

Co-occurring species indicate habitats of the rare *Limonium girardianum*

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Background and aims – The conservation of a rare and endangered plant species requires a clear knowledge of its habitat distribution. Species Distribution Models (SDM) are generally applied to characterize species' suitable habitats and to predict their potential distribution. However, this method is not well suited to rare species that require a fine spatial scale approach. Co-occurring plant species of a targeted species can be used to define suitable habitats taking into account biotic interactions. Our aim was to construct a predictive model of the presence of the rare *Limonium girardianum*, using the species that are the best indicators of its presence.

Methods – In the main sites in the French coastal salt marshes where *L. girardianum* occurs, we investigated 198 quadrats (1 × 1 m) with and without *L. girardianum* in three strata along a topographical gradient. In these quadrats, we recorded plant species and measured the maximum water level during flooding, the soil moisture, salinity and texture. We calculated the species indicator value of the presence of *L. girardianum*. For each quadrat, we added the species indicator values to obtain a score used to model the presence of *L. girardianum*. We compared the predictive power of the model based on co-occurring plant species with a model based on environmental variables.

Key results – The best indicator species of the presence of *L. girardianum* are *Limonium virgatum*, *Hymenolobus procumbens* and *Frankenia pulverulenta*. The predictive power of the model based on the co-occurring plant species appears to be similar to that of the model based on environmental variables, with about 72% of correct predictions. However, the environmental model shows higher False Positive predictions than the plant species model.

Conclusions – The co-occurring plant species can be used to define suitable habitats for *L. girardianum*. The model based on the co-occurring plant species, that integrates the biotic interactions, would appear to be more efficient to define the habitat where *L. girardianum* is most likely to be found. Furthermore, as extensive and numerous vegetation databases are available, this simple method could be used to predict the presence of several species with low abundance.

Key words – Area Under the ROC-curve (AUC), fundamental niche, Generalized Linear Model (GLM), indicator species, *Limonium girardianum*, rare species, realized niche, Receiver Operating Curve (ROC), salt marshes, species distribution models.

INTRODUCTION

The capacity to define suitable habitat is often a crucial parameter in conservation, restoration or reinforcement projects of rare plant species populations, as it requires previous fine knowledge of their ecological requirements and dynamics (Guisan & Thuiller 2005, Wolters et al. 2008, Maschinski et al. 2011).

Data collection of abiotic factors is often time consuming, calls for onerous measurement methods and is not easily realizable by field conservation managers. Nevertheless, currently Species Distribution Models constitute the main procedure for finding suitable habitats (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Their usefulness is however limited by the fact that they do not take into account biotic interactions (Austin 2002, Meier et al. 2010). Hence,

SDMs only illustrate the *fundamental* or Grinnellian niche of species and not their *realized niche* (Pulliam 2000). Finally, co-occurring plant species can be used to develop SDMs and hence to define more precisely suitable habitats for the development of the targeted species.

The endangered *Limonium girardianum* is typically a species with small populations distributed over large Mediterranean coastal salt marshes in France and Spain. It is strictly protected in France (Danton & Baffray 2005), where its habitats are mostly threatened by industrial development and land abandonment (Pavon 2005).

However, since the last decade, coastal salt marshes have endured increasing threats due to the development of human activities such as industry, agriculture, tourism, and pollution (Gedan et al. 2009). Flooding regime, topography, and salinity are the main abiotic factors driving salt marsh functioning and plant community patterns (Chapman 1974, Odum 1988). For more effective management of salt marshes, sensitive species with rapid responses to environmental changes may be used to detect the impact of human-driven change, and they are therefore particularly well-suited for ecosystem monitoring and conservation (Oostermeijer et al. 1994). For example, Carboni et al. (2010) showed that on coastal Mediterranean coastal dunes, native and specialist plant species are sensitive to human-driven changes. Rare species are particularly threatened by habitat destruction and fragmentation or abandonment of human land use (Schröter et al. 2005). Hence, focusing on rare and threatened species by gathering knowledge on them and modeling their habitat would improve management efficiency (Lomba et al. 2010).

