximum and average values of the GREEN model variables were formed and values from datasets pertaining to water bodies were also assigned to land areas, making all environmental variables geographically continuous.

Selection of environmental layers

Since environmental datasets are almost always spatially auto-correlated, there is a high propensity for overly complex models in SDM. To overcome this issue the method presented by Lahoz-Monfort et al. 2010 was applied. This method implies running the MaxEnt model several times excluding one variable at a time (backward elimination). If the Area Under the Curve (AUC) rose when the variable was eliminated, the variable was left out. If the AUC decreased, the variable was inserted again. Thus, a "pruned" set of environmental data layers was created (Tables 1 and 2).

Table 1. Bioclimatic variables and corresponding units from worldclim.org used in the model final version.

Variable	Unit
BIO1 = Annual Mean Temperature	°C
BIO2 = Mean Diurnal Range	°C
BIO3 = Isothermality (P2/P7) (* 100)	dimensionless
BIO4 = Temperature Seasonality	°C
BIO5 = Max Temperature of Warmest Month	°C
BIO6 = Min Temperature of Coldest Month	°C
BIO7 = Temperature Annual Range (P5-P6)	°C
BIO8 = Mean Temperature of Wettest Quarter	°C
BIO9 = Mean Temperature of Driest Quarter	°C
BIO10 = Mean Temperature of Warmest Quarter	°C
BIO11 = Mean Temperature of Coldest Quarter	°C
BIO12 = Annual Precipitation	mm
BIO14 = Precipitation of Driest Month	mm
BIO15 = Precipitation Seasonality	mm
BIO16 = Precipitation of Wettest Quarter	mm
BIO17 = Precipitation of Driest Quarter	mm
BIO18 = Precipitation of Warmest Quarter	mm
BIO19 = Precipitation of Coldest Quarter	mm

Table 2. Variables from the WPI and GREEN models used in the final model, plus corresponding units and description.

Variable	Unit	Description
Mean water velocity	m/s	Average surface water velocity (WPI) per river sub-basin
Maximum water velocity	m/s	Maximum surface water velocity (WPI) per river sub-basin
Mean urban loads	dimensionless	Average pollution index from urban wastes (GREEN model) per river sub-basin
Maximum urban loads	dimensionless	Maximum pollution index from urban wastes (GREEN model) per river sub-basin
Mean Nitrogen concentration	$tons/m^3$	Average nitrogen concentration from both point loads and diffuse loads (GREEN model) per river sub-basin
N:P ratio	dimensionless	Average nitrogen concentration divided by mean phosphorus concentration (GREEN model) river sub-basin
Mean infrastructure	dimensionless	Average of the index of infrastructure in the river floodplain(s) (WPI) per river sub-basin
Minimum infrastructure	dimensionless	Minimum value of the index of infrastructure in the river floodplain(s) (WPI) per river sub-basin
Maximum infrastructure	dimensionless	Maximum value of the index of infrastructure (WPI) in the river floodplain(s) per river sub-basin

Occurrence data

Elodea nuttallii geographical occurrence data were gathered from the European Alien Species Informa-tion Network (EASIN)—which included data from the Global Biodiversity Information Facility (GBIF)—and the Floristic Institute for Belgium and Luxemburg (IBFL). The criteria for data selection were: a) collection date from 1995 or after, as those records were deemed most reliable, b) the inaccuracy estimate (as noted in the downloaded data) was less than 100 m, c) absence of coordinates and spatial issues (e.g. continent-country mismatches, invalid country, failed coordinate re-projection). In addition, the data had to fall within a rectangular geographic space with the corners at the following WGS1984 coordinates: 31.353636N; 28.125W, 67.875541N and 40.078125E, which correspond to the rough boundaries of the European continent. Moreover, when collecting the data from GBIF, only occurrences recorded on the following basis were used: Human observation, machine observation, observation, material sample, living specimen, literature occurrence and specimen. An analysis of GBIF records with the specified settings (GBIF.org 2018) conducted in December 2017 showed that out of 22,671 records 19,546 were field observations, only one was a literature reference, and 3,124 were observations, with no additional specifications.

All data were mapped in ArcGIS, using the projected coordinate system ETRS 1989 LAEA. In order to filter out false or inaccurate data we have used only data points that were inside the area covered by the original water velocity layer, which only included areas in Europe covered by water.

Methodological challenges

Species distribution modelling faces two major methodological challenges: sampling bias (Stolar and Nielsen 2015) and model overfitting (Radosavljevic and Anderson 2013).

Sampling bias

The creation of subsets of distribution data used in this study have been shown to minimize both false positives and false negatives in MaxEnt model predictions (Kramer-Schadt et al. 2013). Sampling bias was therefore tackled by placing two grids over the geographic distribution: one with a grid cell size of 10 × 10 km and one of 20 × 20 km. Subsequently, one occurrence data point per grid cell was extracted, thus forming two sets of input data. These subsets are referred to as subset 1 and subset 2 respectively and are presented graphically in Figure 4A and 4B. The coordinates can be found in Supplementary material Tables S1 and S2, respectively.

In order to further address the issue, version 1.0-27 of the sgeostat package (Gebhardt 2016) in the R programming language (R Core Team 2014) was used to analyze and eliminate spatial autocorrelation, following the method described in Veloz (2009). This package allows for determining the minimum distance between occurrence points at which they are no longer spatially autocorrelated. That distance is determined by fitting variograms to the data to analyze the degree of variance in the values of the environmental variables at the occurrence points. The distance at which that variance reaches a sill is the threshold beyond which the data are no longer spatially autocorrelated. This distance is known as the range and was found to be 60 km.

Subset 1 was subsequently thinned such that all points were at least 60 km apart. Thus subset 3 was created. It is presented graphically in

Figure 6B and its coordinates can be found in Supplementary material Table S3. It contained 149 occurrence points. Creating a similar subset from subset 2 was deemed unnecessary because 60 km is far above the average distance between 20 km occurrence points (which was 26323.5 meters).

The modelling tasks described below were performed on subsets 1, 2 and 3 separately.

