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Present and future distribution of three aquatic plants taxa across the world: decrease in native and increase in invasive ranges

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Abstract Inland aquatic ecosystems are vulnerable to both climate change and biological invasion at broad spatial scales. The aim of this study was to establish the current and future potential distribution of three invasive plant taxa, *Egeria densa*, *Myriophyllum aquaticum* and *Ludwigia* spp., in their native and exotic ranges. We used species distribution models (SDMs), with nine different algorithms and three global circulation models, and we restricted the suitability maps to cells containing aquatic ecosystems. The current bioclimatic range of the taxa was predicted to represent 6.6–12.3% of their suitable habitats at global scale, with a lot of variations between continents. In Europe and North America, their invasive ranges are predicted to increase up to two fold by 2070 with the highest gas emission scenario. Suitable new areas will mainly be located to the north of their current range. In other continents where they are exotic and in their native range (South America), the surface areas of suitable locations are predicted to decrease with climate change, especially for *Ludwigia* spp. in South America (down to −55% by 2070 with RCP 8.5 scenario). This study allows to identify areas vulnerable to ongoing invasions by aquatic plant species and thus could help the prioritisation of monitoring and management, as well as contribute to the public awareness regarding biological invasions.

Keywords Brazilian waterweed · Climate change · Parrot feather · RCP scenarios · Species distribution models · Water primroses

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Introduction

Climate change and biological invasions are two of the main drivers of global change with impacts on health, ecosystems and biodiversity, which induce massive costs for society (e.g., Bradshaw et al. 2016). These drivers are expected to impact all ecosystems, including inland aquatic ecosystems (Dudgeon et al. 2006). Indeed, water temperature are expected to increase, while the modification of precipitation regimes may alter flow regimes (Whitehead et al. 2009; Watts et al. 2015). Moreover, climate change is also expected to have impacts on biological invasions, although the strength and direction of this impact varies between species (Mainka and Howard 2010; Bellard et al. 2013). There are 15 taxa living in inland aquatic ecosystems in the list of the 100 world's worst invasive species from IUCN (Lowe et al. 2004), while this biotope represents less than 1% of the earth's surface.

Most of the aquatic invasive plant species have been introduced into their invasive range by humans for their ornamental characteristics or for their use in the aquarium trade. Once they are released into aquatic environments, their spread is facilitated by flows and flooding events that connect water bodies. Propagules can also be dispersed by recreational boats and by birds. Dense waterweed (*Egeria densa* Planch.; Hydrocharitaceae), water primroses (*Ludwigia hexapetala*, *Ludwigia grandiflora* (Michx.) Greuter and Burdet and *Ludwigia peploides* subsp. *montevidensis* (Spreng.) P.H. Raven; Onagraceae), and parrot feather (*Myriophyllum aquaticum* (Vell.) Verdc.; Haloragaceae) are five aquatic plant species native to South America. They have been introduced into Europe, the USA, Australia and New-Zealand, where they increasingly extended their range (Yarrow et al. 2009; Hussner 2012; Thouvenot et al. 2013a). These taxa are considered invasive species by the IUCN because of their impacts on aquatic ecosystems: by forming dense mats on the water surface, they generate, amongst others, lower water flow, dam obstruction, and cause water navigation problems. In addition, the management costs of these species in invaded areas are high (Thouvenot et al. 2013a).

The control and eradication of invasive species are known to be more efficient during the early stages of the invasion, as well as at early stages of the plant life cycle. Thus, the challenge for managers is to detect the presence of invasive organisms as soon as possible, to avoid the colonisation of new environments and to limit their range expansion. To achieve this objective, species distribution models (SDMs) can be used as tools for the early detection of invasive species (Broennimann et al. 2007; Guisan et al. 2013), especially when establishing predictive scenarios, since such models have generally been proven to reflect the correct response to climate change (Stephens et al. 2016). Many studies have investigated invasive plant species distribution through projection by SDM (Kriticos et al. 2003; Peterson et al. 2008; Qin et al. 2014; Thalmann et al. 2015), but only a few of them have used non-native macrophyte species (Heikkinen et al. 2009; Alahuhta et al. 2011). Thus, knowledge about the current potential distribution of macrophytes species could be of interest for managers worldwide. Indeed, invasion fronts are not stabilised yet and the bioclimatic limits of aquatic plant species in their invasive range under current climates are unknown. Information about their potential bioclimatic and biogeographic extent could help to prioritise the monitoring of species presence in high suitability areas, and thus improve species control. For the same reasons, predicting the future potential distribution of aquatic plant species under different climate change scenarios is also of interest. Indeed, climate change is expected to alter the distribution of areas with suitable climate within the next decades, as shown for other invasive species (Bellard et al. 2013).