To define suitable habitat for *L. girardianum*, the classical SDM based on Geographical Information Systems (GIS) is not applicable as salt marshes represent extensive areas where *L. girardianum* habitat distribution is weak and depends on fine ecological gradients and microhabitats. Here, for *L. girardianum*, we suggest a method that integrates co-occurring species allowing identification of suitable habitats. This method is based on the development of a predictive model of the presence of targeted species.

We address two questions:

- (i) Are co-occurring plant species good indicators of the presence of *L. girardianum*?
- (ii) Do they predict the presence of *L. girardianum* more accurately than environmental variables?

MATERIAL AND METHODS

Study species and sites

Limonium girardianum (Guss.) Fourr. (Plumbaginaceae) is a perennial hemicryptophyte, endemic to the northwestern Mediterranean coastal salt marshes of France and Spain (Erben 1993, Pavon 2005). This species is threatened by habitat disappearance because certain salt marshes have been subjected to increasing human-driven alterations and land abandonment (Pinder & Witherick 1990, Danton & Baffray 2005, Pavon 2005). In addition, *L. girardianum* populations are distributed in few sites with limited range, and for this reason the species is protected in France.

The Mediterranean climate of the French coastal salt marshes is characterized by dry and hot summers with irregular rainfall occurring mainly in autumn and winter that induces irregular flooding periods. Salt marsh soil texture ranges from sandy marine sediments to clayey fluvial sediments of Holocene depositions (Molinier et al. 1964, Corre 1975, Duboul-Ravazet et al. 1982, Somoza et al. 1998). The elevation of salt marshes ranges from 0.5 to 2 m above mean sea level. We studied eleven sites (43°26'2''N to 42°56'58''N and 2°39'56''E to 0°42'12''E) that hold the main French populations of *L. girardianum* (fig. 1) and are classified as priority habitat "Mediterranean salt steppes" (Limonietaia, Natura2000 code: 1510; CORINE code: 15.8 European Habitat Directive 92/43/EEC) (Bissardon et al. 1997).

Sampling and environmental measurements

In order to encompass salt marsh vegetation associated or not with *L. girardianum*, we monitored 198 permanent quadrats of 1 × 1 m in eleven sites. For each site, we considered the three following sampling strata: (i) high topographical position within dunes or grasslands, (ii) mid-topographical position of salt marshes within salt steppes where *L. girardianum* populations occur, and (iii) low topographical position where glasswort species are dominant. Within each stratum and salt marshes, we randomly and equally arranged the quadrats to envelop the whole gradient and presence or absence of *L. girardianum* (Hirzel & Guisan 2002). Within each quadrat of each stratum, we recorded the presence and the absence of *L. girardianum* and we exhaustively inventoried vascular plants with their abundance by estimating the cover rate of ten classes of ten percent of: (i) total vegetation other than *L. girardianum*, (ii) the herbaceous stratum (i.e. inferior to 50 cm height) and (iii) the therophytes.

In addition, we measured eight abiotic variables in each of the quadrats: mean annual water table depth, maximum water level during flooding, winter and summer soil moisture, soil salinity, proportion of clay, fine sand and coarse sand. These soil variables were measured on five soil cores of 1.5 cm diameter by 20 cm depth, sampled at the four corners and at the center of the quadrat. We averaged the value of the five samples of one quadrat for each abiotic variable. To measure water table depth and maximum water level during flooding, we defined the relative topographical elevation of a quadrat to a reference piezometer of 2.5 m depth us-

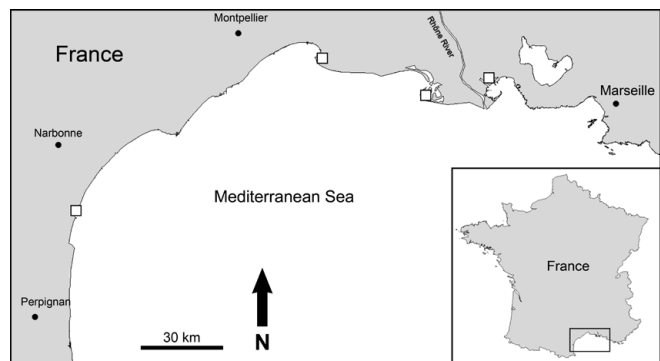


Figure 1 – Map of the study sites (white squares) of *Limonium girardianum*.

