

# An invasion risk map for non-native aquatic macrophytes of the Iberian Peninsula

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## Abstract

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Freshwater systems are particularly susceptible to non-native organisms, owing to their high sensitivity to the impacts that are caused by these organisms. Species distribution models, which are based on both environmental and socio-economic variables, facilitate the identification of the most vulnerable areas for the spread of non-native species. We used MaxEnt to predict the potential distribution of 20 non-native aquatic macrophytes in the Iberian Peninsula. Some selected variables, such as the temperature seasonality and the precipitation in the driest quarter, highlight the importance of the climate on their distribution. Notably, the human influence in the territory appears as a key variable in the distribution of studied species. The model discriminated between favorable and unfavorable areas with high accuracy. We used the model to build an invasion risk map of aquatic macrophytes for the Iberian Peninsula that included results from 20 individual models. It showed that the most vulnerable areas are located near to the sea, the major rivers basins, and the high population density areas. These facts suggest the importance of the human impact on the colonization and distribution of non-native aquatic macrophytes in the Iberian Peninsula, and more precisely agricultural development during the Green Revolution at the end of the 70's. Our work also emphasizes the utility of species distribution models for the prevention and management of biological invasions.

**Keywords:** Aquatic plants, bioclimatic factors, biological invasions, ecological niche models, freshwater ecosystems, map risk assessment, MaxEnt, non-native species, socio-economic factors, species distribution model.

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## INTRODUCTION

Invasive species are one of the main causes of biodiversity loss. At a global scale, they represent a major threat to the ecosystems functioning (Mack & al., 2000; Sala & al., 2000; Brooks & al., 2004). Non-native species may also cause negative effects (Ricciardi & Kipp, 2008; Pyšek & Richardson, 2010) on human health (Hulme, 2006; Chytrý & al., 2009), as well as important economic impacts (Pimentel & al., 2005). Some freshwater systems are

## Resumen

Rodríguez-Merino, A., Fernández-Zamudio, R. & García-Murillo, P. 2017. Mapa de riesgo de invasión de macrófitos acuáticos exóticos de la Península Ibérica. *Anales Jard. Bot. Madrid* 74(1): e055.

Los sistemas acuáticos son especialmente susceptibles a los organismos exóticos debido a su elevada fragilidad y a los impactos que provocan estas especies en este tipo de hábitats. Los modelos de distribución de especies, basados en variables ambientales y socioeconómicas, facilitan la identificación de las áreas más vulnerables ante la expansión de especies exóticas. Se utilizó MaxEnt para predecir la distribución potencial de 20 macrófitos exóticos en la Península Ibérica. Algunas de las variables estudiadas, como la estacionalidad de la temperatura y la precipitación del cuatrimestre más seco, ponen en evidencia la importancia de los factores climáticos en su distribución. Además, la influencia humana en el territorio se presenta como una variable clave en la distribución de las especies estudiadas. El modelo obtenido discrimina claramente entre áreas favorables y desfavorables con mucha precisión. Se utilizó el modelo para construir un mapa de riesgo de invasión de macrófitos acuáticos para la Península Ibérica que incluyó los resultados de 20 modelos individuales y que muestra que las áreas más vulnerables son las zonas cercanas al mar, las cuencas de los grandes ríos y las zonas con una alta densidad de población. Estos resultados vinculan la importancia del impacto humano en la colonización y la distribución de los macrófitos acuáticos exóticos en la Península Ibérica y, más concretamente, con la Revolución Verde de finales de la década de los setenta. Nuestro trabajo enfatiza la utilidad de los modelos de distribución de especies para la prevención y gestión de invasiones biológicas.

**Palabras clave:** Ecosistemas acuáticos continentales, especies exóticas, factores bioclimáticos, factores socioeconómicos, invasiones biológicas, mapa de evaluación de riesgos, MaxEnt, modelos de nicho ecológico, modelos de distribución de especies, plantas acuáticas.

considered biodiversity hotspots (Murphy, 2002; Strayer & Dudgeon, 2010; Brundu, 2015; Serrano & Díaz Paniagua, 2015) and are one of the most threatened ecosystems in the world (Collen & al., 2014; Brundu, 2015; Serrano & Díaz Paniagua, 2015). These systems are particularly susceptible to biological invasions, because of their propensity to shift away from natural conditions and feedbacks that alter colonized habitats (Willby, 2007; Aguiar & Ferreira, 2013; Brundu, 2015; Gallardo & al., 2015). Aquatic macrophytes

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play an important role in the structure and function of freshwater systems (Chambers & al., 2008; García-Murillo & Fernández-Zamudio, 2015) by providing a structurally complex environment (Rennie & Jackson, 2005; Dibble & al., 2006). They contribute to environmental heterogeneity (Harrel & Dibble, 2001) and to increase the diversity of ecological niches. Aquatic invaders features like high productivity, broad ecological tolerances, notable phenotypic plasticity, and a remarkable facility in producing propagules (Santamaría, 2002; Les & al., 2003), have led some invasive freshwater plants to belong to the group of the “100 of the World’s Worst Invasive Alien Species” (Lowe & al., 2004). In addition, the nutrient increase in many water bodies due to human activities and the frequent absence of natural enemies in this group of plants, have led in some cases to absolute dominance in the invaded habitats (García-Murillo & al., 2007; Ruiz & al., 2008).