<u>Model overfitting</u>

The ENMeval (Ecological Niche Modelling Evaluation) package of the R programming language, version 0.2.1 (Muscarella et al. 2014) was used to address this challenge. The package was first debugged, ensuring compatibility between the functions and the input data. This package has previously been used to build cost-effective monitoring schemes for IAS (Costa et al. 2015). The software package is specifically designed to indicate model settings optimal for overfitting minimization. It works as follows: MaxEnt uses several mathematical function types (linear, quadratic, hinge, product, threshold) and the Regularization Multiplier (RM), a controller of model complexity, to identify the relationship between data occurrence and the underlying environmental variables. ENMeval calibrates a MaxEnt model by pointing out the optimal settings of the function types and RM. These settings, indicated for both sets of occurrence data, were subsequently used to run the MaxEnt model on the dataset in question.

The measure used for optimal model settings was the mean difference in AUC values between testing and training data (mean AUC difference), which is expected to be high for models that are overfitted to data (Muscarella et al. 2014). When several values of the RM yielded the same mean AUC difference, the lowest value was selected to ensure maximum discernibility between suitable and unsuitable habitat (Costa et al. 2015). When different combinations of function types indicated the same mean AUC difference, the combination containing most functions was chosen. For subset 1, the output settings were a RM of 0.5, meaning a very rigid boundary between suitable and unsuitable habitat, and all function types. For subset 2, the output was a RM of 2.0 and again all function types. For subset 3, the output was to only use hinge functions and a regularization multiplier of 3.0. These 3 models are referred to as model 1, 2 and 3, respectively.

MaxEnt analysis and alert areas identification

The species distribution models were subsequently run on subset 1, 2 and 3 using MaxEnt, using the indicated optimization settings for each dataset. The AUC outputs for models 1, 2 and 3 were 0.968, 0.948 and 0.917, respectively. These were very high measures of model performance.

The sensitivity-specificity sum maximizer criterion was used to determine the threshold between suitable and unsuitable habitat (Jiménez-Valverde and Lobo 2007). This threshold was 0.081 for model 1, 0.126 for model 2 and 0.114 for model 3.

Priority areas

The outputs of models 1 and 2 and of models 1 and 3 were compared. Areas that had the same output in both models (below or above threshold suitability) were tagged with low uncertainty. Areas with both above threshold suitability and low uncertainty are the areas that should receive conservation priority and are referred to as "priority areas". This combined output was again mapped in ArcGIS.

Alert areas

After the identification of priority areas over the studied EU, the areas that should receive particular attention were identified. These were the areas over 100 km away from the nearest known *E. nuttallii* occurrence point and are referred to as "alert areas". Among these, the ones that fall within areas of the Natura 2000 conservation network (European Environmental Agency 2015) were identified.

Results

The influence of the environmental variables on model performance for models 1, 2 and 3 are given in Figures 1, 2, and 3 respectively. The figures present both the model performance when the variable is used in isolation and the loss in performance when the variable is omitted. In more generic terms, this means that the figures show both a measure of how much predictive information each variable contains and of how much information each variable contains that is not included in other variables. In the case of all 3 models, the variable which gave the greatest model gain when used in isolation was the mean temperature of the driest quarter of the year. In model 1, the variable that reduced the model performance the most when omitted was nitrogen concentration, while in models 2 and 3 it was the N:P ratio. In all three models, water velocity barely influenced model performance, either when omitted or when used in isolation.

The number of occurrence points used in each model are presented in Table 3, as well as graphically in Figures 4A, 4B, 6A and 6B. Figure 4C and 6C display the combined output of both models, including areas with high uncertainty and priority areas. The size of priority areas and alert areas are given in Table 4 (for models 1 and 2) and Table 5 (for models 1 and 3).

The alert areas are presented in Figure 5 for models 1 and 2 and in Figure 7 for models 1 and 3. More details (area name, surface area and Natura 2000 identification code of alert areas inside Natura 2000 sites) can

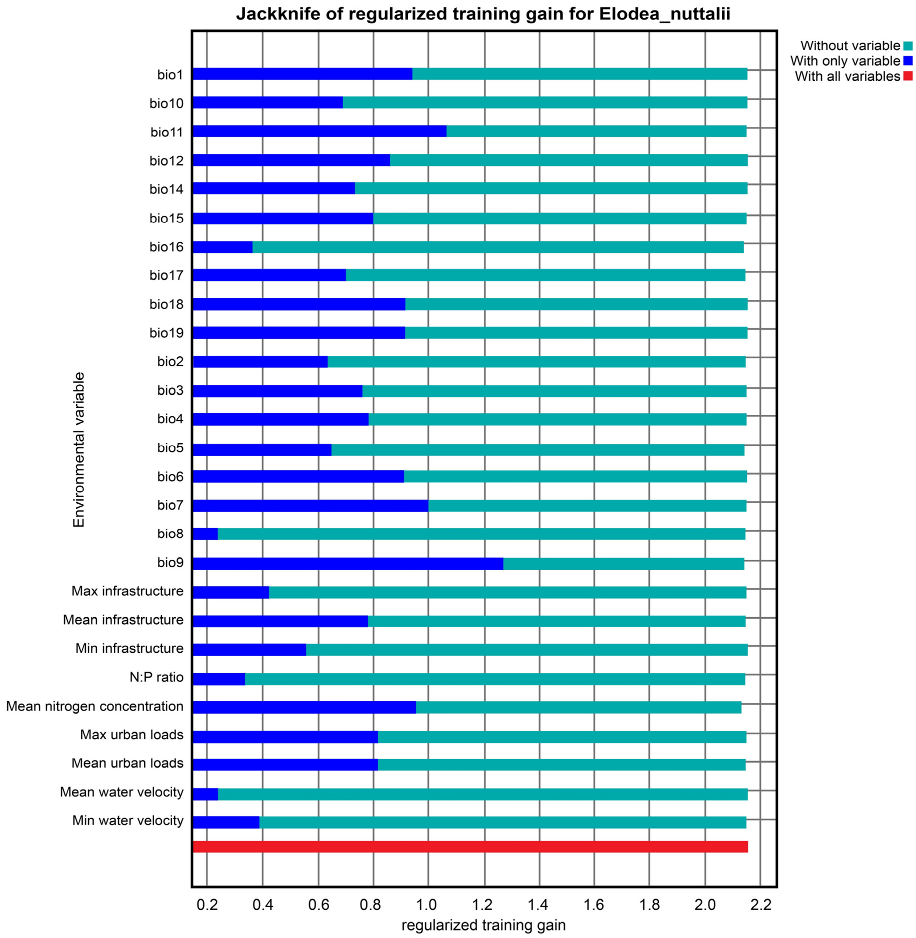

Figure 1. The model performance (regularized training gain) of the MaxEnt model generated using subset 1 of the occurrence data when the variable in question is omitted or used in isolation, compared to the performance of the model when all variables are used.

be found in Supplementary material Table S4 for models 1 and 2 and in Table S5 for models 1 and 3. Final summaries of the surface of priority areas and alert areas in the EU are provided in Tables 4 and 5.