In this study, we focused on the climate change impact on the potential distribution of three invasive macrophyte taxa that have major impacts in their introduced ranges: *E. densa*, *Ludwigia* spp. and *M. aquaticum*. Previous studies considered the distribution of some of these species, but so far they have only been made at a country scale or based on a limited set of algorithms and general circulation models (GCMs) (Gallardo and Aldridge 2013; Kelly et al. 2014). By applying rigorous modelling methods, we aimed (1) to establish the current potential distribution of five invasive macrophytes and (2) to predict the future climate suitability for these species at world and continental scales.

Materials and methods

Species data

Presence data from the entire range (native and non-native) of species are necessary to model the climatic niches of invasive species accurately (Broennimann and Guisan 2008). Occurrences were collected from internet databases (GBIF, GISIN, AVH, speciesLink) completed by occurrences obtained from personal observations, personal communications and from published and grey literature (see Appendices S1 and S2 in Electronic supplementary material). To ensure correspondence with environmental variables, records before 1950 were discarded, and those after 1950 were aggregated into 0.8° cells, i.e. cells of about 10 × 10 km.

Water primroses have very similar morphologies, high phenotypic plasticity, and apart from the flowering period, they are often mistaken for one another when identifying species (Dandelot et al. 2005). Furthermore, the taxonomy of *L. grandiflora* and *L. hexapetala* is controversial. They are respectively called *L. grandiflora* subsp *grandiflora* and *L. grandiflora* subsp *hexapetala* in Europe, and *L. grandiflora* subsp *hexapetala* is sometimes referred to as *L. grandiflora*. These characteristics confuse the identification of the species, and as we could not be sure that the occurrences collected in databases related to the right species, we chose to consider the three taxa together. Hereafter they are called *Ludwigia* spp.

Climate data

We used bioclimatic variables from the WorldClim database (Hijmans et al. 2005), averaged for the 1950–2000 period, at a 5 arc-min resolution ($\approx 0.8°$). We applied a protocol to select relevant predictive variables for each taxa, selecting uncorrelated bioclimatic variables (Pearson's $r < 0.7$) that best predicted the current distribution of the taxa (see Appendix S3 and Leroy et al. 2013; Bellard et al. 2016). The selected variables are shown in Table 1 and S3.3.

To project future changes in distributions with respect to climate change, we used the four representative concentration pathway scenarios of the IPCC (RCP 2.6, 4.5, 6.0 and 8.5), based on different assumptions of greenhouse gas emissions. We chose two future periods: the 2050s and 2070s (30 year periods from 2041 to 2060 and 2061 to 2080). As uncertainty in forecasting future distribution is partially due to GCMs (Buisson et al. 2010), we used three different GCMs that simulated the impact of the different climate scenarios for the two future periods: the Hadley Centre Coupled Model version 3 (HADCM3) (Collins et al. 2001), Coupled Global Climate Model version 3 (CGCM3) (Yukimoto et al. 2012) and Community Climate System Model version 4 (CCSM4) (Gent et al. 2011). CGCM3 and CCSM4 were downloaded from WorldClim at 5 arc-min resolution.

Modelling methods

Species occurrence data with no corresponding climate data were removed so that occurrence points had obligatory bioclimatic correspondence. After this operation, the number of 0.8° cells used to train

Table 1 Effect of selected climatic predictor variables, based on the fitted response curves (Appendix S4)

Variable	*Egeria densa*	*Ludwigia* spp.	*Myriophyllum aquaticum*
Mean annual temperature		Limiting < 13 °C	
Mean diurnal range	Slightly negative	Slightly limiting	
Annual temperature range	Limiting		
	<15 and >39 °C		
Mean temperature of warmest quarter	Limiting		
	<15 and >28 °C	>27.5 °C	<12 and >37.5 °C
Mean temperature of coldest quarter			Limiting
			<2 and >19 °C
Annual precipitation	Slightly limiting	Slightly negative	
Precipitation seasonality	Slightly limiting	Slightly negative	
Precipitation of driest quarter	Slightly limiting	Limiting	
		>480 mm	>500 mm
Precipitation of coldest quarter	Slightly limiting		Slightly negative

A variable was considered to have a slightly negative effect when the taxa response remained above 0.75, a slightly limiting effect when the response was between 0.5 and 0.75 for some values of the variable, and a limiting effect when the taxa response fell below 0.5. When there is a limiting effect, the variable values that limit the species response under 0.75 are indicated on the line below models was 837 for *E. densa*, 1454 for *Ludwigia* spp. and 1422 for *M. aquaticum*.