An early detection of the arrival of non-native species can increase the success in their eradication before the establishment, preventing future invasions (Broennimann & Guisan, 2008; Williams & Grosholz, 2008; Crafton, 2015). For this reason, it should be necessary to identify the most exposed areas of invasion risk (Reshetnikov & Ficetola, 2011). But aquatic habitats in general and aquatic macrophytes in particular are difficult to be monitored (Brundu, 2015). So, the development and use of alternative methodologies for the prevention and control of exotic species are essential for the identification of areas with a high invasion risk. This kind of methodologies will allow us to manage potential non-native species while preserving native species (Gallardo & al., 2012).

Species distribution models have the potential to predict invasiveness and have become common in the study and management of biological invasions (Peterson, 2003; Thuiller & al., 2005). Significant recent advances have been achieved in the development of species distribution models (v.gr., Elith & Leathwick, 2009). Appropriate factors in modeling the potential distribution of species, as well as the use of suitable occurrence data, are essential to execute more accurate models. In our case, we have chosen the algorithm MaxEnt (Phillips & al., 2006), based on the maximum entropy principle, for modeling the potential distribution of non-native aquatic macrophytes. Several authors propose that MaxEnt model is better than other algorithms based on presence-only data (Elith & al., 2006; Elith & Leathwick, 2009; Mateo & al., 2010).

The Iberian Peninsula has been considered as a plant biodiversity hotspot (Molina & al., 2015), including aquatic plants (Chappuis & al., 2012). But over the last decades a significant transformation seems to have occurred in some important Iberian inland aquatic ecosystems. In essence, we have observed an expansion of some non-native aquatic plants and the decrease in some other native ones (Cirujano & al., 2014). The aim of this study is to predict the potential priority risk areas for invasion of aquatic plants in the Iberian Peninsula. To accomplish this objective we have employed a species distribution model. We firstly determined the influence of environmental and socio-economic factors over 20 non-native aquatic macrophytes at a global scale. Secondly, we overlapped the individual models to achieve a map that shows the higher vulnerable areas, due to the effect of multiple invasions.

Finally, we compared the most vulnerable regions with the irrigated agricultural areas in order to find an explanation for the distribution of the studied species.

## MATERIAL AND METHODS

### *Study area*

The Iberian Peninsula is located in the southwestern Europe. It is restricted by the Atlantic Ocean and the Mediterranean Sea. The Pyrenees separate it from the rest of Europe, and the Strait of Gibraltar from Africa. The climate diversity of the study area and the rugged topography of the land along with the geographic isolation, are key elements to develop an outstanding biodiversity (López-López & al., 2011). Concerning aquatic plants, this territory shows a high diversity of aquatic ecosystems and water bodies. Thus, we can find several types of rivers, streams, creeks, lakes, ponds —temporary or permanent—, bogs, and marshlands.

### *Species selection*

We have modeled the distribution of 20 non-native aquatic macrophytes which are currently established in the Iberian Peninsula (Table 1). The non-native species belong to 13 genus and 9 families and were selected from Cirujano & al. (2014) complemented with the European and Mediterranean Plant Protection Organization list —EPPO, see <http://www.eppo.int> — and the Delivering Alien Invasive Species Inventories for Europe list —DAISIE, see <http://www.europe-alien.org>.

The global spatial occurrences of 20 species were obtained from the Global Biodiversity Information Facility (GBIF, 2015). We tested the Iberian Peninsula occurrences with data showed by the Anthos Project (Anthos, 2015). The case of *Ludwigia peploides* subsp. *monteviden-sis* (Spreng.) P.H. Raven was checked in other additional sources (Verloove & Sánchez, 2008; Bou & Font, 2016). Records were considered from 1950 to the present to match the timeframe for the current climate data. In order to avoid underestimating the potential niche we counted all occurrences available for each species, showing the native and invasive ranges of species (Jiménez-Valverde & al., 2011).

We used the statistical software R (R Development Core Team, 2014) to clean data and removed duplicates, data without date, and erroneous occurrences in both taxonomic and geographic data. Furthermore, we also reduced the spatial autocorrelation of the data to not violate the assumption of independence (Heffner & al., 1996). Thus, the distance between data pairs was reduced to 10 km; the same distance was used for modeling the species’ potential distribution.

### *Predictor variables*

The 19 bioclimatic layers and altitude —Digital Elevation Model, DEM— were taken from WorldClim-Global Climate Data (Hijmans & al., 2005; Worldclim, 2015). The resolution of the environmental layers used was 5 arc-min —~10 km at the equator.