Discussion

Elodea nuttallii is known to cause severe damage to the environment and to impact human activities in Europe (Josefsson 2011). It is considered a weed species in its native range, while in Europe it is included in the list of invasive alien plants of the European and Mediterranean Plant Protection Organization (EPPO 2016) and in the black listed species for Belgium (Branquart 2007). The species has been recently included in the IAS list of Union concern (EU 2017), in the framework of the IAS Regulation. As a result, EU Member States (MS) are obliged to prevent the introduction and spread of *E. nuttallii*, and to enforce effective early detection and rapid eradication mechanisms for tackling new introductions of the species.

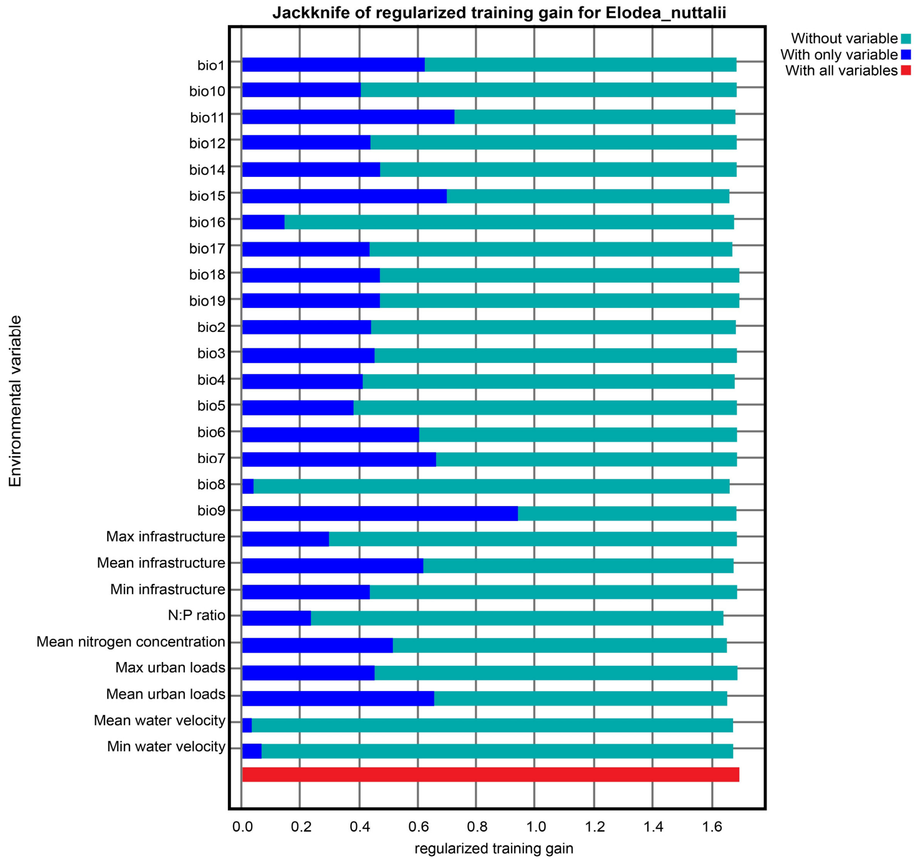

Figure 2. The model performance (regularized training gain) of the MaxEnt model generated using subset 2 of the occurrence data when the variable in question is omitted or used in isolation, compared to the performance of the model when all variables are used.

Table 3. Model information

Model	No. of occurrence points	No. of occurrence points inside study area	Area of modelled suitable habitat (km^2)
10 × 10 km	720	607	200,116.7
20 × 20 km	273	235	447,928.5
60 × 60 km	149	149	416,402.6

Prevention is more environmentally desirable and cost-effective than remediation, and should be prioritized, targeting species at an early stage of invasion (EU 2014). Europe has a high density and abundance of natural freshwaters susceptible to colonization by *E. nuttallii,* which can facilitate its subsequent survival, development and multiplication. *Elodea nuttallii* is already established in 19 EU countries. Preventing establishment in the other MS, such as the Baltic and Southern EU countries, and generally in areas where this species is not yet present, is crucial. Therefore, early warning is important to prevent introductions in non-infested areas.

Our results highlight those areas in Europe which are most suitable for successful establishment of *E. nuttallii*. However, many of these areas are already occupied by *E. nuttallii* populations. This is likely because *E. nuttallii* is a longstanding problem, as the species has been present in Europe since 1914 (Josefsson 2011), and since then has been spreading rapidly across European waterbodies through vegetative reproduction