ing Leica Builder R100 theodolite (Leica Instruments) with a resolution of 1 cm. The depth of the water table and the level of water during flooding were monitored at the reference piezometer bimonthly during one year. The measured value was reported for each neighbouring quadrat and the relative position of each quadrat was added to the reference piezometer. We measured soil moisture during the dry period in early September 2009 and during the flood period in early January 2010. Clammy soil cores were weighed and air dried at 85°C during 72 h. Then, we weighed dried soil samples and calculated soil moisture as follows: $100 \times [(clammy\ soil\ mass) - (dry\ soil\ mass)] / (clammy\ soil\ mass)$. Soil moisture is expressed in percent of water. Soil granulometry was analyzed using a laser granulometer (Beckman Coulter LS-13320) giving 130 soil fractions. We clustered soil fractions in three classes: from 0.04 μm to 20 μm as ‘clay and slime’ class; from 20 μm to 200 μm as ‘fine sand’ class; and from 200 μm to 2 mm as ‘coarse sand’ class. Soil salinity was measured on dried and homogenized soil samples in the laboratory using InoLab® Cond 730 conductimeter. This was done by diluting ten grams of each soil sample into 50 ml of distilled water at 20°C. We measured the conductivity of the soil solution and converted conductivity values, expressed in $\mu\text{S}\cdot\text{cm}^{-1}$, to gram of NaCl per kilogram of dry soil. We log-transformed salinity values prior to statistical analyses.

Data analysis and modeling

We defined the habitat of *L. girardianum* and the relationship between vegetation community and environmental variables by performing a Canonical Correspondence Analysis (CCA) (Legendre & Legendre 1998). We performed a Monte Carlo permutation test (999 permutations) to assess the significance of the relationship between vegetation and environmental variables.

In order to define the best indicator species of the presence of *L. girardianum*, we separated the data set into two clusters, i.e. plots with *L. girardianum* and plots without *L. girardianum*. These two clusters were used to calculate the indicator value of each plant species (Dufrêne & Legendre 1997, Legendre & Legendre 1998, De Cáceres et al. 2010). This method consists in calculation of an indicator value for each species within clusters with regard to their relative frequency and abundance in each cluster. The indicator value of the species i in the cluster j is calculated as follows: $\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$ where A_{ij} corresponds to the specificity of the species i and is equal to the mean abundance of the species i in cluster j divided by the total abundance of the species in data set. B_{ij} corresponds to the fidelity and is equal to the number of quadrats of cluster j occupied by the species i divided by the number of quadrats in cluster j . In our case, we calculated IndVal of each species as follows: $\text{IndVal}_{i,Lg} = A_{i,Lg} \times B_{i,Lg} \times 100$ where $A_{i,Lg}$ and $B_{i,Lg}$ correspond to specificity and fidelity to *L. girardianum*.

For the best indicator species of presence or absence of *L. girardianum*, we performed simple Student test comparisons of the mean value of environmental variables between *L. girardianum* and other plant species.

To construct the predictive model of the presence of *L. girardianum* using vegetation composition, we used species

IndVal to predict the presence of *L. girardianum* according to plant species composition of the quadrat. For each quadrat, we calculated a score of IndVal ($\text{IndVal}_{\text{score}}$) as the sum of the IndVal of plant species recorded in the quadrat. We removed *L. girardianum* in the calculation of $\text{IndVal}_{\text{score}}$. Then, we fitted a linear model using simple logistic regression between $\text{IndVal}_{\text{score}}$ and presence/absence (binomial response 0 or 1) with Generalized Linear Model (GLM).

In order to estimate the predictive power of the vegetation model, we calculated a ‘mistake ratio’ as follow: $\text{Misratio}_{\text{plant}} = 100 \times \text{number of wrong predictions in quadrats} / \text{total number of quadrats}$. We considered the prediction as wrong when the model predicted a probability between 0 and 0.5 (considered as absence) while the observed value was 1 (presence), and, in the same way, when the model predicted a probability between 0.5 and 1 (considered as presence) while the observed value is 0 (absence). We detailed prediction errors by taking into account ‘False Positive’ (FP) predictions and ‘False Negative’ (FN) predictions (Fielding & Bell 1997). FP constitutes a prediction of ‘presence’ by the model while the observed value is ‘absence’, whereas FN constitutes a prediction of ‘absence’ while the observation is ‘presence’. Hence, a model that presents a higher proportion of FP concerning its Misratio overestimates potentially suitable habitats.