**Table 1.** List of non-native aquatic macrophytes selected for the Iberian Peninsula.

Family	Genus	Species
Azollaceae	<i>Azolla</i>	<i>A. filiculoides</i> Lam. (incl. <i>A. caroliniana</i> Willd.)
Araceae	<i>Lemna</i>	<i>L. minuta</i> Kunth
		<i>L. valdiviana</i> Phil.
		<i>Pistia</i>
Haloragaceae	<i>Myriophyllum</i>	<i>M. aquaticum</i> (Vell.) Verdc.
		<i>M. heterophyllum</i> Michx.
Hydrocharitaceae	<i>Egeria</i>	<i>E. densa</i> Planch.
	<i>Elodea</i>	<i>E. canadensis</i> Michx.
	<i>Lagarosiphon</i>	<i>L. major</i> (Ridley) Moss ex Wager
Nymphaeaceae	<i>Nymphaea</i>	<i>N. mexicana</i> Zucc.
Onagraceae	<i>Ludwigia</i>	<i>L. grandiflora</i> (Michx.) Greuter & Burdet
		<i>L. peploides</i> subsp. <i>montevidensis</i> (Spreng.) P.H. Raven
		<i>L. repens</i> J.R. Forst.
Pontederiaceae	<i>Eichhornia</i>	<i>E. crassipes</i> (Mart.) Solms
	<i>Heteranthera</i>	<i>H. limosa</i> (Sw.) Willd.
		<i>H. reniformis</i> Ruiz & Pav.
		<i>H. rotundifolia</i> (Kunth) Griseb.
Apiaceae	<i>Hydrocotyle</i>	<i>H. ranunculoides</i> L. f.
Salviniaceae	<i>Salvinia</i>	<i>H. verticillata</i> Thunb.
		<i>S. natans</i> (L.) All.

Slope was derived from DEM layer using the software ArcGIS 9.3.1 (ESRI, 2008). The human footprint was considered a socio-economic factor that reflects the human influence on the territory following Sanderson & al. (2002). This authors used as proxies of this footprint several variables such as various human land uses, population density or distance to major roads, railways and rivers. The information was obtained from Socioeconomic Data and Applications Center (SEDAC, 2015) and its resolution is 30 arc-sec  $\sim$  1 km.

The resolution of 22 variables (Table 2) was turned into 5 arc-min and was projected using the World Geodetic System 1984 projection. The spatial correlation between variables was analyzed by Raster package (Hijmans & van Etten, 2015). After obtaining the correlation tree, the variables were selected by a threshold limit of 0.5. In addition, to remove the linear combination between variables in the model, the Variance Inflation Factor —VIF— was calculated using the package HH, and taking 5 as limit value (Heiberger, 2015).

### Species distribution modeling

We developed the species distribution models with the machine learning MaxEnt version 3.3.3.k (Phillips & al., 2006), which estimates species distribution by the principle of maximum entropy. This method was chosen because is one of the most effective species distribution model, and shows a high quality achievement with low sample sizes and moderate georeferencing errors (Elith & al., 2006; Wisz & al., 2008; Mateo & al., 2010).

The parameters employed for this study were taken from Phillips & al. (2006), Phillips & Dudík (2008), and Elith & al. (2011). Default parameters were convergence threshold = 0.00001, maximum iterations = 1,000, and

**Table 2.** List and description of used variables.

Variable	Description
Bio 1	Annual mean temperature
Bio 2	Mean diurnal range [mean of monthly (max temp – min temp)]
Bio 3	Isothermality [(Bio 2 / Bio 7) * 100]
Bio 4	Temperature seasonality
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
DEM	Digital Elevation Model
Slope	Slope
HFP	Human Footprint

prevalence = 0.5, multiple regularization —default is 1— was changed to 2.5 to reduce the probability of overfitting models following Elith & al. (2010). Models were fitted with the 70% occurrences data and the remaining 30% was used to

evaluate the obtained models. Besides, we used 10-fold cross-validations to estimate the errors around the fitted functions and the predictive performance on the held-out data (Elith & al., 2011). We created 10,000 background points to simulate pseudo-absences (Phillips & Dudík, 2008; Elith & al., 2011). Likewise, we interpreted the logistic output as a habitat suitability map for each species. The model accuracy was estimated using the area under the receiving operating characteristic —ROC— curve —AUC—. According to it, the results within a value of 0.5 do not discriminate better than the random, while a model with a perfect discrimination would have an AUC of 1, and values bigger or equal than 0.7 correspond to the highest predictive models (Hosmer & Lemeshow, 2000). Finally, we calculated the AUC for each model and determined the average AUC for each set of 10 replicates (Barnes & al., 2014). 10<sup>th</sup> percentile training presence threshold was chosen because it shows a good ability to predict correctly the presence of invasive species (Pearson & al., 2007; Reshetnikov & Ficetola, 2011), representing the species distribution in suboptimal habitats (Kelly & al., 2014).