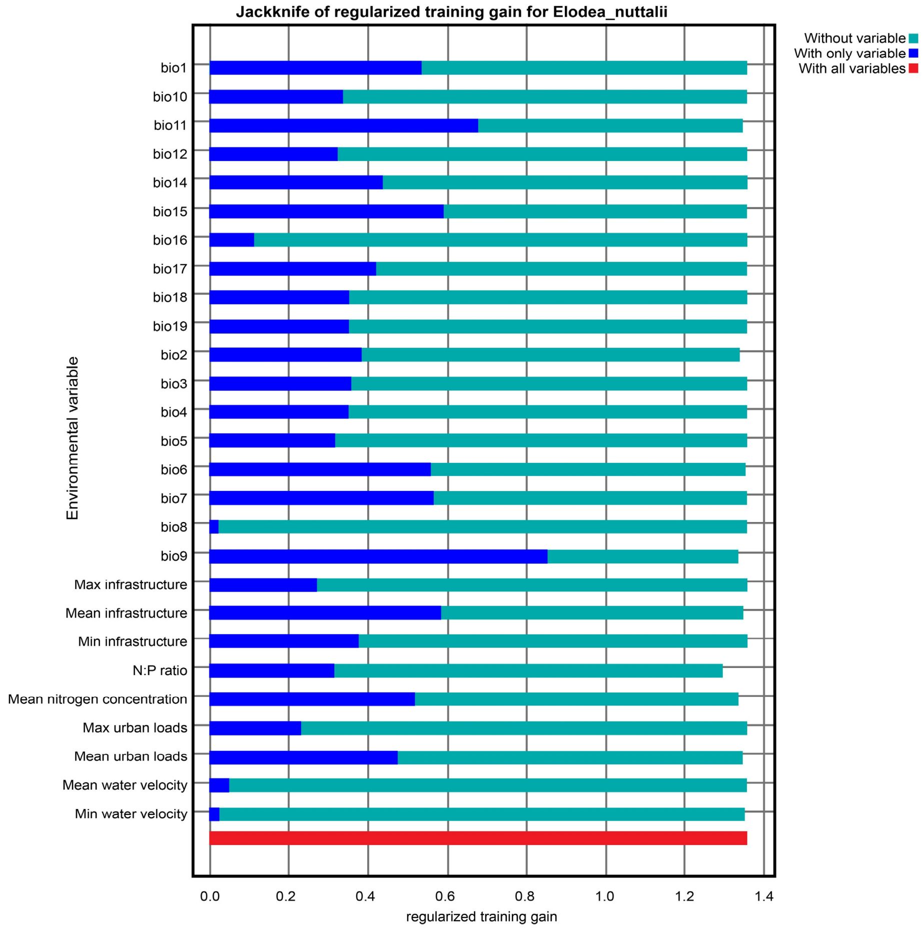

Figure 3. The model performance (regularized training gain) of the MaxEnt model generated using subset 3 of the occurrence data when the variable in question is omitted or used in isolation, compared to the performance of the model when all variables are used.

Table 4. Surface area of priority areas (i.e. areas of low uncertainty and above threshold suitability) and alert areas (i.e. areas of low uncertainty, above threshold suitability and over 100 km away from the nearest *Elodea nuttallii* occurrence point) generated by the models using subset 1 and subset 2 of the occurrence data, split up between Natura 2000 and non-Natura 2000 areas.

Total surface of priority areas (km^2)	179,811.5
Alert areas outside Natura 2000 (km^2)	6,603.4
Alert areas inside Natura 2000 (km^2)	979.3g

Table 5. Surface area of priority areas (i.e. areas of low uncertainty and above threshold suitability) and alert areas (i.e. areas of low uncertainty, above threshold suitability and over 100 km away from the nearest *Elodea nuttallii* occurrence point) generated by the models using subset 1 and subset 3 of the occurrence data, split up between Natura 2000 and non-Natura 2000 areas.

Total surface of priority areas (km^2)	156,522.6
Alert areas outside Natura 2000 (km^2)	9984.9
Alert areas inside Natura 2000 (km^2)	1289.3

(Cook 1987; Escobar et al. 2011). The vast majority of known records are from the Netherlands, Flanders and the west of Germany, densely populated areas with a long botanical research tradition where the presence of *E. nuttallii* is more likely to be noted. The bias in the distribution of

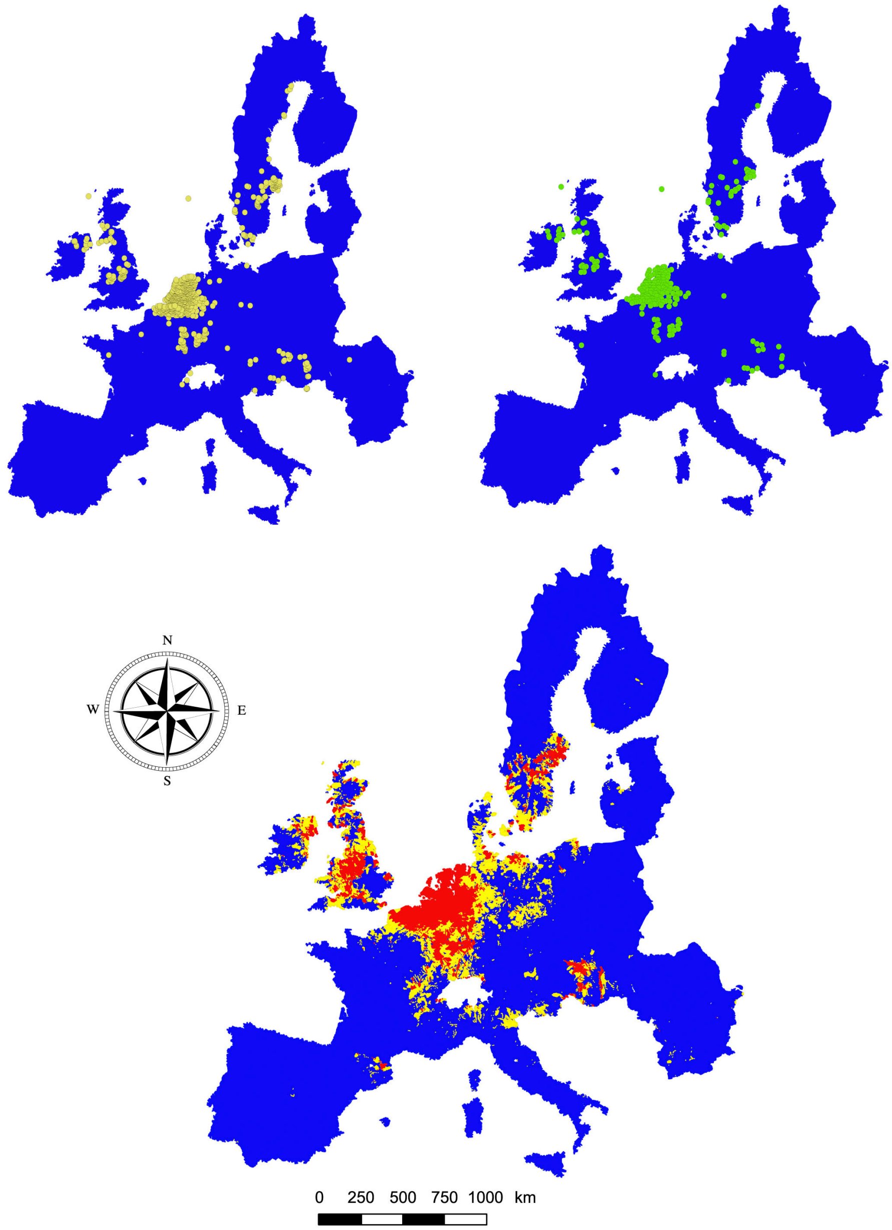

Figure 4. The occurrence with data thinned by extraction from subset 1 (A) and subset 2 (B) of occurrence data. The combined output of both is also presented (C). Areas with low uncertainty and above the habitat suitability threshold (i.e. priority areas) are marked in red while areas with high uncertainty are marked in yellow. The grid size of all 3 maps is 1 km^2.

