

Climatic niche shift of aquatic plant invaders between native and invasive ranges: a test using 10 species across different biomes on a global scale

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Abstract – Environmental niche conservatism defines a concept, stating that species could live in the same environmental condition in both native and invasive ranges. Niche modeling often used this as basis for the prediction of the range of invasive plants. However, it is debatable whether environmental niches of invasive plant species are conserved or shift between native and invasive ranges. Only few studies have investigated such a shift in aquatic plant invaders (APIs) on a meaningful global scale. Environmental niche modeling was used to project climatic niche distributions of 10 APIs based both on the native range and the invasive range of species. We found that niche shifts of APIs between native and invasive ranges may occur throughout the world. Moreover, we found niche shifts of APIs between native and invasive ranges across different biomes. The largest climatic niche shift was detected for *Najas minor* and the smallest for *Alternanthera philoxeroides*. For all 10 APIs, overlap between both ranges was maximal for large river deltas, while overlap was minimal for temperate floodplain rivers and wetlands. For APIs, the suitability of the climatic habitat was highest in temperate coastal rivers for invasive models in invasive ranges. More importantly, based on invasive models, climatic suitability was significantly higher for temperate coastal rivers and temperate floodplain rivers and wetlands in invasive ranges and compared to native models. We suggest to integrate climatic niches of both native and invasive ranges into projections of the global climatic niche distribution of APIs.

Keywords: climatic niche shift / aquatic plant species / biomes / niche overlap / plant invasion

Résumé – **Changement de niche climatique de plantes aquatiques invasives des habitats natifs aux habitats envahis: un test utilisant 10 espèces de différents biomes à une échelle globale.** Le conservatisme de niche environnementale définit un concept, affirmant que les espèces pourraient vivre dans les mêmes conditions environnementales dans les habitats indigènes et invasifs. La modélisation de niche a souvent servi de base à la prédiction de l'extension des plantes envahissantes. Cependant, cela est discutable si les niches environnementales des espèces de plantes envahissantes sont conservées ou se modifient entre les aires indigènes et invasives. Seules quelques études ont étudié un tel changement chez les plantes aquatiques invasives (API) à une échelle mondiale significative. La modélisation de niche environnementale a été utilisée pour projeter des distributions de niches climatiques de 10 API basées à la fois sur la répartition native et invasive d'espèces. Nous avons constaté que des changements de niche des API entre les aires indigènes et invasives peuvent se produire dans le monde entier. En outre, nous avons trouvé des changements de niche des API entre les aires indigènes et invasives entre différents biomes. Le plus grand changement de niche climatique a été détecté chez *Najas minor* et le plus petit pour *Alternanthera philoxeroides*. Pour les 10 API, le chevauchement entre les deux aires de répartition était maximal pour les grands deltas des rivières, alors que le chevauchement était minimal pour les rivières de plaine inondable et les zones humides. Plus important encore, selon les modèles d'invasion, la pertinence climatique était significativement plus élevée pour les rivières côtières tempérées et les rivières de plaine inondable et les zones humides tempérées dans les aires envahies comparées aux aires indigènes. Nous suggérons d'intégrer les niches climatiques des aires indigènes et invasives dans les projections de la répartition mondiale des niches climatiques des API.

Mots-clés : changement de niche climatique / plantes aquatiques / biomes / chevauchement de niche / plantes invasives

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1 Introduction

From an environmental management perspective, aquatic plant invaders (APIs) are a growing concern, because they constitute 11% (4 of 36) of the world's most invasive plant species; additionally, they pose a threat to biodiversity, ecosystem balance, and water bodies (Hussner, 2012; Leppäkoski *et al.*, 2013; Svirčev *et al.*, 2014; Luque *et al.*, 2014). The environmental niche describes the response of APIs to the distribution of suitable habitats. The expansion and evolution of APIs in non-native ranges, and their propagation along barriers may instill an environmental niche shift. Previous studies have also shown that environmental niche shift is related to human influence (Riis *et al.*, 2012; Hussner, 2012; Donoghue and Edwards, 2014; Svirčev *et al.*, 2014; Nunes *et al.*, 2015). API seedlings have been imported to non-native regions for ecological restoration, agricultural production, or even as ornamental plants (De Groot *et al.*, 2002; Leppäkoski *et al.*, 2013; Riis *et al.*, 2012; Kaufman and Kaufman, 2013). Additionally, a period of repeated human colonization in relation to plasticity, establishment, and genetic evolution can result in a successful niche shift. Plasticity is the ability of an individual plant species to alter its physiology or morphology in response to changes of environmental conditions (Nunes *et al.*, 2015; Donoghue and Edwards, 2014; Guisan *et al.*, 2014). Hence, some degree of plasticity allowing at least the temporarily establishment of individual plants enables subsequent climatic niche evolution (Zhu *et al.*, 2013; Guisan *et al.*, 2014; Nunes *et al.*, 2015). The interaction between the climatic niche shift of APIs and their expansion into invasive ranges is rather complex (Petitpierre *et al.*, 2012; Guisan *et al.*, 2014; Larson *et al.*, 2014). This report uses the premise of climatic niche shifts as basis for a risk assessment of APIs.