We performed the species distribution modelling and ensemble forecasting using the biomod2 package (Thuiller et al. 2009) with R Development Core Team (2015). We used nine different algorithms implemented in biomod2, including: three regression methods, (1) a generalized linear model (GLM) (McCullagh and Nelder 1989), (2) a generalized additive model (GAM) (Hastie and Tibshirani 1990) and (3) multivariate adaptive regression splines (MARS) (Friedman 1991); two classification methods, (4) classification tree analysis (CTA) (Breiman et al. 1984) and (5) flexible discriminant analysis (FDA) (Hastie et al. 1994); and four machine learning methods (6) artificial neural network (ANN) (Ripley 1996), (7) generalized boosted models (GBM) (Ridgeway 1999), (8) maximum entropy (MAXENT) (Phillips et al. 2006) and (9) random forest (RF) (Breiman 2001). These algorithms require datasets with both presence and absence, and we had presence-only records, so we randomly generated three sets of pseudo-absences with equal numbers of presences (Barbet-Massin et al. 2012).

We calibrated the models with 70% of randomly selected data, and evaluated the performance of each model with the remaining 30%. The evaluation stage was performed with three evaluation metrics, the area under the relative operating characteristic curve (ROC), the true skill statistic (TSS) and a similarity index, the Jaccard index (Jaccard 1901). Indeed, Leroy et al. (submitted) suggested that both AUC (area under the curve) and TSS were dependent on prevalence, so they recommended the use of an alternative similarity index to evaluate model performances, as done by Finch et al. (2006) and Ebeling et al. (2008) and also recommended by Li and Guo (2013). We repeated the calibration and evaluation operations three times to obtain an average value of model performance. We evaluated the response of the taxa to climatic predictors with the evaluation strip method (Elith et al. 2005). We used the ensemble forecast method implemented in the BIOMOD platform to combine the nine model outputs, and thus provide a robust forecast of our model taxa distributions. Probability maps were transformed into binary maps of suitable areas or non-suitable areas using the probability threshold that maximised the TSS value (Liu et al. 2005). We generated one current binary distribution map and three future binary distribution maps per scenario and per study period (i.e. 2050 and 2070). Consensus binary maps were obtained by committee averaging, i.e. by attributing presence in a cell when at least two of the three GCMs predicted presence, otherwise we assigned absence (Araújo and New 2007; Gallien et al. 2012).

Suitable aquatic environments

Since our model taxa have aquatic habitat requirements, we filtered our projected suitability maps to only include cells containing aquatic ecosystems adapted to our taxa. We downloaded land use datasets from the Global Lakes and Wetlands Database (GLWD) (Lehner and Döll 2004), and aggregated data into 0.8° cells, corresponding to the resolution of our projection raster. We selected lakes, reservoirs and rivers for *E. densa*, which is strictly affiliated to water, and added layers corresponding to freshwater marshes, floodplains, swamp forests, flooded forests, coastal wetlands, intermittent wetland and wetlands for *Ludwigia* spp. and *M. aquaticum*, which are amphiphyte taxa. For each taxa, we counted the number of cells occupied by suitable aquatic environments, and the number of those cells where models predicted presence of the taxa. Results of potential taxa distribution under current and future climates were expressed as a percentage of suitable aquatic environments, per scenario and per year, at the world scale and for six continents. Variability in future projections has been quantified per scenario and per taxa by calculating the standard deviation across the three GCMs, for the same extents the results of potential taxa distribution.

Results

Model evaluations

The fitted response curves of the three taxa showed a strong response to the selected predictor variables (Appendix S4). For the three taxa, the most limiting determinants for species distribution were temperature variables, especially the mean temperature of the warmest quarter which limited the response of all three taxa (Table 1).

For the three taxa, all the calibrated models had ROC values above 0.8, TSS values above 0.6 and Jaccard indices above 0.3 (meaning that all models predicted correctly at least 30% of presences in the cross-validation dataset) (Appendix S5), with an average ROC value, TSS value and Jaccard Index value higher than 0.9, 0.7 and 0.4, respectively (Table 2). Thus, all the calibrated models were included in the ensemble forecast.