occurrence records could also be explained by the presence of herbaria. *Elodea nuttallii* is known to spread through release from decorative aquaria and escape from ornamental planting (EASIN 2018). Regional bias in herbarium collection distribution (Loiselle et al. 2008) significantly affects the range of invasive species (Delisle et al. 2003), and herbarium collections are themselves distributed along climatic gradients with considerable bias. However, species distribution models have been shown to be robust enough to account for this (Daru et al. 2018). Despite this, the presence of herbaria is a probable reason for occurrence records around Stockholm and London, as well as for the abundance in Flanders and the Netherlands. On

Figure 5. "Alert areas", i.e. areas with high probability to be invaded by *Elodea nuttallii* that are at least 100 km away from any known occurrence point of the species, divided by being inside or outside Natura 2000 site, generated using subset 1 and subset 2 of occurrence data.

the other hand, the species' preference for slow, moving, shallow and eutrophic waters may explain its high abundance in the Netherlands and Flanders which have an extensive system of canals and polders, several of which face eutrophication problems (Van Puijenbroek et al. 2014; Van Landuyt et al. 2008). Still, it is important to be cautious when selecting occurrence records for SDM.

The findings described here are consistent with previous studies using SDM and global climatic models, in that climatic variables are more important than nutrient loads. We found that the temperature of the driest quarter was the greatest determinant, in contrast with Kelly et al. (2014), who highlighted the minimum temperature of the coldest month. However, this study focused on Ireland alone and the temperature of the driest month

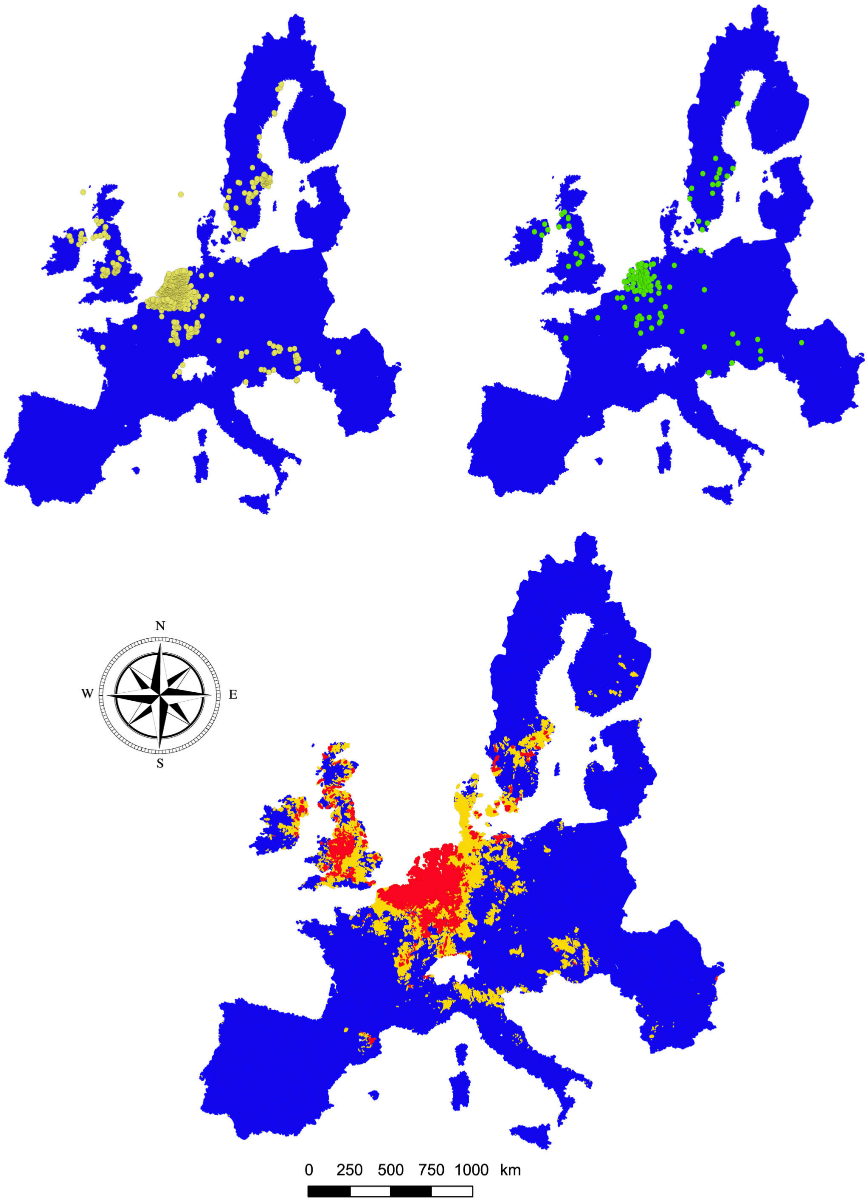

Figure 6. The occurrence with data from subset 1 (A) and subset 3 (B). The combined output of both is also presented (C). Areas with low uncertainty and above the habitat suitability threshold (i.e. priority areas) are marked in red while areas with high uncertainty are marked in yellow. The grid size of all 3 maps is 1 km^2.

was not input into the model. There were also some inconsistencies between model output and the ecological background information for the species, for instance the limited effect of water velocity on AUC. A likely explanation for this is that the 1 km^2 resolution of the data was too coarse. The low water velocities preferred by *E. nuttallii* are probably side branches of rivers, or canals, which cannot be represented accurately at 1 km^2 resolution. The mean temperature of the driest quarter was the variable that had the best model performance when used in isolation. This is justified by the fact that *E. nuttallii* is a temperate species which thrives only at a certain optimum temperature. In addition, evaporation in the generally shallow low-velocity waters may expose the plant's shoots and

Figure 7. "Alert areas", i.e. areas with high probability to be invaded by *Elodea nuttallii* that are at least 100 km away from any known occurrence point of the species, divided by being inside or outside Natura 2000 site, generated using subset 1 and subset 3 of occurrence data.

limit its spread via water. Evapotranspiration has been identified as a strong determinant of invasive freshwater species prevalence (Reshetnikov and Ficetola 2011; Luizza et al. 2016).

