

On the origin of *Echinodorus grandiflorus* (Alismataceae) in Florida (“*E. floridanus*”), and its estimated potential as an invasive species

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Abstract A large semi-aquatic plant, *Echinodorus floridanus*, was described and considered as a rare Floridian endemic only 10 years ago. Recent phylogenetic studies revealed that the new species actually belongs into a South American species, *E. grandiflorus*. This species has been cultivated in Florida as an ornamental aquarium plant at least since the 1980s. This only known wild population in Florida most likely originated by escaping from cultivation, or it was intentionally planted. A maximum entropy niche model suggests a potential range expansion in the southern USA, although the suitability of this area is predicted to be relatively low for the species. Apparently low risk of invasion is also demonstrated by the non-invasive history of this only known wild population. The species may, however, threaten the local flora via hybridization with native *Echinodorus* species, and hence eradication of the species should be considered.

Keywords Aquatic plants · Conservation · Endemic species · Florida burhead · Invasive plants · Rare plants

Introduction

In 1981, a large marsh plant belonging to the genus *Echinodorus* (Alismataceae) was collected from Pensacola, Florida. This specimen was later noticed to represent a species previously unknown in the USA and a new name *Echinodorus floridanus* Haynes & Burkhalter (Florida burhead) was established (Haynes & Burkhalter, 1998). No other locations of occurrence are known to the USA, and the only existing population consisting of several hundreds of individuals is bisected by a highway (Haynes & Burkhalter, 1998; Haynes & Hellquist, 2000). Hence, the species was considered to be a rare endemic and a status for threatened or endangered species was suggested by Haynes & Burkhalter (1998), and the species was mentioned to be of a conservation concern in Flora of North America (Haynes & Hellquist, 2000).

However, this status now appears to be an artifact of erroneous taxonomy (Lehtonen, 2008). Recent advances in *Echinodorus* systematics (Lehtonen, 2006; Lehtonen & Myllys, 2008) revealed several unnatural species and subspecies level rankings in previous classifications, which resulted in a partial revision of the genus (Lehtonen, 2008). The close affinity of *Echinodorus floridanus* with a South American species *E. grandiflorus* was already suspected by Haynes & Burkhalter (1998), and the conspecific status of the two was confirmed by morphological (Lehtonen, 2006) and molecular evidence (Lehtonen & Myllys, 2008). This led to the

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formal synonymization of the name *E. floridanus* under *E. grandiflorus* (Cham. & Schltld.) Micheli (Lehtonen, 2008).

Echinodorus is one of the most popular ornamental plants in aquaria (Kasselmann, 2001) with a cultivation history dating back into the early twentieth century (Rataj, 1978). After a short boom of production in South America, a large-scale production began in Southeast Asia, Europe, and USA (Lehtonen & Rodríguez Arévalo, 2005). Due to the favorable climatic conditions, Florida became the center of aquatic plant nurseries in the North America (McLane, 1969).

In the USA, numerous naturalized aquatic plant species became introduced in the nature via the aquarium pathway (Les & Mehrhoff, 1999; Kay & Hoyle, 2001; Maki & Galatowitsch, 2004; Cohen et al., 2007; Keller & Lodge, 2007), and many are causing immense threats to the native species and ecosystem services (Les & Mehrhoff, 1999). These species are of various geographical origins, and represent widely divergent taxonomic groups (Les & Mehrhoff, 1999). Since it has been recognized that the family Alismataceae is over-represented by invasive species (Daehler, 1998) and Florida provides exceptionally suitable landscapes for various nonindigenous aquatic plants (McLane, 1969), it is possible that *E. grandiflorus* possesses a threat of becoming a nuisance in Florida.

Further risk is introgression of nonindigenous genes into native populations, commonly recognized as one of the main threats for biodiversity (Seehausen et al., 2008). Even quite remotely related *Echinodorus* species are commonly crossed in order to produce new cultivars for the ornamental use in aquaria (Kasselmann, 2001). Two native *Echinodorus* species are present in Florida: *E. cordifolius* (L.) Griseb. and *E. berteroi* (Spreng.) Fassett (Haynes & Hellquist, 2000). In this article, the origin of the *E. grandiflorus* population in Florida, its invasive potential, and possible risks of hybridization with the native species are discussed.