### Invasion risk map

The invasion risks map was calculated by overlaying the 20 species distribution individual models (Aranda & Lobo, 2011; Fajardo & al., 2014) using the Geographic Information System ArcGIS 9.3.1 (ESRI, 2008). Thereby we obtained a cartography that reflects the cumulative risk of invasion, which represent the most favorable areas for colonization and spread for the studied species in the Iberian Peninsula.

## RESULTS

A total of 8,892 records were used for modeling the global potential distribution of species. The number of records varied widely among species —*Nymphaea*

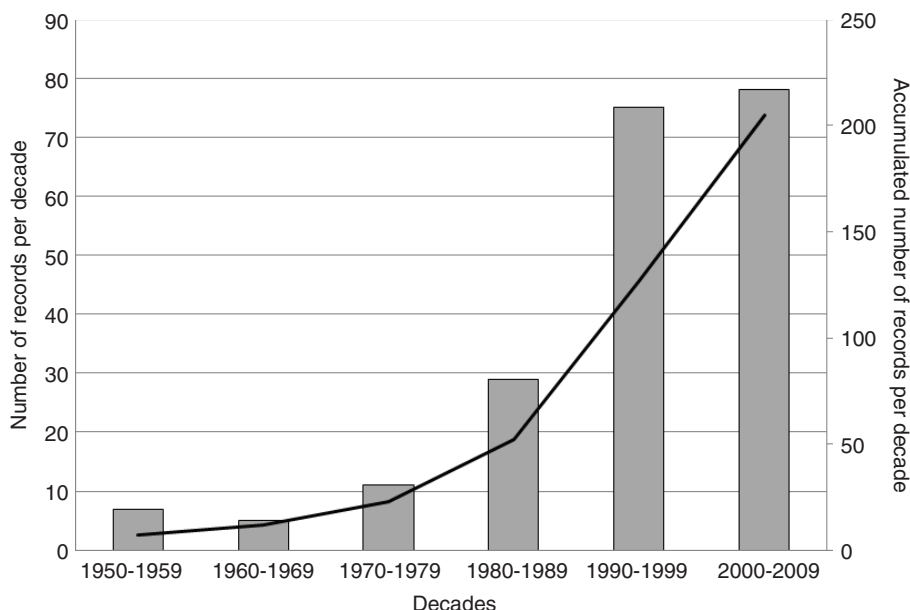
*mexicana* Zucc. minimum global occurrence points: 46 and *Azolla filiculoides* Lam. maximum occurrence points: 1,617, after cleaning data—. Fig. 1 shows the number of records per decade and the accumulated number of records per decade, and Fig. 2 shows the current presences of studied species on the Iberian Peninsula.

The final factors included as predictors in MaxEnt were mean diurnal range —Bio 2—, temperature seasonality (Bio 4), annual precipitation —Bio 12—, precipitation seasonality —Bio 15—, precipitation in the driest quarter —Bio 17—, altitude, slope, and human footprint —HFP.