Current potential distribution

The current bioclimatic range of the three taxa was predicted to represent 6.6–12.3% of their suitable habitats, with a large variation between continents (Table 3). In their native continent (South America), *Ludwigia* spp. and *E. densa* are predicted to have a suitable bioclimatic range in around 30% of the aquatic habitats and/or water bodies, while 14.5% of aquatic habitats are likely to be climatically suitable for *M. aquaticum.*

Outside their native continent, Oceania was the most suitable continent with 17.3% (*M. aquaticum*), 30.3% (*Ludwigia* spp.) and 69.5% (*E. densa*) of suitable aquatic habitats. In New-Zealand, a large proportion of the aquatic habitats was predicted to be suitable for the three taxa, except at high altitudes in South Island. In Australia, the suitable areas were located in the north-east, south-east and in Tasmania, while the centre and north of the country were not predicted to be suitable. Asia was the least suitable continent with less than 5% of their aquatic habitats predicted to be suitable for all taxa. Differences occurred between taxa, e.g. Africa was predicted to be almost unsuitable for *M. aquaticum* (1.6%), but suitable for both *E. densa* (20.3%) and *Ludwigia* spp. (13.5%). In Europe and North America, the two continents where the three taxa are invasive, their potential current distribution represented respectively 12–25% and 7–10% of their specific suitable habitats (Table 3; Fig. 1).

Future potential distribution

Europe and North America are the only two continents where our models predicted future increases in the size of the bioclimatic range for the three aquatic taxa (Fig. 1, Appendix S6), which were proportional to gas emission scenarios. According to the results using the RCP 8.5 scenario, by 2070, the three macrophyte taxa will increase their range up to 2.2-fold in Europe and between 1.4-fold and 1.8-fold in North America (Fig. 1).

In Europe, new areas, such as Iceland, are predicted to become suitable to *M. aquaticum* after 2050, even with the low gas emission increase scenario (Fig. 2). Although the climatic conditions of southern Norway and southern Sweden are predicted to be currently suitable for *E. densa* and *M. aquaticum*, their bioclimatic ranges will probably move further north and inland, independently of the future period or of the scenario considered (Fig. 2, Appendix S7). The bioclimatic range of *L.* spp., which is currently at lower latitudes than those of the other taxa, is predicted to increase northwards, especially into Ireland, the UK, Germany, the Netherlands and Denmark. Some areas in Central and Eastern Europe are predicted to become suitable for the three taxa, more or less severely, depending on the period and on the gas emission scenario considered (Fig. 2, Appendix S7). On the other hand, the ranges of the three macrophytes are predicted to decrease in the Mediterranean region, particularly under high gas emission scenarios.

In North America, the climate of the Great Lake region is predicted to become suitable for the studied taxa from 2050, even with RCP 2.6, and especially for Lakes Ontario and Erie, and for the south of Lakes Huron and Michigan (Fig. 3). Climates of other large lakes of Canada are not predicted to become suitable for the three taxa (Fig. 3), which explains the relatively low increase of the percentage of suitable areas for future climates for this continent (Fig. 1). Other regions of North America are predicted to

Table 2 Models evaluation metrics

Species	Mean values (calibrated models)			Ensemble modelling values	
	ROC	TSS	Jaccard	ROC	TSS
Egeria densa	0.94	0.78	0.41	0.97	0.83
Ludwigia spp.	0.92	0.74	0.44	0.96	0.80
Myriophyllum aquaticum	0.95	0.83	0.46	0.98	0.84

Table 3 Results of potential current species distribution at the world and continental scales, expressed in percentage of suitable water bodies for *Egeria densa*, and in percentage of water bodies and wetlands for *Ludwigia* spp. and *Myriophyllum aquaticum*

	% of suitable environment		
	Egeria densa	*Ludwigia* spp.	*Myriophyllum aquaticum*
World	12.3	9.1	6.6
Africa	20.3	13.5	1.6
Asia	4.1	1.5	2.7
Oceania	69.5	30.3	17.3
Europe	24.6	12.5	17.5
North America	10.4	7.5	6.6
South America	31.6	29.2	14.5