Materials and methods

Ecological niche modeling has become a common practice to predict species' potential ranges and their invasive potential in nonindigenous areas (Peterson &

Vieglais, 2001). This author used Maxent ver. 3.3.0 (Maximum entropy modeling; Phillips et al., 2006; software available at <http://www.cs.princeton.edu/~schapire/maxent>) to predict the potential range of *E. grandiflorus* in southern USA. In order to produce an ecological niche model for *E. grandiflorus*, the author used 46 georeferenced occurrence points from the species native range, based on the herbarium specimens collected between 1925 and 2004 and deposited at BA, BM, BR, H, K, MVFA, MVFQ, MVJB, MVM, SI, TUR, UC, and UNA [herbarium codes according to Thiers (continuously updated)]. South America was used as a background to build the model, which was then projected onto southern USA to predict the potential distribution.

The niche models were based on 19 bioclimatic variables (Table 1) from high resolution (2.5 arc minutes) climatic surfaces (Hijmans et al., 2005; <http://www.worldclim.org>). The climatic data are based on records of the 1950–2000 period (Hijmans et al., 2005). For evaluating model, performance data were divided into training data (75% of occurrence points) and test data for model validation (25% of occurrence points). Since the prediction may depend upon the data partitioning, this author replicated the

Table 1 Bioclimatic variables used in Maxent modelling

BIO1	Annual mean temperature
BIO2	Mean diurnal range [mean of monthly (max temp – min temp)]
BIO3	Isothermality (P2/P7) ($\times 100$)
BIO4	Temperature seasonality (standard deviation $\times 100$)
BIO5	Max temperature of warmest month
BIO6	Min temperature of coldest month
BIO7	Temperature annual range (P5–P6)
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

modeling 10 times using repeated subsampling. Linear, quadratic, and hinge functions of the predictor variables were included in the models. Convergence threshold was set to 10^{-5} and maximum iterations at 500. The results were outputted as logistic values, which give an estimate between 0 and 1 of probability of presence.

Other environmental variables, such as topography and availability of habitats, could have been incorporated into the model as well. Within its native range, *E. grandiflorus* is the most common along rivers, river deltas, and other lowland areas (pers. obs.), which also typify Florida and southern USA more broadly. Aquatic habitats possibly suitable for the species are also common in the area, as can be observed from the wide occurrence of closely related *E. cordifolius* and more distantly related *E. berteroi* in the southern states (Haynes & Hellquist, 2000; Lehtonen, 2008). Since idea of the study is to broadly limit an area where the species potentially could sustain itself, the more detailed habitat-level information is not as relevant for this study, and consequently is not included in the model.

In addition to previously mentioned collections, herbarium specimens collected from Floridian aquarium plant nurseries were found from herbaria AAU and FLAS. These specimens were not included in the niche model, but they were used to date the cultivation history of *E. grandiflorus* in Florida.

Results

The oldest herbarium specimen representing a wild population of *E. grandiflorus* in Florida was collected in 1981 (*Wilhelm 9464* USF!), and further collections from the same population have been made in 1986 (*Burkhalter 10310* FSU), 1989 (*Burkhalter & de Graaf 11539* FSU), 1997 (*Haynes & Burkhalter 9717* UNA!), 2000 (*Reese 1* UNA!), and 2002 (*Junge s.n.* M!). The population is located at sea level in a *Taxodium*-dominated swamp forest (Haynes & Burkhalter, 1998), thus resembling the native gallery forests habitats. However, these are not the only specimens of *E. grandiflorus* collected from Florida. At least one other herbarium collection of the species has been made from the aquarium plant nursery: *McClade s.n.* 19/07/1985 (AAU!) from Broward County, with Brazil mentioned as the original source.

Ridings & Zettler (1973) studied *Aphanomyces* disease in the Floridian aquarium plant nurseries and its effect on the different cultivated *Echinodorus* species. Their voucher collections are located in FLAS (accession numbers 109518–109524), but does not include *E. grandiflorus*. Hence, it appears reasonable to believe that *E. grandiflorus* was not yet imported into Florida at the time of the *Aphanomyces* invasion in the early 1970s.