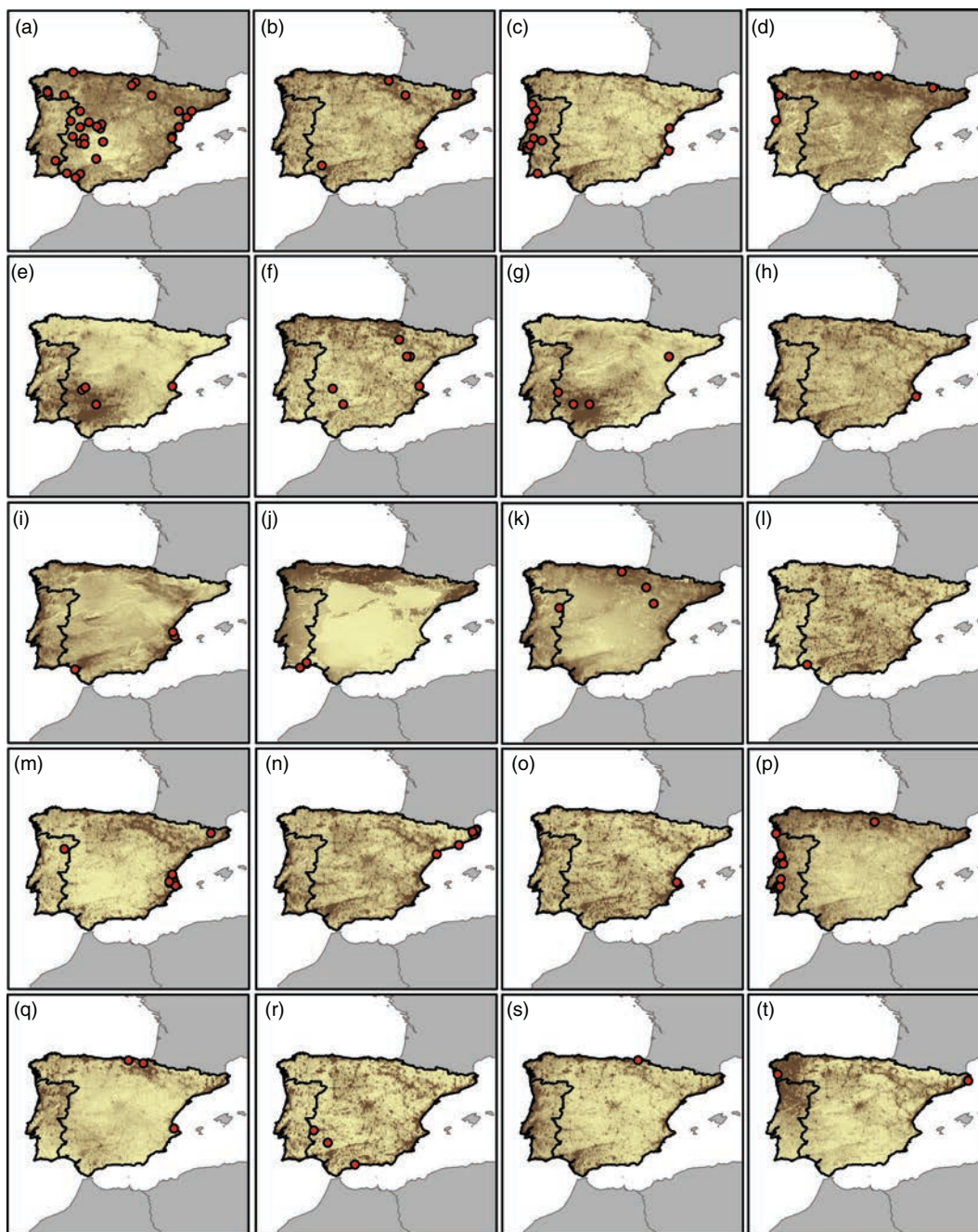
In Table 3 we show the main results for each studied species. The accuracy scores of models ranged between 0.918 and 0.981, which shows that our models provide a good performance (Hosmer & Lemeshow, 2000) indicating a better discrimination than random chance for the species analyzed (Phillips & al., 2006). The binomial test of omission showed statistical significance — $p < 0.001$ — for each of the 10 replicates (Phillips & al., 2006), supporting the reliability of the models. The use of 10<sup>th</sup> percentile training presence threshold allowed us to discriminate correctly the presence of non-native species (Pearson & al., 2007; Reshetnikov & Ficetola, 2011) in both optimal and suboptimal areas (Jiménez-Valverde & al., 2011; Kelly & al., 2014).

The best predictor of potential distribution for the majority of the species was the human footprint. In relation to *Azolla filiculoides*, *Hydrocotyle verticillata* Thunb., *Lagarosiphon major* (Ridl.) Moss ex Wager, and *Pistia stratiotes* L., the best predictor was the temperature seasonality; for *Heteranthera rotundifolia* (Kunth) Griseb. the mean diurnal range, and for *Myriophyllum heterophyllum* Michx. the precipitation in the driest quarter. Besides, for these species the human footprint was included among the three best predictors (Table 3).

The suitable habitat models for the invasion risk varied broadly between species (Fig. 2), showing a large favorable distribution for species as *Azolla filiculoides*,



**Fig. 1.** Number of records per decade and accumulated number of records per decade of all the aquatic macrophytes studied in the Iberian Peninsula.



**Fig. 2.** Potential distribution models for the selected species: **a**, *Azolla filiculoides*; **b**, *Egeria densa*; **c**, *Eichhornia crassipes*; **d**, *Elodea canadensis*; **e**, *Heteranthera limosa*; **f**, *Heteranthera reniformis*; **g**, *Heteranthera rotundifolia*; **h**, *Hydrocotyle ranunculoides*; **i**, *Hydrocotyle verticillata*; **j**, *Lagarosiphon major*; **k**, *Lemna minuta*; **l**, *Lemna valdiviana*; **m**, *Ludwigia grandiflora*; **n**, *Ludwigia peploides* subsp. *montevidensis*; **o**, *Ludwigia repens*; **p**, *Myriophyllum aquaticum*; **q**, *Myriophyllum heterophyllum*; **r**, *Nymphaea mexicana*; **s**, *Pistia stratiotes*; **t**, *Salvinia natans*. Darker areas correspond with higher suitability areas; red spots indicate the presence of occurrences of the studied species in the Iberian Peninsula — after data cleaning process.

*Egeria densa* Planch., *Elodea canadensis* Michx., *Lemna valdiviana* Phil., *Nymphaea mexicana*, and *Ludwigia repens* J.R. Forst.

The combination of the 20 individual models is the risk map for non-native Iberian aquatic macrophytes (Fig. 3). It shows the suitability of presence of the species according to the factors selected in the model building. The most vulnerable areas coincide with the littoral fringe, the high population density sectors, and the large river basins.