Environmental niche modeling (ENM) was used to predict the ability of alien plant species to inhabit and thrive in invasive ranges, based on environmental niche conservatism. In fact, invasion ecologists have used ENMs to model suitable climatic habitats of APIs, based on climatic factors for the risk assessment of API invasion (Zhu *et al.*, 2013; Montecino *et al.*, 2014; Natalie and Myla, 2015). In particular, a study by Natalie and Myla (2015) modeled both range expansion and habitat preferences of three APIs in the United States. Their results led to the suggestion that land managers in the northeastern United States should concentrate on both early detection and rapid response management for API invasion in lakes, ponds, and man-made wetland habitats. Furthermore, Zhu *et al.* (2013) used MAXENT modeling to project potential distributions of *Spartina alterniflora* on a global scale, based on the transferability of ENM predictions between native and invasive ranges. Climatic niche conservatism is the key assumption for the evaluation of the impact of climate change on distributions of invasive plant species (Petitpierre *et al.*, 2012; Wiens and Graham, 2005; Töpel *et al.*, 2012; Corlett and Westcott, 2013). Previous studies reported climatic factors to be an important driving force behind plant invasion into non-native regions, because invasive plant species typically spread into areas with climatic conditions, similar to their native habitat; this is referred to as climatic niche conservatism (Petitpierre *et al.*, 2012; Corlett and Westcott, 2013; Donoghue and Edwards, 2014). Climatic niche conservatism is widespread among terrestrial plant invaders (Petitpierre *et al.*,

2012). However, it has recently been reported that large-scale validations of the equilibrium assumption, using native and naturalized distributions, are not generally applicable. This was based on a comparison between climatic niches that had been evaluated by occurrence records of native ranges and invasive ranges (Early and Sax, 2014). Considerable variability within published data renders the principle of climatic niche conservatism debatable. However, these studies all focused on climatic niche shifts of terrestrial plant invaders, while only few studies have provided evidence of climatic niche shifts in APIs (Petitpierre *et al.*, 2012).

ENMs can be used to evaluate the expansion risk of particular APIs into non-native regions based on their climatic niche. Furthermore, suggestions for both prevention and control of APIs have been proposed based on the potential API distribution, using data provided by ENMs (Zhu *et al.*, 2013; Montecino *et al.*, 2014; Natalie and Myla, 2015). Modeling the potential distribution of invaded species should ideally be based on occurrence data of the native ranges, rather than that of the invasive ranges, since the species might not reach the full range of habitable space an invaded region (Medley, 2010; Petitpierre *et al.*, 2012). Moreover, climatic niche shifts of APIs between native and invasive ranges increase uncertainty levels of niche structure and species lability, thus decreasing the reliability of ENMs for invasion risk predictions (Petitpierre *et al.*, 2012).

Based on all of the previously described information, we addressed two scientific questions: (1) what is the extent of climatic niche shift between the native and invasive ranges of APIs? and (2) what are the differences in niche shifts of APIs between native and invasive niches across different freshwater biomes?

A biome is a formation of plant species with common characteristics due to similar climatic conditions that can be found across various continents (Abell *et al.*, 2008). Hence, biomes may provide novel insights into the climatic niche of APIs (Petitpierre *et al.*, 2012; Larson *et al.*, 2014). Here, 10 APIs with the most extensive global invasion were used to model the climate space of native and invasive ranges to test the niche shift of these APIs on a global scale. The niche shifts of APIs across different freshwater biomes were also examined.

2 Method and materials

2.1 Species data

The Invasive Species Specialist Group (ISSG) identified several species that provide a representative set of the most widespread and dangerous APIs in the world (<http://www.issg.org/>; accessed in August 2016). These APIs share two main characteristics: they significantly impact the invaded ecosystems and they possess general functional traits that promote invasion (<http://www.issg.org/>; accessed in August 2016) (Lowe *et al.*, 2000). In addition to API identification, the ISSG also identified their invasive and native ranges. Occurrence data and primary geographic coordinates for each API were obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org; accessed in August 2016). Duplicate occurrences of recorded data for species in 5.0-arc-minute grid pixels (10 km at the equator) were removed to avoid georeferencing errors (Beck *et al.*, 2014). To decrease the

Table 1. Number of occurrence localities, AUC values, and climatic niche overlap between native and invasive models for aquatic plant invaders (APIs). Native and invasive (the subscripts in this table) represent native and invasive models, respectively. Record represents the number of occurrence localities based on both native and invasive models, respectively. AUC represents the AUC values of MAXENT modeling based on the occurrence localities of native and invasive models, respectively. D_{obs} represents Schoener's D for APIs between native and invasive models and D_{null} represents Schoener's D outside of the 95% confidence limits for each API based on the null model. D_{obs} values smaller than D_{null} significantly support niche shift. VS NA and VS IN (the subscripts in this table) represent niche overlap between all models and the native models (or invasive models). The code of I was similar to D . Bold values represent significant climatic niche shift between native and invasive ranges based on the null model. SD, standard deviation.