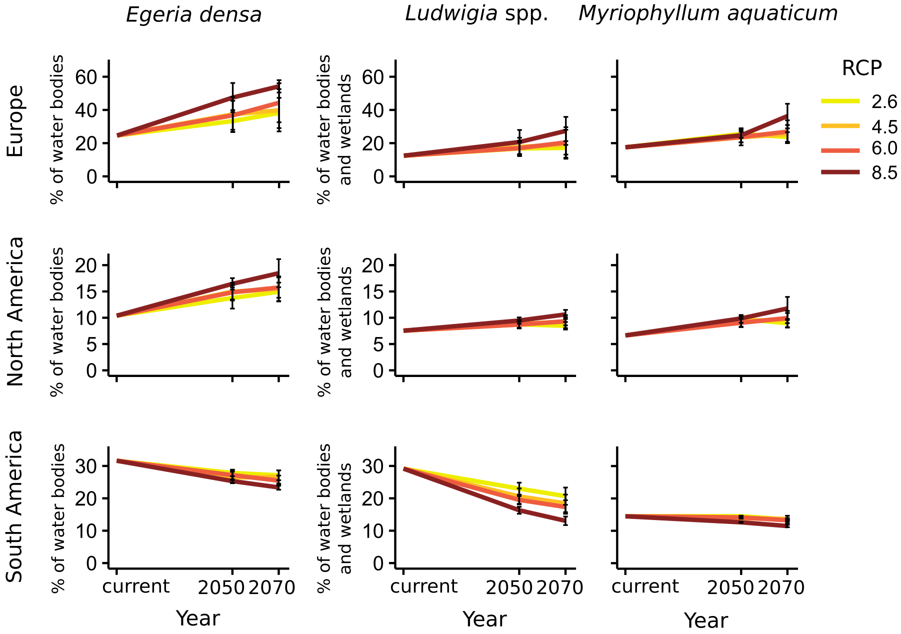

Fig. 1 Percentage of suitable areas for *Egeria densa*, *Ludwigia* spp. and *Myriophyllum aquaticum* with current climatic conditions, and for 2050 and 2070 with the four RCP scenarios in Europe, North America and South America. The *error bars* are standard deviation across the three GCMs, represented for each future scenario

become suitable for the taxa, with a global progression northwards, in particular on the coasts, but with differences between taxa. The four scenarios show that water bodies located at the eastern border between Canada and the US are predicted to become suitable for *M. aquaticum*, while *E. densa* could even reach water bodies located on the left bank of the St Lawrence River (Fig. 3). The west of British Columbia and South Alaska are likewise predicted to become suitable areas for these two taxa. The range of *Ludwigia* spp. is also predicted to move further north than at present, particularly in the Great Lakes region, and some aquatic ecosystems in central US will become suitable environments. For the three macrophyte taxa, some areas which are currently suitable, are predicted to become unsuitable, especially in Mexico, Cuba, the central US and southern Florida under some scenarios.

In their native range, the distribution ranges of our model taxa will decrease proportionally to greenhouse gas emission scenarios (Fig. 1). Under the RCP 8.5 scenario, *E. densa*, *Ludwigia* spp. and *M. aquaticum* are predicted to lose 26, 55, and 20% respectively, of their current suitable areas. In other continents, future climate change will either decrease the proportion of areas suitable for these taxa, or maintain it, such as for