A possible criticism of the methods presented here is that biological invasions, particularly by plants, may cause a niche shift (Broennimann and Guisan 2008). It is therefore important to consider the stage of invasion when employing climatic variables in species distribution models (Guisan et al. 2014). However, since *E. nuttallii* has been shown to be present in Europe since 1918 (EASIN 2018), it is likely that the species has already gained equilibrium. It is also possible that the invasion by *E. nuttallii* occurred earlier than literature suggests, because it can easily be mistaken for *Elodea canadensis* (CABI 2018). We cannot draw upon literature to determine whether the niche shift has happened or not, because remarkably little is known about the environmental niche of *E. nuttallii* in its native range

(Thiébaut and Di Nino 2009) except that it tolerates waters contaminated with nutrients (Angelstein and Schubert 2008) and is a temperate species (CABI 2018; Hickman 1993). In addition, the WPI and GREEN model indicators used in this study do not span beyond Europe, which makes reproducing the model for America impossible. However, our results do coincide with the known presence of *E. nuttallii* in Italy. Though no occurrence records from Italy were found in this study, the species is present in Northern Italy, specifically the regions of Piemonte, Lombardy, Emilia Romagna, Trentino, Veneto and Friuli (Portale della Flora d'Italia 2013; Conti et al. 2005). Since its arrival in 1994 (EASIN 2018), however, the species has remained relatively isolated, perhaps indicating that this is the edge of *E. nuttallii*'s ecological niche in Europe. This may be explained by the findings of this study; the mean temperature of the driest quarter may well be a strong determinant. Another possibility is that an equilibrium state has been reached: although 1994 to the present is a short time for this to occur, since *E. nuttallii* is often mistaken for *E. canadensis* it may have arrived much earlier.

Our study could be supplemented with economic variables, such as river trade routes and ports. In this way, we could also predict and simulate *E. nuttallii*'s expansion through human mediated activities (e.g. release from aquariums, secondary dispersal (through vegetative propagation) through man-made canals, etc). Finally, the same methodology may be applied to other species and different taxonomic groups, including mobile species. With the main challenges in species distribution modelling compensated for, this methodology may have the potential for modelling many species' potential distribution besides the kingdom Plantae.

Our results indicate that there are still many areas within the EU which are free from *E. nuttallii*. We do not know where the species will disperse to next, but considering its rapid spread and the highly connected waterbodies across Europe, it is very likely that these areas will be invaded in the near future. Our study highlights specific non-infested areas that present high probability of invasion. Among these, several areas coincide with Natura 2000 sites. These "alert areas" are the ones that should receive top priority due to their natural biodiversity value and vulnerability to invasion. In addition, legislation for the protection of nature in these sites may be conducive to conservation efforts. In these areas, the water bodies should be checked regularly, particularly in places where eutrophication and high levels of available iron are common, such as near agricultural fields, cities and old construction sites. Early warning systems and rapid response mechanisms should be locally developed. Increased awareness and early detection through citizen science initiatives could also play an important role in tackling introductions of *E. nuttallii* in these areas. Upon detection of the species, rapid remediation activities should be performed, though prevention is highly preferable.

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References

Angelstein S, Schubert H (2008) *Elodea nuttallii*: uptake, translocation and release of phosphorus. *Aquatic Biology* 3: 209–216, https://doi.org/10.3354/ab00080

Baker R, Cannon R, Bartlett P, Barker I (2005) Novel strategies for assessing and managing the risks posed by invasive alien species to global crop production and biodiversity. *Annals of Applied Biology* 146: 177–191, https://doi.org/10.1111/j.1744-7348.2005.040071.x

Barrat-Segretain MH (2005) Competition between invasive and indigenous species: impact of spatial pattern and developmental stage. *Plant Ecology* 180: 153–160, https://doi.org/10.1007/s11258-004-7374-7

Bouraoui F, Grizzetti B, Aloe A (2011) Long term nutrient loads entering European seas. Joint Research Centre (JRC). JRC scientific and technical reports EUR 24726 EN, 72 pp

Branquart E (2007) Alert, black and watch lists of invasive species in Belgium. *Elodea nuttallii* – Nuttall's waterweed. Belgian Forum on Invasive Species. http://ias.biodiversity.be (accessed 24 July 2017)

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biology Letters* 4: 585–589, https://doi.org/10.1098/rsbl.2008.0254

CABI (2018) CABI – Invasive Species Compendium datasheet – *Elodea nuttallii*. Center for Agricultural and Biosciences International - CABI. https://www.cabi.org/isc (Accessed 16 January 2018)

Conti F, Abbate G, Alessandrini A, Blasi C (2005) An annotated checklist of the Italian vascular flora. Palombi & Partner S.r.l., Roma, Italy, 420 pp

Cook CDK (1987) Dispersion in aquatic and amphibious vascular plants. In: Crawford RMM (ed), Plant life in aquatic and amphibious habitats. Blackwell Scientific Publications, Oxford, UK, pp 179–190

Costa H, Ponte NB, Azevedo EB, Gil A (2015) Fuzzy set theory for predicting the potential distribution and cost-effective monitoring of invasive species. *Ecological Modelling* 316: 122–132, https://doi.org/10.1016/j.ecolmodel.2015.07.034

Crall AW, Jarnevich CS, Panke B, Young N, Renz M, Morisette J (2013) Using habitat suitability models to target invasive plant species surveys. *Ecological Applications* 23: 60–72, https://doi.org/10.1890/12-0465.1

Daru BH, Park DS, Primack RB, Willis CG, Barrington DS, Whitfeld TJ, Seidler TG, Sweeney PW, Foster DR, Ellison AM, Davis CC (2018) Widespread sampling biases in herbaria revealed from large-scale digitization. *New Phytology* 217: 939–955, https://doi.org/10.1111/nph.14855

Delisle F, Lavoie C, Jean M, Lachance D (2003) Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. *Journal of Biogeography* 30: 1033–1042, https://doi.org/10.1046/j.1365-2699.2003.00897.x

Di Nino F, Thiébaut G, Muller S (2005) Response of *Elodea nuttallii* to manual harvesting in the North-East of France. *Hydrobiologia* 551: 147–157, https://doi.org/10.1007/s10750-005-4457-y

EASIN (2018) European Alien Species Information Network (EASIN). http://alien.jrc.ec.europa.eu/SpeciesMapper (accessed 2018)

European Environmental Agency (2015) EEA. http://www.eea.europa.eu (accessed March 2017)