Species	Record _{Native}	Record _{Invasive}	AUC _{Native}	AUC _{Invasive}	D_{obs}	D_{null}	I_{obs}	I_{null}	$D_{\text{VS NA}}$	$D_{\text{VS IN}}$	$I_{\text{VS NA}}$	$I_{\text{VS IN}}$
<i>Alternanthera philoxeroides</i>	58	199	0.969	0.967	0.600	0.609	0.841	0.840	0.675	0.874	0.899	0.985
<i>Ceratophyllum demersum</i>	572	156	0.958	0.933	0.363	0.823	0.709	0.975	0.796	0.532	0.972	0.831
<i>Crassula helmsii</i>	395	860	0.956	0.950	0.539	0.769	0.770	0.966	0.815	0.678	0.962	0.885
<i>Elodea canadensis</i>	287	935	0.969	0.944	0.495	0.728	0.789	0.948	0.694	0.748	0.929	0.941
<i>Hydrilla verticillata</i>	64	102	0.989	0.993	0.307	0.752	0.633	0.928	0.470	0.812	0.791	0.959
<i>Ludwigia peruviana</i>	356	64	0.980	0.979	0.423	0.734	0.698	0.933	0.899	0.479	0.982	0.766
<i>Najas minor</i>	266	106	0.986	0.992	0.151	0.689	0.425	0.893	0.455	0.565	0.773	0.843
<i>Pistia stratiotes</i>	107	162	0.986	0.969	0.487	0.769	0.785	0.951	0.647	0.789	0.896	0.963
<i>Potamogeton crispus</i>	367	316	0.972	0.970	0.437	0.854	0.720	0.977	0.598	0.797	0.844	0.965
<i>Sagittaria platyphylla</i>	81	107	0.989	0.985	0.324	0.727	0.651	0.894	0.628	0.601	0.882	0.880
Mean	255.3	300.7	0.975	0.968	0.413	0.745	0.702	0.931	0.668	0.688	0.893	0.902
SD	164.757	306.079	0.012	0.019	0.124	0.064	0.111	0.041	0.135	0.129	0.069	0.069

negative effect of sampling bias on the performance of ENMs, 10 species with more than 50 unique records for both native and invasive ranges were selected; the entire globe was used as the extent of the input data (Varela *et al.*, 2014) (Tab. 1). The distribution of the species occurrence data as the training dataset of ENM was obtained from the ISSG to incorporate global distribution data. Invasive and native ranges were obtained from the ISSG (<http://www.issg.org/>; accessed in August 2016; Tab. S1).

2.2 Climatic variables

Nineteen bioclimatic variables, ranging from 1950 to 2000 (with 5.0-arc-minute spatial resolution) were downloaded from the WorldClim database (www.worldclim.org; accessed in August 2016). A multi-collinearity test was conducted among the 19 bio-climatic variables based on the Pearson's correlation coefficient to eliminate highly correlated variables from the final modeling procedure. We excluded variables with a cross-correlation coefficient value of $> \pm 0.8$. The resulting eight bioclimatic variables represent numerous factors, including general trends (means), variation (seasonality), and limiting variables (minimum and maximum temperatures) and are closely related to both distribution and physiological performance of plant species (Tab. S2; Grimaldo *et al.*, 2016).

2.3 Climatic niche shift analysis

We used two methods to analyze climatic niche shifts of APIs between native and invasive ranges: principal component analysis (PCA) and ENM.

First, we used PCA to quantify the climatic space, thus illustrating environmental niche shifts of APIs between native and invasive ranges, based on occurrence records and relevant climatic variables (Medley, 2010). Based on the observed

occurrences for each species, a two-dimensional climatic space was defined where the first two axes were identified *via* PCA (Medley, 2010). Thus, the observed climatic niches of APIs between native and invasive ranges could be obtained *via* PCA (Medley, 2010). The PCA was conducted in JMP 10.0 (SAS, USA).

Then, we generated reciprocal models by running one model with the native occurrence records based on ENM, while running the other model using the invasive occurrence records in both native and invasive ranges (Medley, 2010). Reciprocal models are good tools to reveal niche shifts for plant invasion (Medley, 2010). MAXENT (ver.3.3.3; <http://www.cs.princeton.edu/~schapire/maxent/>; accessed in August 2016) was used as a common ENM to model native and invasive niches of APIs in climatic space. This was done based on bioclimatic variables and occurrence localities using native (native model), invasive ranges (invasive model), and both native and invasive ranges (all model) (Warren *et al.*, 2008; Václavík *et al.*, 2012). All pixels were regarded as parts of the possible climate space of native and invasive ranges for the globally distributed APIs (Kolanowska, 2013). A logistic output format was used to visualize the identified potential niches of these APIs in the climate space of native and invasive ranges based on MAXENT modeling (Václavík *et al.*, 2012). For climatic niche maps based on native and invasive ranges, each pixel had a value ranging from 0 to 1, with 0 representing the lowest climatic suitability of (not suitable at all) and representing 1 the highest climatic suitability (completely suitable) (Phillips *et al.*, 2006; Warren *et al.*, 2008). In accordance with a previously described protocol (Phillips *et al.*, 2006), 10,000 background points were selected for pseudo-absence data based on the native and invasive ranges. Auto features were used and other values were retained at default settings provided by Warren *et al.* (2008).