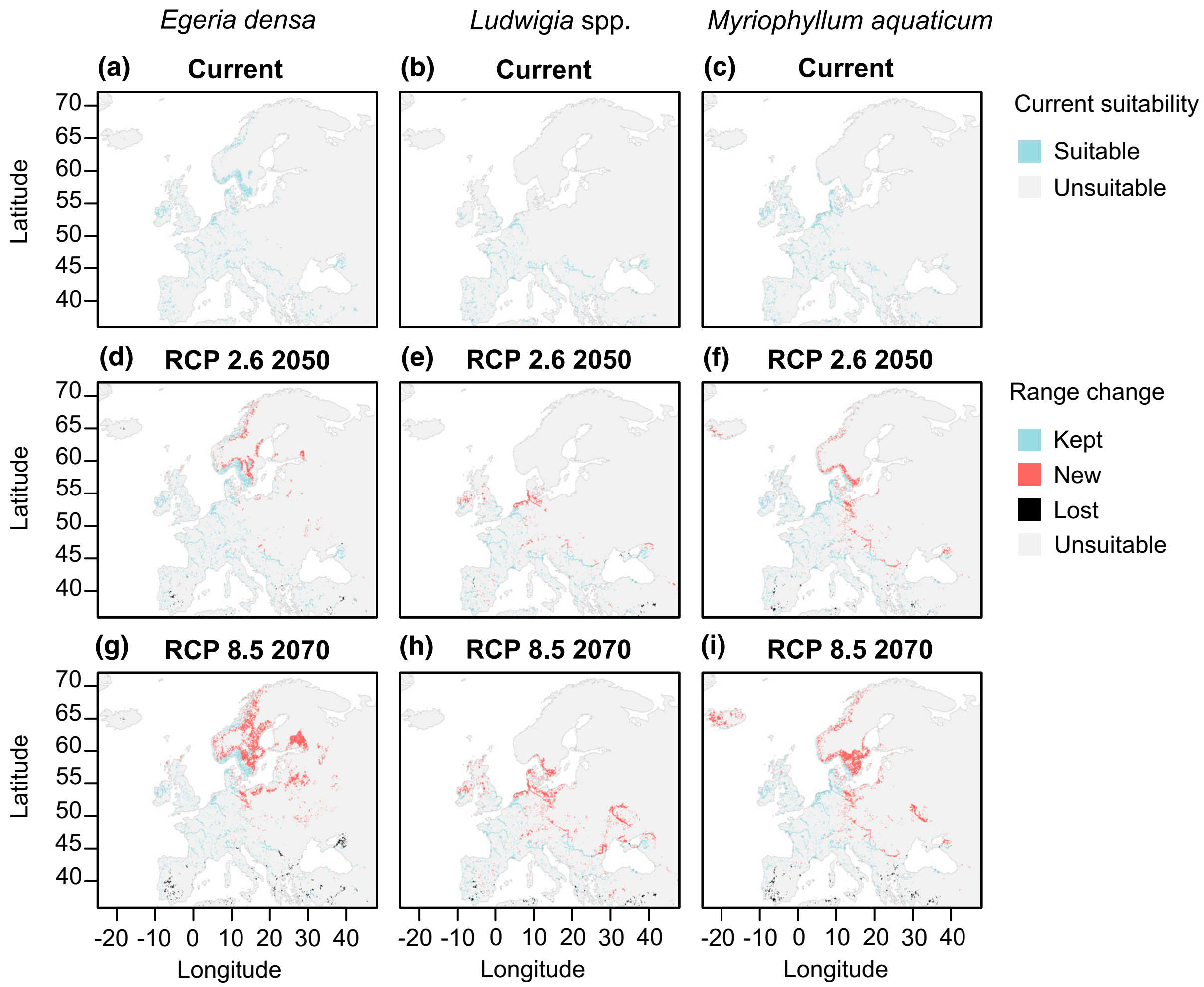

Fig. 2 Current and projected future environmental suitability of Europe for *Egeria densa*, *Ludwigia* spp. and *Myriophyllum aquaticum*, according to two different climate scenarios (RCP 2.6 and RCP 8.5). **a–c** Current climate suitability; **d–f** changes in the predicted distribution range of the species by 2050 according to RCP scenario 2.6; **g–i** changes in the predicted distribution range of the species by 2070 according to RCP scenario 8.5

E. densa in Oceania, where suitable environments are predicted to decrease slightly in Australia, but to increase in New Zealand (Appendix S6).

Discussion

In this study, we predicted the global changes in climate suitability for three invasive aquatic taxa which have massive economic and ecological impacts: dense waterweed (*E. densa*), water primroses (*Ludwigia* spp.), and parrot feather (*M. aquaticum*). Our results highlighted that large portions of aquatic ecosystems are predicted to be suitable for these taxa in most regions of the world. In addition, our results showed that climate change is predicted to have negative impacts in their native range, but positive impacts in their invasive range, which has important implications for their management. This work represents the first large-scale study of climate change impacts on invasive macrophyte distribution.

Taxa bioclimatic ranges and impacts of climate change

The predicted responses of taxa to bioclimatic variables (see Table 2) are consistent with known temperature tolerance and preferences (Getsinger and