Elith J (2017) Chapter 5: Predicting distributions of invasive species. In: Walshe TR, Robinson A, Nunn M, Burgman MA (eds), Invasive Species: Risk Assessment and Management Cambridge University Press, Cambridge, United Kingdom, pp 93–129, https://doi.org/10.1017/9781139019606.006

EPPO (2016) European Plant Protection Organization (EPPO). http://www.eppo.int/INVASIVE_PLANTS/ias_lists.htm#A1A2Lists (accessed 15 February 2016)

Escobar MM, Voyevoda M, Fühner C, Zehnsdorf A (2011) Potential uses of *Elodea nuttallii* -harvested biomass. *Energy, Sustainability and Society* 1(4): 1–8

ESRI (2011) ArcGIS Desktop: Release 10. Environmental Systems Research Institute (ESRI). Redlands, California, USA

EU (2014) Regulation (EU) No 1143/2014 of the European Parliament and of the Council on the prevention and management of the introduction and spread of invasive alien species. *Official Journal of the European Union* L 317/35

EU (2017) Commission Implementing Regulation (EU) 2017/1263 of 12 July 2017 updating the list of invasive alien species of Union concern established by Implementing Regulation (EU) 2016/1141 pursuant to Regulation (EU) No 1143/2014 of the European Parliament and of the Council. *Official Journal of the European Union* L 182/37

Gallardo B, Aldridge DC (2013) The 'dirty dozen': socio-economic factors amplify the invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. *Journal of Applied Ecology* 50: 757–766, https://doi.org/10.1111/1365-2664.12079

GBIF.org (2018) GBIF Occurrence Download. https://doi.org/10.15468/dl.oufswz (accessed 05 May 2018)

Gebhardt A (2016) sgeostat: An Object-Oriented Framework for Geostatistical Modeling in S+. R package version 1.0-27

Genovesi P, Shine C (2004) European strategy on invasive alien species. Nature and environment (137). Council of Europe Publishing, Strasbourg, France, 67 pp

Greulich S, Trémolières M (2006) Present distribution of the genus *Elodea* in the Alsatian Upper Rhine floodplain (France) with a special focus on the expansion of *Elodea nuttallii* St. John during recent decades. *Hydrobiologia* 570: 249–255, https://doi.org/10.1007/s10750-006-0188-y

Grizzetti B (2006) Modelling nitrogen and phosphorus fate from point and diffuse sources at European scale. PhD thesis, University of Pierre et Marie Curie, Paris, France, 192 pp

Grizzetti B, Bouraoi F, Aloe A (2012) Changes of nitrogen and phosphorus loads to European seas. *Global Change Biology* 18: 769–782, https://doi.org/10.1111/j.1365-2486.2011.02576.x

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift studies: insights from biological invasions. *Trends in Ecology & Evolution* 29: 260–269, https://doi.org/10.1016/j.tree.2014.02.009

Heink U, Herzele Van A, Bela G, Kaloczkai A, Jaz K (2016) Different arguments, same conclusions: how is action against invasive alien species justified in the context of European policy? *Biodiversity and Conservation* 27: 1659–1677, https://doi.org/10.1007/s10531-016-1170-2

Hickman JC (1993). The Jepson Manual: higher plants of California. University of California Press, Berkeley, California, USA, 1400 pp

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978, https://doi.org/10.1002/joc.1276

Ikusima I (1984) Aquatic macrophytes. In: Hiroe S (ed), Lake Biwa. Dr. Junk Publishers, Dordrecht, The Netherlands, pp 303–311

Jarvenish SC, Young N (2015) Using the MAXENT Program for Species Distribution Modelling to Assess Invasion Risk. In: Venette RC (ed), Pest Risk Modelling and Mapping for Invasive Alien Species. USDA Forest Service, USA, pp 65–81

Jeschke JM, Bacher S, Blackburn TM, Dick JTA, Ess F, Evans T, Gaertner M, Hulme PE, Kühn I, Mrugała A, Perg J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Winter M, Kumschick S (2014) Defining the impact of non-native species. *Conservation Biology* 28: 1188–1194, https://doi.org/10.1111/cobi.12299

Jiménez-Valverde A, Lobo JM (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica* 31: 361–369, https://doi.org/10.1016/j.actao.2007.02.001

Jones JI, Eaton JW, Hardwick K (1993) Physiological plasticity in *Elodea nuttallii* (Planch.) St. John. *Journal of Aquatic Plant Management* 31: 88–94

Josefsson M (2011) NOBANIS - Invasive Species Fact Sheet – *Elodea canadensis*, *Elodea nuttallii* and *Elodea callitrichoides*. Online Database of the European Network on Invasive Alien Species – NOBANIS. http://www.nobanis.org (accessed 21/12/2017)

Kelly R, Leach K, Cameron A, Maggs CA, Reid N (2014) Combining global climate and regional landscape models to improve prediction of invasion risk. *Diversity and Distributions* 20: 1–11, https://doi.org/10.1111/ddi.12194

Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U (2009) Technical support to EU strategy on invasive alien species (IAS) - Assessment of the impacts of IAS in Europe and the EU. Institute for European Environmental Policy (IEEP), Brussels, Belgium, 44 pp + Annexes

Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfre, R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, Wilting A (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19: 1366–1379, https://doi.org/10.1111/ddi.12096

Lahoz-Monfort JJ, Guillera-Arroita G, Milner-Gulland EJ, Young RP, Nicholson E (2010) Satellite imagery as a single source of predictor variables for habitat suitability modelling: how Landsat can inform the conservation of a critically endangered lemur. *Journal of Applied Ecology* 47: 1094–1102, https://doi.org/10.1111/j.1365-2664.2010.01854.x

Larson D (2003) Predicting the threats to ecosystem function and economy of alien vascular plants in freshwater environments. Literature review. Sveriges Lantbruksuniversitet report 2003: 7

Loiselle BA, Jørgensen PM, Consiglio T, Jiménez I, Blake JG, Lohmann LG, Montiel OM (2008) Predicting Species Distributions from Herbarium Collections: Does Climate Bias in Collection Sampling Influence Model Outcomes? *Journal of Biogeography* 35(1): 105–116

Luizza MW, Evangelista PH, Jarnevich CS, West A, Stewart HA (2016) Integrating subsistence practice and species distribution modeling: assessing invasive elodea's potential impact on Native Alaskan subsistence of Chinook salmon and whitefish. *Environmental Management* 58: 144–163, https://doi.org/10.1007/s00267-016-0692-4