Fig. 4 shows the overlapping between the irrigated agricultural areas taken from European Environment Agency

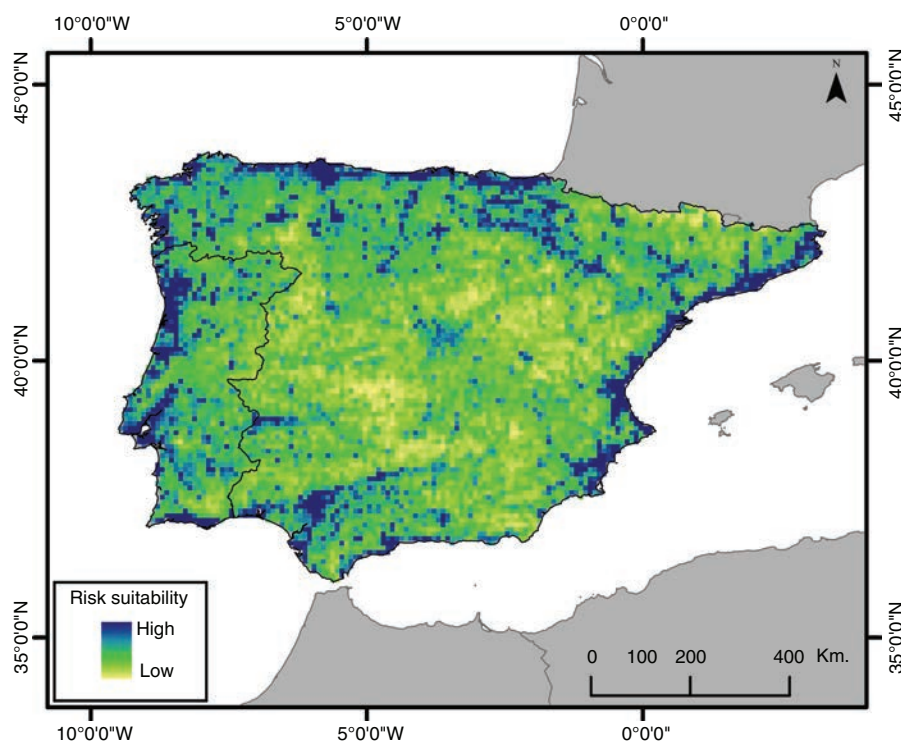
(2015) and the most vulnerable region in the invasion risk map.

## DISCUSSION

Our results show the first geographical representation of the potential invasion risk by non-native aquatic macrophytes in the Iberian Peninsula. The combination of both environmental and socio-economic factors allows us to identify those areas more susceptible to be invaded by non-native aquatic plants.

**Table 3.** AUC values  $\pm$  SD and percent contribution of each of the variables taken into account for the models. In bold the best factor in the potential distribution of each species.