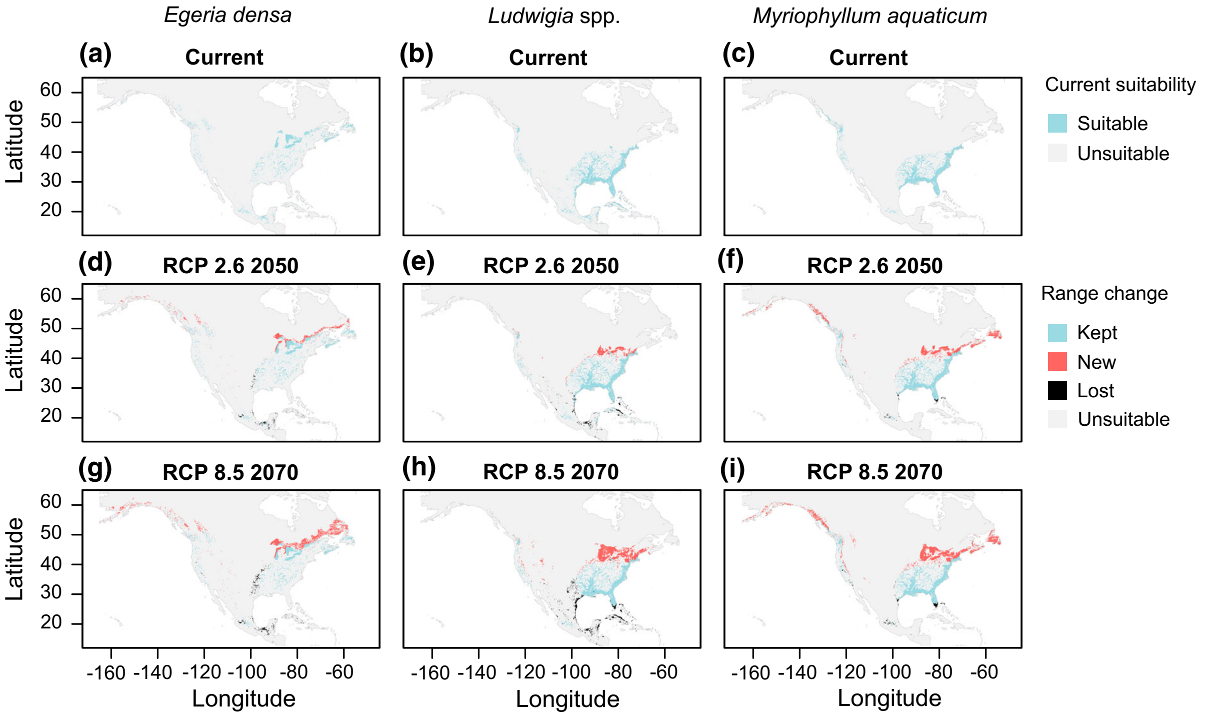

Fig. 3 Current and projected future environmental suitability of North America for *Egeria densa*, *Ludwigia* spp. and *Myriophyllum aquaticum*, according to two different climate scenarios (RCP 2.6 and RCP 8.5). **a**–**c** Current climate suitability; **d**–**f** changes in the predicted distribution range of the species by 2050 according to RCP scenario 2.6; **g**–**i** changes in the predicted distribution range of the species by 2070 according to RCP scenario 8.5

Dillon 1984; Hussner and Champion 2011; Thouvenot et al. 2013a). Our results suggested large differences in the proportion of suitable aquatic ecosystems between taxa for some regions of the world (*e.g.*, Asia, Africa), with *E. densa* generally having the highest habitat suitability and *M. aquaticum* having the lowest suitability throughout the world. These differences can be explained by their different climatic niches, but also by the differences between the types of aquatic environments considered suitable for the different taxa. For example, in Oceania, water bodies are rare, and most of them are in areas with suitable climates for *E. densa*, which explains the high proportion of this taxa in this particular range. Another example is the difference between *M. aquaticum* and *Ludwigia* spp. which have similar life forms (amphiphytes) but different environmental preferences. The predicted range of *M. aquaticum* shows that this species has suitable bioclimatic areas at latitudes which are further north than those suitable for *Ludwigia* spp., a result consistent with models by Kelly et al. (2014) in Ireland. The higher cold tolerance of *M. aquaticum* and *E. densa* may allow them to proliferate in Nordic countries and in southern Alaska from 2050 onwards, contrary to *Ludwigia* spp. Our results suggest that all three taxa will benefit from climate change in their invasive range, where they could expand their distribution. Unsurprisingly, their range is predicted to shift northwards in Europe and North America, with a more severe progression for high greenhouse gas concentration scenarios. This result is consistent with the predictions of Gallardo and Aldridge (2013) and Kelly et al. (2014) in Ireland and in Great Britain, but also with predictions for other macrophyte species (Heikkinen et al. 2009; Alahuhta et al. 2011). However, the proportion of suitable environments is predicted to decrease in the future in their native range, as well as in other areas of the world where they have not yet been reported. In general, higher greenhouse gas concentration scenarios should create less suitable climatic niches than lower ones. *Ludwigia* spp. is the taxa which may undergo the most severe loss of environmental niches in South America, and suitable climatic conditions are predicted to almost disappear from parts of the continent, which may threaten the taxa in its native range.

Sources of uncertainties

The protocol applied here was devised with the aim to mitigate uncertainties. The high number of occurrences used to calibrate the models ensured good precision for the niche modelling, even though there is more monitoring and knowledge about taxa presence in their invaded ranges.

Our predictions illustrate the potential bioclimatic range of species based on their modelled environmental niches, and the occurrence of species within their suitable bioclimatic range is conditional upon multiple factors that can impede the colonisation of new environments by these plant taxa (see Fig. 1 in Guisan and Thuiller 2005). Firstly, species have to disperse to a suitable area, which happens mainly by vegetative reproduction and is often human mediated. Prevention of the species dispersion by humans might be more manageable and efficient than controlling the invasive species once they have colonised new sites (see below).