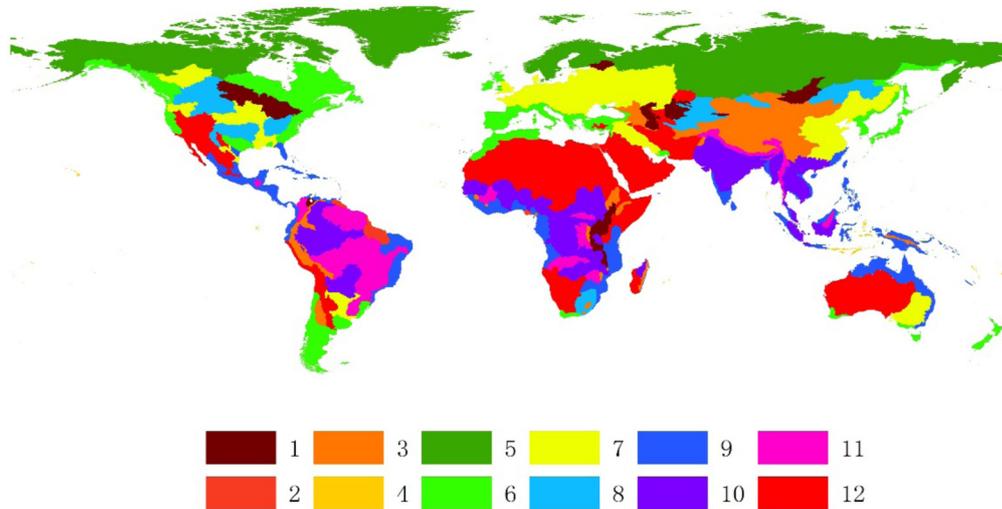


Fig. 1. Global distribution of freshwater biomes. Codes: 1, large lakes; 2, large river deltas; 3, montane freshwaters; 4, oceanic islands; 5, polar freshwaters; 6, temperate coastal rivers; 7, temperate floodplain rivers and wetlands; 8, temperate upland rivers; 9, tropical and subtropical coastal rivers; 10, tropical and subtropical floodplain rivers and wetland complexes; 11, tropical and subtropical upland rivers; 12, xeric freshwaters and endorheic (closed) basins.

Shifts between climatic niches in native and invasive ranges on a global scale were also examined based on the niche overlap (Schoener's D (D)) and a measure derived from the Hellinger distance (I); this was evaluated using ENMTools 1.4.4 (Warren *et al.*, 2008, 2010; Oke and Thompson, 2015). Furthermore, the niche overlaps between all models and native models or invasive models were quantified *via* D and I . We then used the background randomization test of ENMTools 1.4.4 to test this null model, thus ensuring any observed climatic niches and the API background environment were divergent in the same way for each API (Warren *et al.*, 2008, 2010). Each pseudo-replicate dataset was produced as follows: the number of background points of the pseudo-replicate datasets for the native range equaled the number of known occurrences in the native range; furthermore, the number of background points in the pseudo-replicate datasets for the invasive range equaled the number of known occurrences in the invasive range. Niche overlap was determined with the same method to build climatic niche models based on 100 pseudo-replicate datasets (Warren *et al.*, 2008, 2010). Using a one tailed t-test, the observed niche overlap (D_{obs} and I_{obs}) between native and invasive models was compared to the niche overlap from the null distributions (D_{null} and I_{null}). The observed niche overlap (D_{null} and I_{null}) was considered significant if it was outside the 95% confidence limits of D_{null} (or I_{null}). Based on the observed and null D and I values, climatic niche relationships were determined and a niche shift was defined significant when D_{obs} (or I_{obs}) < D_{null} (or I_{null} ; Warren *et al.*, 2008, 2010).

Finally, we computed D values for each API in the native and invasive ranges based on climate spaces between native and invasive models across 12 freshwater biomes (Abell *et al.*, 2008). The following classes were used to facilitate interpretation of niche overlap based on D values: 0–0.2=no or very limited overlap, 0.2–0.4=low overlap, 0.4–0.6=moderate overlap, 0.6–0.8=high overlap, 0.8–1.0=very high overlap (Rödder and Engler, 2011).

We used the following equation to compute climatic suitability of 12 freshwater biomes based on native and invasive models in both native and invasive ranges, respectively:

$$S_j = \sum_{i=1}^n X_i Y_i,$$

where S_j is the climatic suitability for each API in the biome j ; n is the total number of pixels in the biome j ; X_i is the value of climatic suitability of API i in each pixel; and Y_i is the area percentage of climatic suitability of API i in biome j . The global scale map of 12 main freshwater biomes was downloaded from www.feow.org (accessed in August 2016; Abell *et al.*, 2008; Rödder and Engler, 2011) (Fig. 1). Then, we tested for climatic suitability, using non-parametric tests based on ten APIs to assess differences between native and invasive models across 12 freshwater biomes.