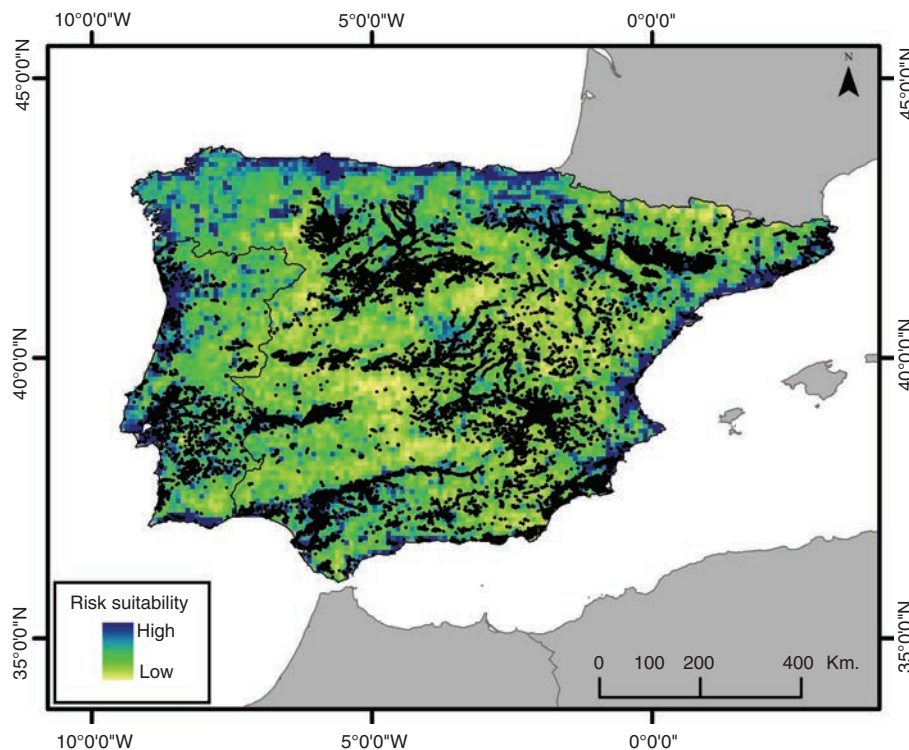
Species	AUC $\pm$ SD	Variables							
		Bio 2	Bio 4	Bio 12	Bio 15	Bio 17	Altitude	Slope	HFP
<i>A. filiculoides</i>	0.923 $\pm$ 0.003	0.3	<b>43.9</b>	4.2	18.6	1.6	1.2	0.0	29.6
<i>E. densa</i>	0.956 $\pm$ 0.009	1.5	20.3	2.4	1.9	12.6	1.5	1.1	<b>58.7</b>
<i>E. crassipes</i>	0.918 $\pm$ 0.014	2.6	33.2	15.4	1.2	4.3	6.7	0.4	<b>36.3</b>
<i>E. canadensis</i>	0.919 $\pm$ 0.008	0.2	20.3	5.2	11.4	25.9	0.8	0.1	<b>36.1</b>
<i>H. limosa</i>	0.956 $\pm$ 0.016	18.4	15.6	15.4	8.4	8.5	2.7	1.7	<b>29.4</b>
<i>H. ranunculoides</i>	0.940 $\pm$ 0.014	1.9	26.7	5.4	5.0	1.2	4.0	0.9	<b>55.0</b>
<i>H. reniformis</i>	0.952 $\pm$ 0.009	1.9	30.5	21.9	2.5	5.1	0.2	3.8	<b>34.0</b>
<i>H. rotundifolia</i>	0.960 $\pm$ 0.012	<b>26.6</b>	11.0	21	5.5	9.1	2.4	2.2	22.3
<i>H. verticillata</i>	0.947 $\pm$ 0.011	9.8	<b>49.4</b>	1.4	6.7	3.2	9.3	2.0	18.3
<i>L. major</i>	0.971 $\pm$ 0.004	16.2	<b>27.9</b>	4.0	19.8	6.7	0.2	0.1	25.1
<i>L. minuta</i>	0.944 $\pm$ 0.007	4.3	19.5	4.0	28.0	7.7	3.5	0.0	<b>32.9</b>
<i>L. valdiviana</i>	0.932 $\pm$ 0.031	18.5	11.1	2.9	1.0	6.1	0.4	6.4	<b>53.7</b>
<i>L. grandiflora</i>	0.981 $\pm$ 0.005	1.1	22.4	1.0	15.0	16.7	6.9	0.5	<b>36.4</b>
<i>L. peploides</i> subsp. <i>montevidensis</i>	0.936 $\pm$ 0.014	6.7	32.0	2.1	2.9	4.2	3.8	1.2	<b>47.2</b>
<i>L. repens</i>	0.937 $\pm$ 0.029	11.8	21.5	1.3	0.7	1.2	3.5	2.6	<b>57.4</b>
<i>M. aquaticum</i>	0.948 $\pm$ 0.005	0.5	27.6	2.1	2.1	20.6	5.7	0.2	<b>41.2</b>
<i>M. heterophyllum</i>	0.973 $\pm$ 0.012	3.9	14.0	20.9	13.5	<b>23.7</b>	2.9	0.7	20.4
<i>N. mexicana</i>	0.967 $\pm$ 0.031	4.2	24.0	1.2	1.8	1.7	0.4	0.6	<b>66.0</b>
<i>P. stratiotes</i>	0.919 $\pm$ 0.010	1.1	<b>39.0</b>	26.0	1.4	0.3	13.4	0.5	18.3
<i>S. natans</i>	0.966 $\pm$ 0.013	6.8	16.8	4.8	4.5	22.9	1.5	1.1	<b>41.6</b>

**Fig. 3.** Invasion risk map representing the risk suitability of 20 non-native aquatic macrophytes species in the Iberian Peninsula.

Large areas of the Iberian Peninsula were suitable to the invasion by different non-native aquatic macrophytes, like *Azolla filiculoides*, *Egeria densa*, *Elodea canadensis*, *Lemna valdiviana*, *Ludwigia repens*, *Myriophyllum aquaticum* (Vell.) Verdc., and *Nymphaea mexicana* (Fig. 2). Most

of them are widely distributed in Europe, being *Azolla filiculoides* and *Elodea canadensis* the species present in more European countries (Hussner, 2012).

Temperature seasonality and precipitation in the driest quarter are key factors in the probability distribution of



**Fig. 4.** Map showing the irrigated agricultural areas—black polygons—over suitable habitats for 20 non-native aquatic macrophyte species.

the studied species. This result is supported by the fact that the climatic characteristics of an area act as key elements for a successful colonization of non-native species (Thuiller & al., 2005; Broennimann & al., 2007). For instance, the temperature could limit the survival, growth, and reproduction in plants (Woodward & Willians, 1987), and the precipitation in the driest quarter is associated to water availability of water bodies (Reshetnikov & Ficetola, 2011), which acts as the principal factor for the persistence of aquatic plants communities. Similar results were obtained by others authors (Gallardo & Aldridge, 2013; Barnes & al., 2014; Kelly & al., 2014), implying that non-native aquatic macrophytes are able to tolerate a wide range of environmental conditions—v.gr., seasonality in Mediterranean environments—and extreme events. This ability benefits them versus native species (Rahel & Olden, 2008; Gallardo & Aldridge, 2013). Several authors (Pearson & Dawson, 2003; Broennimann & al., 2007; Walther & al., 2009) have suggested that shifts in climate could benefit non-native species, which often tolerate temperature and precipitation ranges broader than the native ones.