Secondly, our models did not consider local factors such as water body size, water depth, or water quality (pH, nutrients, turbidity, etc.) which can greatly influence the suitability of aquatic environments for the taxa studied (Feijoó et al. 2002; Hussner et al. 2009; Hussner 2010; Bornette and Puijalon 2010). In addition, photoperiod is another factor that was not represented in the predictive variables, even though it influences plant growth, and could limit their spread, especially at high latitudes. Nonetheless, large differences in photoperiod during the year also have consequences on local climates, and thus should be reflected indirectly in the climatic variables used. Include non-climatic variables to the models could allow to improve the spatial accuracy of the predictions.

Thirdly, the spread of the studied taxa throughout wetlands and water bodies might be impacted by competition with other native and invasive plant taxa. For example, several studies demonstrated that species from the Hydrocharitaceae family such as *Elodea canadensis* or *Elodea nutallii* recently experienced a northward range shift (Heikkinen et al. 2009; Carey et al. 2016), while the current potential distribution of *Hydrilla verticillata* is comparable with that of *E. densa* (Peterson et al. 2003). These species may therefore colonise the same water bodies than our studied species. Nonetheless, as many invasive species, the taxa investigated in this study do not seem to be adversely affected by competition with other species (Stiers et al. 2011; Thouvenot et al. 2013b). Thus, the colonisation of the same sites by these species might be more likely to lead to a succession of dominant invasives, or to communities of invasive plants. Consistent with this idea, Gallardo and Aldridge (2013) showed that the invasive species richness of aquatic plants may increase in Ireland in the future.

In addition, the GLWD database used in this study to limit the potential presence of the taxa to aquatic environments and wetlands, represents current locations of water bodies and wetlands. In the future, a decrease in precipitation and the modification of rainfall frequency could lead to modifications of water bodies and wetland size and location. To be more accurate in our predictions, we need an estimation of the future potential distribution of water bodies and wetlands.

Finally, the modelled distribution of *Ludwigia* spp. might be either more or less accurate than for the two other taxa studied, as it groups together three different species from the Ludwigia genus. The results presented in this study represent average potential distributions and if the three Onagraceae species do not have the same climatic limits, the results might be under- or overestimated compared with an analysis of individual species. On the other hand, if they present similar bioclimatic niches, considering them together might have enhanced the prediction.

Prioritisation of management policy

Our predictions of the current climate ranges of the three invasive taxa presented in this study do not reflect their current distribution, especially outside their native range. Indeed, taxa have not yet been introduced into every continent, and, among other factors, the time since introduction of the taxa into their invasive range has not always allowed them to be in equilibrium with the environment, so they probably have not reached all of their suitable environments yet. Our results therefore highlight, not only an imminent risk of colonisation of new areas by the taxa, but also an opportunity to control the progression of the invasion front. The taxa spread mainly vegetatively in their exotic ranges, but *Ludwigia* spp. are also capable of sexual reproduction, which could increase their dispersion capacity (Ruaux et al. 2009). In water bodies already colonised, propagules are mainly dispersed by water flow (Santamaría 2002; Li 2014). However, the colonisation of new watersheds can occur when propagules are transported by birds (Santamaría 2002), even though humans are the main vector of introduction and spread through water bodies (Zhang and Boyle 2010; Gallardo and Aldridge 2013).

In order to control the invasion front, part of the policy could be to sensitise people who are susceptible to use the water bodies to recognise the species, and to report presences to local organisations or to a database. Fishermen would therefore be able to remove invasive plant fragments from their boats when moving from one water body to another. Limiting the trade of these taxa could also be a solution, if coupled with increasing the awareness of people owning aquariums and garden ponds to the necessity of not introducing the species into natural ecosystems. Given the high human influence on the dispersion of aquatic plant species (Gallardo and Aldridge 2013), educating people about the species could be a solution to preclude these macrophytes from reaching new suitable environments.

In conclusion, our models predicted future northward shifts in the bioclimatic ranges of the taxa in their invasive ranges (Europe and North America). The increase in bioclimatic suitability may accelerate the rate of expansion of their northernmost invasion front. In addition, the possible increase in flooding events due to more frequent heavy precipitation events (IPCC 2012) may facilitate the ability of these taxa to disperse into new habitats, both within and outside their invasive ranges. Consequently, future monitoring of species presence should be prioritised both in current and future unoccupied but suitable habitats, within and to the north of current potential distributions. In Europe, the climate of Iceland is currently unsuitable for the three taxa, but is predicted to become suitable for *E. densa* and *M. aquaticum* under future climatic conditions. Given the known sensitivity of islands to invasion, any importations of these species to Iceland should be avoided. Water bodies of Australia and New-Zealand are predicted to remain highly suitable for *E. densa*, but the long distances between some water bodies in Australia could prevent the dispersion of this species across the whole of the southeastern and southwestern parts of the country.

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