2.4 Model evaluation

The area under the receiver operating characteristic curve (AUC) was used to evaluate the MAXENT accuracy. Models with AUC values below 0.7 were not taken into account based on a study by Phillips *et al.* (2006), suggesting these cutoff values to increase model accuracy (Phillips *et al.*, 2006). We then used a binomial test based on omission rate to evaluate the performance of MAXENT modeling for the 10 APIs (Phillips *et al.*, 2006). Training omission rate was the proportion of test occurrence localities measured in pixels of predicted absence (Phillips *et al.*, 2006). These one-sided tests evaluate the null hypothesis that test points are predicted no better than *via* random prediction (Phillips *et al.*, 2006). Binomial probabilities were based on eight common thresholds defaulted by MAXENT modeling (for detailed information, see Tab. S3). Although the training omission rate may not have been sufficient, an omission rate below 17% is a prerequisite for a suitable model (Phillips *et al.*, 2006).

3 Results

All the climatic niche models (including native and invasive models based on 100 pseudo-replicate datasets) had AUC values above 0.7 for the training data sets and a low training omission rate (below 17%), indicating good accuracy of each model (Tab. 1). Based on PCA, we found a possible climatic niche shift between native and invasive ranges across some species such as *Ceratophyllum demersum*, *Crassula helmsii*, *Elodea canadensis*, *Hydrilla verticillata*, *Najas minor*, *Potamogeton crispus*, and *Sagittaria platyphylla* (Fig. 2). Using the null model, the number of D_{obs} (or I_{obs}) below D_{null} (or I_{null}) was 100 for each API, except for the I value of *A. philoxeroides* (namely, outside the 100% confidence limits of D_{null} (or I_{null}) for APIs). Hence, a significant niche shift was present between the native and invasive models in all 10 APIs ($D_{\text{obs}} < D_{\text{null}}$ and $I_{\text{obs}} < I_{\text{null}}$ except for *A. philoxeroides*; Tab. 1).

D for these 10 APIs ranged from 0.151 to 0.600 (mean \pm SD: 0.413 ± 0.124) indicating low or moderate niche overlap between native and invasive models, and a range of I from 0.425 to 0.841 (mean \pm SD: 0.702 ± 0.111 ; Tabs. 1 and S2; Fig. S1). Both D and I were minimal for *N. minor*, while they were maximal for *A. philoxeroides* (Tab. 1; Fig. S1). For *N. minor*, we found that the distribution of high climatic suitability did not match the invasive ranges based on the native model. Furthermore, we could not use the invasive model to predict distributions of suitable climatic habitats in native ranges, further indicating large climatic niche shifts between native and invasive ranges (Fig. 3). Moreover, we found that the niche overlap between the set of all models and native models [mean D : 0.668; mean I : 0.688] or invasive models (mean D : 0.893; mean I : 0.902) was larger than the overlap between native and invasive models across all 10 APIs (Tab. 1). This result indicates that the use of native and invasive occurrence records could decrease prediction uncertainty due to an environmental niche shift between native and invasive ranges (Tab. 1). Consequently, the model transferability of APIs between native and invasive ranges could be improved.

The range of climatic niche overlap between both models (calculated D values) varied from 0.392 ± 0.123 to 0.882 ± 0.187 , suggesting low, moderate, high, and very high niche overlap across different freshwater biomes. The calculated I values varied from 0.698 ± 0.122 to 0.958 ± 0.073 based on 12 freshwater biomes (Tab. 2; Fig. 1). These results indicate maximal overlap between native and invasive models in large river deltas, while temperate floodplain rivers and wetlands have minimal overlap (Tab. 2; Fig. 1). We found maximal climatic habitat suitability of APIs for tropical and subtropical coastal rivers based on native models, and for temperate coastal rivers based on the invasive models of invasive ranges. Suitability was minimal for polar freshwaters of native ranges and for large river deltas of invasive ranges for both models (Tab. 2). Based on native ranges and between models, we detected significant differences of climatic suitability for large lakes, temperate coastal rivers, temperate floodplain rivers and wetlands, tropical and subtropical coastal rivers, and tropical and subtropical upland rivers (all P values < 0.05). Compared