Maxent modeling yielded an average test AUC (area under the curve, see Phillips et al., 2006) of 0.959 for the replicated runs, with a standard deviation of 0.061. The prediction maps averaged over all the 10 models are presented as logistic outputs in Figs. 1 (projected into native range) and 2 (projected into southern USA). The logistic output gives an relative probability of presence (Phillips & Dudík, 2008). The models did not predict Florida to be generally suitable for *E. grandiflorus*, but a relatively narrow coastal region from Houston to New Orleans appeared as more suitable. Three variables with the largest contribution to the Maxent

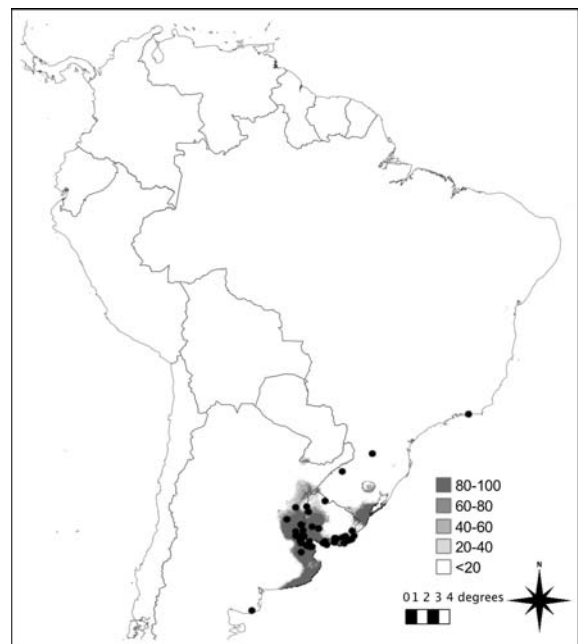


Fig. 1 Native locations of *E. grandiflorus* used for Maxent bioclimatic modeling, with a predicted potential range in South America. The prediction is averaged logistic output of 10 Maxent models, each using randomly selected 25% of data points in model evaluation. The color scale indicates relative probability of occurrence

Fig. 2 Potential range for *E. grandiflorus* in southern USA. The prediction is averaged logistic output of 10 Maxent models, each using randomly selected 25% of data points in model evaluation. The only known wild population in Pensacola, Florida (marked with a dot), was not incorporated in the modeling. The color scale indicates relative probability of occurrence

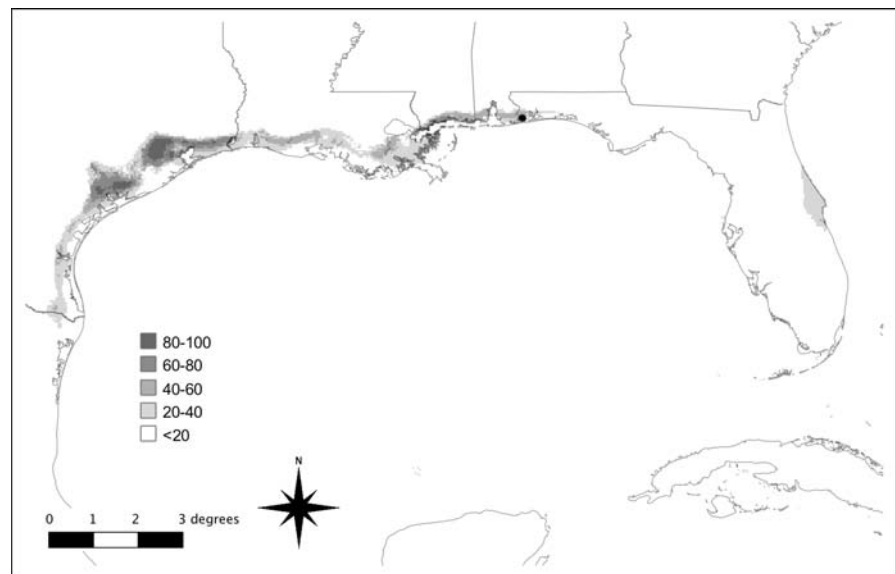


Table 2 The percent contribution of the 10 most important environmental variables to the Maxent model

Variable	Percent contribution
Mean temperature of wettest quarter	32.8
Precipitation seasonality	9.9
Precipitation of driest month	9.9
Isothermality	8.2
Precipitation of warmest quarter	7.4
Mean diurnal range	6.4
Min temperature of coldest month	4.8
Temperature seasonality	4.2
Precipitation of coldest quarter	3.4
Mean temperature of coldest quarter	2.9

Values shown are averages over 10 replicate runs

model were mean temperature of the wettest quarter, precipitation seasonality, and precipitation of driest month (Table 2). According to the jackknife test, annual mean temperature is the variable including most useful information by itself.