The human footprint was positively associated with the presence of all studied species. This association reflects the easiness these species have to establish in disturbed habitats (Chytrý & al., 2009; Kelly & al., 2014), due to the increased presence of introduction vectors and pathways like as channels, roads or railways by which these species can be introduced and the disturbances in land uses in the studied area by human activity (Catford & al., 2011; Gallardo & Aldridge, 2013).

For example, the increase of nutrients on watercourses and water bodies, which contributes to the growth of algal blooms and the rise of turbidity levels (Carter &

Rybicki, 1990; Santamaría & al., 1996) is associated with human activities. It provokes the reduction of light and oxygen availability, stopping the growth of the submerged vegetation (Moss, 1990) but enhancing floating aquatic macrophytes (Egerston & al., 2004). The new ecological scheme will promote the establishment of non-native macrophytes, which are able to colonize degraded habitats, where native macrophytes are unable to survive (Quinn & al., 2001; Catford & Downes, 2010; Chappuis & al., 2011).

Areas under the highest risk of multiple invasions include large rivers basins, highly populated areas, and the coastline (Fig. 3). An important part of the areas for colonization and expansion of these non-native species coincide with territories with agricultural development increase over the last decades. From 1970, the number of records of non-native species in the Iberian Peninsula began to rise (Fig. 1). This period overlaps with the industrialization of agriculture—the Green Revolution—when traditional non-irrigated farming was transformed into huge irrigation areas (Ruiz & al., 2008) in the Iberian Peninsula.

In this period, the high dependence on agricultural chemicals has affected freshwater ecosystems (Galil & al., 2007). Hydrological alterations and the increase of dissolved nutrients, have contributed to the eutrophication of aquatic ecosystems (Chappuis & al., 2011; Quinn & al., 2011), and the intensive land use has favored sedimentation events (Allan, 2004). All these changes have facilitated the expansion of non-native aquatic macrophytes (Egertson & al., 2004; Chappuis & al., 2011; Quinn & al., 2011). Moreover, the increment of sedimentation events caused by an intensive land use also benefits submerged non-native species. Principal

areas of irrigated agriculture in the Iberian Peninsula overlap with the most susceptible areas to be invaded by non-native macrophytes (Fig. 4). This phenomenon has been reported previously by García-Murillo & al. (2007) and Ruiz & al. (2008) for *Azolla filiculoides* and *Eichhornia crassipes* (Mart.) Solms expansion, respectively. Both studies support the hypothesis, together with ours, that the quick expansion of non-native macrophytes is due to the nutrients increase contributed by adjacent agricultural areas.

In addition, we also have observed that some areas predicted as being suitable (Fig. 3) were currently unoccupied—see Fig. 2, current presences of studied species—. This may be due to different causes: areas where species have been successfully eradicated—v.gr., *Pistia stratiotes* in neighborhood Doñana National Park, Southern Spain, as pointed up by García-Murillo & al. (2005)—or areas with geographical barriers or species interactions that limited its distributions—v.gr., *Azolla filiculoides* has not been detected in temporary ponds and marshes in Doñana National Park while the weevil *Stenopelmus rufinanus* Gyllenhal was present in samples, as pointed up by Florencio & al. (2015)—. Besides, they can also be areas where species have not been detected yet due to the lack of studies in these places, or because this species may have not been able to colonize these suitable areas yet (Liu & al., 2011) as a consequence of they are still in the early stages of the invasion process. These two last points are crucial for proper management and early control of non-native species.

Among the species studied in this work, we consider that the most harmful are *Azolla filiculoides* and *Eichhornia crassipes*, both present in the major part of the World, being the two more potentially invasive species in Europe and the Mediterranean basin (Hussner, 2012; Kriticos & Brunel, 2016). Their invasion capacity is due not only to climate tolerance and the adapting ability to eutrophic environments, but also to a high rate of vegetative reproduction that ensure the success of colonization in invaded habitats and a high competition with others species (Ruiz & al., 2008; Fernández-Zamudio & al., 2013).

In conclusion, our study, based on the global distribution of 20 non-native aquatic macrophyte species, contributes to the understanding of the distribution patterns of non-native aquatic macrophytes in the Iberian Peninsula, and it may be used as a base to develop useful tools to manage successfully the Iberian biodiversity in future conservation planning, and for the conservation and management of aquatic ecosystems in other lands. Species distribution models should not be a substitute for field work, but they are a first step that allows an early identification of the most vulnerable areas to implement more effective management efforts preventing biological invasions.

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