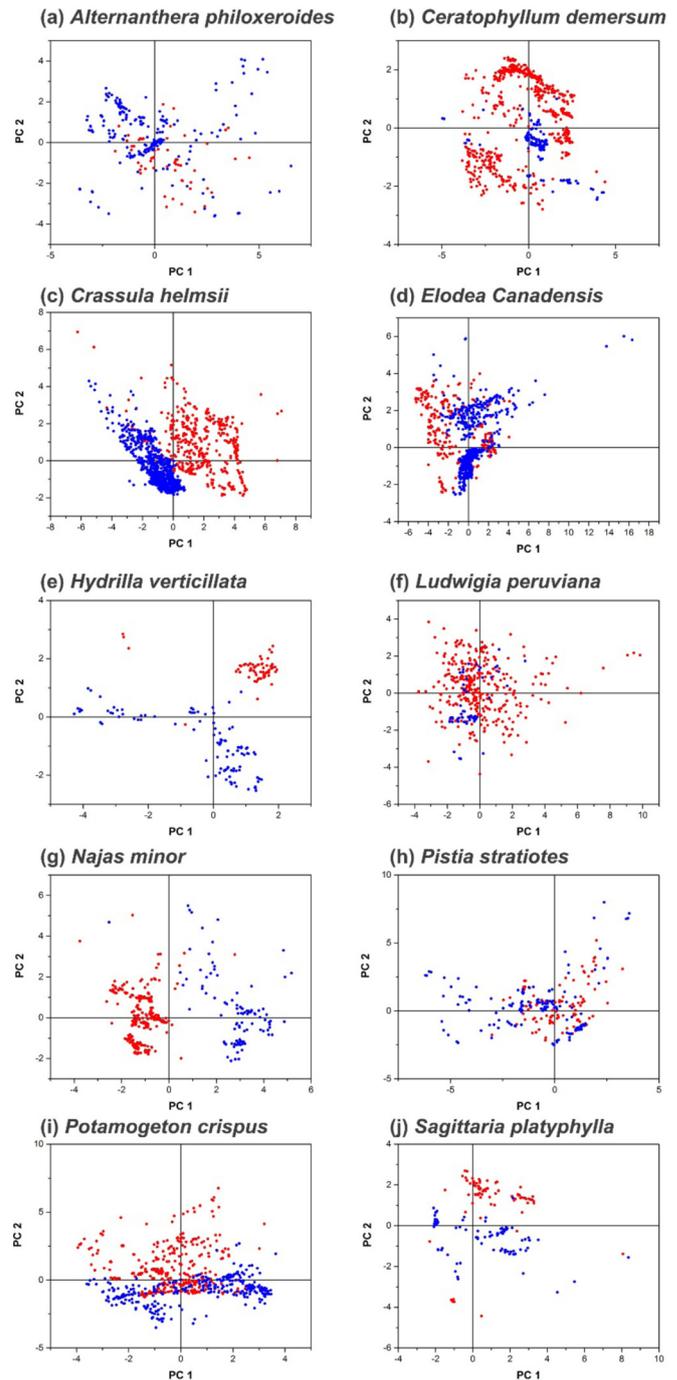


Fig. 2. Climatic space of aquatic plant invaders based on principal component analysis. Red points represent occurrence records of native regions, while blue points represent occurrence records of invasive regions.

to native models, climatic suitability was significantly better for invasive models in temperate coastal rivers, and temperate floodplain rivers and wetlands, based on invasive ranges (Tab. 2; Fig. 1). Furthermore, the climatic suitability of APIs for native ranges was significantly lower for the invasive model compared to the native model (all P values < 0.05 ; Tab. 2).