Discussion and conclusions

Several *Echinodorus* species have outlying populations remote from their main distribution area. This pattern can be found for at least the following species: *E. berteroi* has its main distribution in North America and the Caribbean Islands, but several

isolated populations are known from Ecuador, Peru, Paraguay, and Argentina (Lehtonen, 2008); *E. horizontalis* has its main distribution in western Amazonia, but isolated populations have been found in the mouth of the Orinoco and Amazon rivers, in Guyana, and one collection from central Amazonia (Rataj, 1978; Lehtonen, 2008); *E. longipetalus* has its main distribution in Paraguay and southern Brazil (Lehtonen, 2008), with two known collections from Suriname (*Rombouts 447 U!*, *Oldenburger et al. 292 U!*), and one from Venezuela (*Delascio 15335 VEN!*); *E. cordifolius*, with its main distribution in the USA, but collected also from South Brazil (Lehtonen, 2008); and *E. grandiflorus*, with its main distribution along the Atlantic coast of South Brazil, Uruguay, and Argentina, but one population in Florida (Lehtonen, 2008).

Most of these outlying populations are located in uninhabited and remote areas and are therefore probably natural. Furthermore, several *Echinodorus* species are distributed in various Caribbean Islands, or have otherwise wide ranges in South America, suggesting well developed long-distance dispersal capacity. However, old cultivation history may have changed distribution of some species, such as *E. horizontalis* in Amazonia (see Lehtonen & Rodríguez Arévalo, 2005). This is even more probable for *E. grandiflorus* in Florida; the species is a well-known aquarium plant (Kasselman, 2001). In their review of nonindigenous aquatic plants of

New England, Les & Mehrhoff (1999) found that 88% of the species had their origin in cultivation, whereas only 12% of the species had been accidentally introduced or dispersed by themselves. Aquatic plant growers in Florida have intentionally introduced exotic species in the wild to guarantee constant supply and low production costs (McLane, 1969). Therefore, it seems most likely that *E. grandiflorus* in Florida originated either by escaping from cultivation, or it was intentionally planted.

The risk of *E. grandiflorus* invasion in Florida seems to be low. Several lines of evidence support this view: the species distribution modeling revealed no areas with high predicted suitability in Florida. However, the coastal region of Texas, Louisiana, Mississippi, and Alabama apparently could support the species. Historical evidence suggests a low invasive potential as well; despite almost 30 years of existence in Florida, *E. grandiflorus* still inhabits only one relatively small patch. Nevertheless, it should be taken into consideration that some aquatic plants have not become invasive until decades after the initial introduction, and a common means of invasion in a large number of species have included intentional planting and escapes from the cultivation (Les & Mehrhoff, 1999). Hence, even though *E. grandiflorus* has not been an aggressive invader in Florida, new populations may become repeatedly established via the aquarium pathway, and this would be a risk especially in the more suitable coastal regions of Texas, Louisiana, and Alabama.

Changing climate, or introduction of new genes, for example, through hybridization with native *Echinodorus* species, could trigger more rapid expansion in the future. Two *Echinodorus* species are native to southern USA: *E. cordifolius* and *E. berteroi* (Haynes & Hellquist, 2000). Both of these species are common in the area predicted to be the most suitable for *E. grandiflorus* in the USA (Haynes & Hellquist, 2000). *Echinodorus grandiflorus* is known to produce offspring in crossings with closely related *E. longiscapus* Arechav. and *E. floribundus* (Seub.) Seub. (Rataj, 1970). *Echinodorus cordifolius* belongs to the same group of closely related species (Lehtonen & Myllys, 2008), thus possibly allowing gene transfer between *E. grandiflorus* and native *Echinodorus* species in Florida. The risk naturally gets higher if more *E. grandiflorus* populations become established via aquarium pathway or range expansion.

The distribution predictions presented are based on bioclimatic variables only. The real potential distribution area is affected by a multitude of other factors as well, such as habitat availability, dispersal capacity, biotic interactions, and so on. These factors are much harder to model, and were not included here. It is here assumed that the presence of closely related species, obvious dispersal capacity of the genus and common outbreaks of various nonindigenous aquatic plants in southern USA are strong indicators that the landscape itself would allow the range expansion of *E. grandiflorus*, but only if the species can tolerate the prevailing climate. So far, *E. grandiflorus* is present as only one small population in Florida and can be quite easily eradicated, if considered appropriate.

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