Millane M, Caffrey J, O'Flynn C (2016) Risk Assessment of *Elodea nuttallii* – submission for consideration of Union listing under EU IAS Regulation No. 1143/2014. EU amended template for submission February, 2016. Version 1.2.1. In: European Commission (2016) Meeting of the scientific forum on invasive alien species. Brussels, Belgium, 4-5 April, 2016, 10 pp

Muller S (2004) Plantes invasives en France: état des connaissances et propositions d'actions. Publications Scientifiques du Muséum national d'histoire naturelle, Paris, France, 168 pp

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution* 5: 1198–1205, https://doi.org/10.1111/2041-210X.12261

Phillips SJ, Dudík M, Schapire RE (2004) A Maximum Entropy Approach to Species Distribution Modeling. In: Greiner R, Schuurmans D (eds), Proceedings of the 21st International Machine Learning Conference. ACM Press, New York City, New York, USA, pp 655–662, https://doi.org/10.1145/1015330.1015412

Pistocchi A, Aloe A, Bizzi S, Bouraoui F, Burek P, de Roo A, Grizzetti B, Van de Bund W, Liquete C, Pastori M, Salas F, Stips A, Weissteiner C, Bidoglio G (2015) Assessment of the effectiveness of reported Water Framework Directive Programmes of Measures. Part I – Pan-European scale screening of the pressures addressed by member states. JRC Report EUR 27465. Publications Office of the European Union, Luxemburg, 88 pp

Portale della Flora d'Italia (2013) http://dryades.units.it/euganei/index.php (accessed 13 October, 2018)

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Radosavljevic A, Anderson RP (2013) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography* 4(41): 629–643

Reshetnikov AN, Ficetola GF (2011) Potential range of the invasive fish rotan (*Perccottus glenii*) in the Holarctic. *Biological Invasions* 13: 2967–2980, https://doi.org/10.1007/s10530-011-9982-1

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress towards understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282, https://doi.org/10.1890/13-0183.1

Rodda GH, Jarnevich CS, Reed RN (2011) Challenges in Identifying Sites Climatically Matched to the Native Ranges of Animal Invaders. *PLoS ONE* 6: 1–18, https://doi.org/10.1371/journal.pone.0014670

Roura-Pascual N, Suarez VA (2008) The utility of species distribution models to predict the spread of invasive ants (Hymenoptera: Formicidae) and to anticipate changes in their ranges in the face of global climate change. *Myrmecological News* 11: 67–77

Sarukhán J, Whyte A, MA Board of Review Editors (2005) Millennium Ecosystem Assessment (MEA). Ecosystems and Human Well-being: Biodiversity Synthesis. Island Press, Washington, DC, USA, 137 pp

Simpson DA (1990) Displacement of *Elodea canadensis* Michx by *Elodea nuttallii* (Planch.) H. St John in the British Isles. *Watsonia* 18(2): 173–177

Stolar J, Nielsen SE (2015) Accounting for spatially biased sampling effort in presence-only species distribution modelling. *Diversity and Distributions* 5: 595–608, https://doi.org/10.1111/ddi.12279

Thiébaut G, Di Nino F (2009) Morphological variations of natural populations of an aquatic macrophyte *Elodea nuttallii* in their native and in their introduced ranges. *Aquatic Invasions* 4: 311–320, https://doi.org/10.3391/ai.2009.4.2.2

Thiébaut G, Rolland T, Robach F, Tremolieres M, Muller S (1997) Quelques conséquences de l'introduction de deux espèces de macrophytes, *Elodea canadensis* Michaux et *Elodea nuttallii* St. John, dans les écosystèmes aquatiques continentaux: exemple de la plaine d'Alsace et des Vosges du Nord (Nord-Est de la France). *Bulletin Francais de la Péche et de la Pisciculture* 344–345: 441–452, https://doi.org/10.1051/kmae:1997040

Van Landuyt W, Vanhecke L, Hoste I (2008) Changes in the distribution area of vascular plants in Flanders (northern Belgium): eutrophication as a major driving force. *Biodiversity Conservation* 17: 3045–3060, https://doi.org/10.1007/s10531-008-9415-3

Van Puijenbroek PJTM, Cleij P, Visser H (2014) Aggregated indices for trends in eutrophication of different types of fresh water in the Netherlands. *Ecological Indicators* 36: 456–462, https://doi.org/10.1016/j.ecolind.2013.08.022

Vaz S, Martin CS, Eastwood PD, Ernande B, Carpentier A, Meaden GJ, Coppin F (2008) Modelling species distributions using regression quantiles. *Journal of Applied Ecology* 45: 204–217, https://doi.org/10.1111/j.1365-2664.2007.01392.x

Veloz SD (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Bio-geography* 36: 2290–2299, https://doi.org/10.1111/j.1365-2699.2009.02174.x

Venette RC (2015) The Challenge of Modelling and Mapping the Future Distribution and Impact of Invasive Alien Species. In: Venette RC (ed), Pest Risk Modelling and Mapping for Invasive Alien Species. USDA Forest Service, Newtown Square, Pennsylvania, USA, pp 1–17, https://doi.org/10.1079/9781780643946.0001

Ward DF (2007) Modelling the potential geographic distribution of invasive ant species in New Zealand. *Biological Invasions* 9: 723–735, https://doi.org/10.1007/s10530-006-9072-y

Wyse-Jackson P (2014) Ireland's Generous Nature. The Past and Present Uses of Wild Plants in Ireland. Missouri Botanical Garden Press, Saint Louis, Missouri, USA, 750 pp

Xu W, Hu W, Deng J, Zhu J, Li O (2016) How do water depth and harvest intensity affect the growth and reproduction of *Elodea nuttallii* (Planch.) St. John? *Journal of Plant Ecology* 9: 212–223, https://doi.org/10.1093/jpe/rtv048

Supplementary material

The following supplementary material is available for this article:

Table S1. Coordinates of subset 1 of occurrence records in ETRS89 LAEA.
Table S2. Coordinates of subset 2 of occurrence records in ETRS89 LAEA.
Table S3. Coordinates of subset 3 of occurrence records in ETRS89 LAEA.
Table S4. "Alert areas" inside Natura 2000 areas, as per the models generated using subset 1 and subset 2 of occurrence data.
Table S5. "Alert areas" inside Natura 2000 areas, as per the models generated using subset 1 and subset 3 of occurrence data.

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