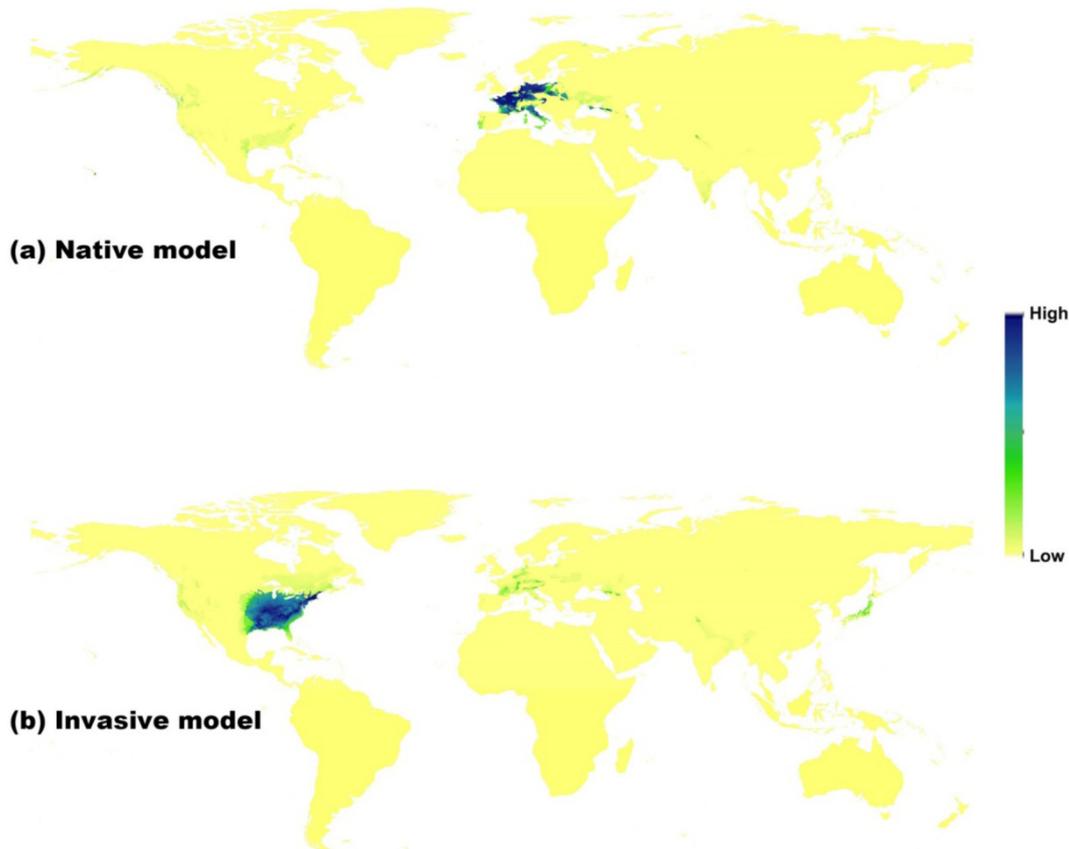


Fig. 3. Map of climatic suitability of *Najas minor* for native (a) and invasive models (b).

4 Discussion

Climatic niche shift of APIs between native and invasive ranges is a valuable component for an appropriate prediction of plant invasion (Donoghue and Edwards, 2014; Guisan *et al.*, 2014; Petitpierre *et al.*, 2012; Wiens and Graham, 2005; Early and Sax, 2014). Issues of climatic niche shift have widely been discussed for plant invaders based on ENMs (Petitpierre *et al.*, 2012; Kolanowska, 2013; Montecino *et al.*, 2014; Wiens and Graham, 2005; Early and Sax, 2014). Here, we focused on aquatic invasive species using MAXENT modeling as a common ENM. Interestingly, our data indicate that based on null model testing using MAXENT modeling, the climatic niches of all 10 tested APIs changed on a global scale between native and invasive ranges (Tab. 1).

Collectively, these studies provide an important basis through which existing models can be improved or new models can be developed; these studies can also be used to predict the distribution of invasive plants, both terrestrial and aquatic. However, it is necessary to consider niche conservatism of APIs with respect to native climatic conditions when using ENMs to predict suitable climatic habitat distributions. Niche conservatism implies that the plant species grow and survive in invasive environmental conditions that are similar to their native ranges. The theory of niche conservatism is the basis to maintain the transferability of ENMs and to improve model performance. However, the considerable climatic niche shift of APIs between native and invasive ranges may result in a reduction of ENM transferability, and the climatic suitability of

APIs may significantly increase in invasive ranges for several biomes (for detailed information, see Tab. 2). Hence, we must take into account the effects of climatic niche shift on habitat suitability in invasive ranges, when these are modeled *via* ENMs. We found that occurrence records of native ranges combined with invasive ranges improve model transferability of APIs between native and invasive ranges. Based on our results (Tab. 1) and considering previous studies, we suggest the use of occurrence locality records of both native and invasive ranges in ENMs to increase the accuracy of projections of climatic niche distributions of APIs on a global scale (Broennimann and Guisan, 2008; Kolanowska, 2013; Kelly *et al.*, 2014; Fernández and Hamilton, 2015; Mainali *et al.*, 2015). For example, Mainali *et al.* (2015) reported improved prediction performance of ENMs of *Parthenium hysterophorus* L. (Asteraceae) with the distribution occurrences from both native and invasive ranges. Therefore, it is important to obtain a large volume of occurrences to generate accurate predictions with ENMs (Donaldson *et al.*, 2014; Mainali *et al.*, 2015). Additionally, our study may provide an important theoretical basis for the future prediction of APIs in invasive ranges based on ENMs and aid further studies that study invasion mechanism(s) of APIs on a global scale.

Niche evolution of APIs may promote niche shift in invasive ranges along a biome gradient *via* population dynamics, community interactions, and genetics of colonization (Donoghue and Edwards, 2014; Wiens and Graham, 2005). Medley (2010) suggested that niche shifts should be indicated if the overlap between native and invasive models in

Table 2. Summary of climatic suitability and niche overlap for all 10 aquatic plant invaders (APIs) in all 12 freshwater biomes. Numerical data is represented as mean \pm SD; *D* represents Schoener's *D* for APIs between native and invasive models on both native and invasive ranges; *I* represents a measure derived from the Hellinger distance and is called *I* based on both the native and invasive ranges; the biome codes are identical to those in Figure 1. The invasive model is based on the distribution records of invasive ranges and the native model is based on the distribution records of native ranges. Bold values represent significant differences between native and invasive models based on the null model. SD, standard deviation.

Biome	Native range		Invasive range		<i>D</i>	<i>I</i>
	Native model	Invasive model	Native model	Invasive model		
1	0.204 \pm 0.179	0.067 \pm 0.059	0.026 \pm 0.051	0.116 \pm 0.171	0.594 \pm 0.182	0.835 \pm 0.107
2	0.044 \pm 0.074	0.016 \pm 0.024	0.000 \pm 0.000	0.000 \pm 0.000	0.882 \pm 0.187	0.958 \pm 0.073
3	0.070 \pm 0.093	0.035 \pm 0.035	0.088 \pm 0.124	0.046 \pm 0.062	0.573 \pm 0.256	0.810 \pm 0.157
4	0.181 \pm 0.245	0.205 \pm 0.205	0.117 \pm 0.131	0.151 \pm 0.162	0.632 \pm 0.189	0.858 \pm 0.121
5	0.019 \pm 0.053	0.011 \pm 0.027	0.024 \pm 0.050	0.090 \pm 0.163	0.645 \pm 0.172	0.855 \pm 0.099
6	0.294 \pm 0.200	0.149 \pm 0.117	0.115 \pm 0.127	0.230 \pm 0.101	0.439 \pm 0.127	0.733 \pm 0.114
7	0.281 \pm 0.171	0.144 \pm 0.145	0.051 \pm 0.047	0.161 \pm 0.087	0.392 \pm 0.123	0.698 \pm 0.122
8	0.102 \pm 0.180	0.015 \pm 0.030	0.027 \pm 0.045	0.087 \pm 0.087	0.640 \pm 0.169	0.864 \pm 0.092
9	0.211 \pm 0.145	0.096 \pm 0.065	0.128 \pm 0.118	0.183 \pm 0.136	0.534 \pm 0.129	0.810 \pm 0.086
10	0.098 \pm 0.126	0.050 \pm 0.062	0.059 \pm 0.074	0.089 \pm 0.126	0.736 \pm 0.205	0.907 \pm 0.087
11	0.139 \pm 0.127	0.072 \pm 0.063	0.081 \pm 0.124	0.093 \pm 0.139	0.718 \pm 0.176	0.913 \pm 0.088
12	0.126 \pm 0.148	0.043 \pm 0.053	0.011 \pm 0.012	0.066 \pm 0.085	0.428 \pm 0.112	0.730 \pm 0.099

native and invasive ranges is small. Our results indicate the existence of API niche shifts between native and invasive ranges across different biomes (Tab. 2). Climatic suitability of APIs was maximal for all 12 biomes, except for tropical and subtropical coastal rivers. Furthermore, the climatic suitability of APIs was higher based on invasive models as compared to native models in temperate coastal rivers, as well as temperate floodplain rivers and wetlands for invasive ranges (Tab. 2). Human activities are the main driving force for plant invasion; *e.g.*, human introduction has been reported to disperse invasive plant species over long distances either on footwear or water sports equipment (Brinson and Malvárez, 2002; Donaldson *et al.*, 2014; Callen and Miller, 2015). Furthermore, hydrological processes of catchments may affect the habitat distribution of species in freshwater biomes (Abell *et al.*, 2008). Various human activities (such as agriculture, urban expansion, and drainage and road construction) in temperate coastal rivers as well as temperate floodplain rivers and wetlands potentially promote the spread of APIs on a global scale due to the outstanding abilities of APIs to adapt to novel conditions (Brinson and Malvárez, 2002). Large river deltas form freshwater ecoregions and these are important interfaces between continents and oceans for material fluxes which have a global impact on marine biogeochemistry (Abell *et al.*, 2008; Bianchi and Allison, 2009). The prediction overlap between native and invasive ranges of APIs may be high due to a considerable overlap between native and invasive models for the invasive range. However, climatic habitat suitability of APIs was low for large river deltas (Tab. 2), due to large areas of habitats that are unsuitable for plants such as northern Africa and central Australia (Donoghue and Edwards, 2014; Fernández and Hamilton, 2015). Hence, API invasion will unlikely occur in invasive ranges of large river deltas.

We need to pay more attention to biomes with high climatic suitability for invasive ranges as well as small niche shifts

between native and invasive ranges (*e.g.* oceanic islands). The same rule may not apply to minimal climatic niche overlap between the ranges, which occurred in temperate floodplain rivers and wetlands (Tab. 2). Due to their negative impact on aquatic and wetland ecosystems, both the prevention and control of API invasions are vitally important for maintaining ecosystem stability (Warfe *et al.*, 2013; Kaufman and Kaufman, 2013; Luque *et al.*, 2014; Svirčev *et al.*, 2014; Nunes *et al.*, 2015). Our results provide novel insights for risk assessments of API invasions. APIs have a large global potential to threaten ecosystems of temperate coastal rivers and oceanic islands (Kueffer *et al.*, 2010). Hence, we assessed the degree of climatic niche shift between native and invasive ranges on a biome scale. Our results suggest that APIs could invade novel habitats of temperate coastal rivers as well as temperate floodplain rivers and wetlands, despite large niche shifts between native and invasive ranges. Due to a small niche shift, APIs currently expand into empty sites within oceanic islands, where climatic conditions mirror those in their native range (Callen and Miller, 2015).

A variety of factors, including human activity and climate change, may promote the adaptation of plant species to novel climatic conditions in non-native regions, resulting in a climatic niche shift between native and invasive ranges (Nunes *et al.*, 2015). Hence, the transferability of ENMs supports the necessity for an accurate determination of climatic niche distributions of APIs in invasive ranges based on observed habitat suitability in both native and invasive ranges (Mainali *et al.*, 2015; Wan *et al.*, 2017).

Supplementary Material

The Supplementary Material is available at <http://www.kmae-journal.org/10.1051/kmae/2017019/olm>.

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