To compare the predictive power of this method with the predictive power of environmental variables, we calculated a ‘mistake ratio’, $\text{Misratio}_{\text{env}}$, in the same way as for vegetation, i.e. between predicted probabilities of presence and observations. The prediction model was constructed applying a multiple regression of all environmental variables (except the vegetation, herbaceous and therophyte cover). Model selection was performed considering AIC criterion (Arnold 2010) with backward stepwise variable selection.

In order to validate the two models, based on vegetation or environmental variables, we used Receiver Operating Characteristic (ROC) curve (Fielding & Bell 1997). The associated Area Under the ROC-curve (AUC) indicates the accuracy of the model. Usually the model’s AUC values of 0.5 to 0.7 correspond to low accuracy, 0.7 to 0.9 indicate useful application and values above 0.9 indicate high accuracy (Swets 1988). To compare the accuracy of the two models, the vegetation based model and the environmental variable based model, we tested the difference between corresponding AUC.

All statistical analyses were carried out with R software v 2.10.1 (R Development Core Team 2010), with ‘vegan’ and ‘pROC’ libraries. Statistical significance was fixed at $p\text{-value} < 0.05$.

RESULTS

Among the best indicator species, *Hymenolobus procumbens* (L.) Hedge & Lamond and *Limonium virgatum* Fourr. showed similar mean values of environmental variables (table 1). Most of the indicator species of the presence of *L. girardianum* showed the same requirement concerning the maximum water level. These species were found between 8.7 and 28.7 above the maximum water level during flooding

Table 1 – List of the ten best indicator species in clusters with and without *L. girardianum* and their mean values (\pm standard deviation) of environmental variables. Significant differences of mean value of environmental variables between *L. girardianum* and others species are noted by “*”.

Indicative species	Indicator Value (%)	IndVAL <i>p</i> -value	Mean water table depth (cm)	Maximum of water level (cm)	Winter soil moisture (%)	Summer soil moisture (%)	Soil salinity (g NaCl. kg ⁻¹ of dry soil)	Litter cover (%)	Vegetation cover (%)	Herbaceous cover (%)	Therophyte cover (%)	Clay and siltine (%)	Fine sand (%)	Coarse sand (%)
Cluster PRESENCE of <i>Limonium girardianum</i>														
<i>Limonium girardianum</i>	-	-	54.3 ± 53.3	-11 ± 28.5	11.1 ± 2.9	4.9 ± 4.5	30.9 ± 3	9 ± 9.7	33.1 ± 30.1	13.8 ± 23.1	13.3 ± 14.4	17.6 ± 12.1	58.5 ± 25.4	23.9 ± 30.8
<i>Limonium virgatum</i>	34,68	0.001	64.3 ± 41.9	-16.8 ± 16.1	10.4 ± 2.6	3.9 ± 3	21.6 ± 2.4*	10.7 ± 12.4	40.7 ± 30.2*	27.6 ± 34.9*	19.1 ± 21.1	15.8 ± 11.9	55.8 ± 20.9	28.4 ± 27.4
<i>Hymenolobus procumbens</i>	32,31	0.001	82.4 ± 48.6*	-26.3 ± 41.3*	10.8 ± 3	4.4 ± 3.3	38.8 ± 2.3	11.4 ± 10.4	33.2 ± 19.2	20 ± 21.1	15.2 ± 10.6	20.3 ± 11.4	58.4 ± 18.1	21.3 ± 23.1
<i>Frankenia pulverulenta</i> L.	32,03	0.001	82.9 ± 43.9*	-13.4 ± 25	11.4 ± 2.4	4.3 ± 2.6	48.3 ± 2.7*	8.5 ± 9	29.2 ± 18.6	17.9 ± 19.7	16.2 ± 12.1	26.6 ± 12.8*	63.1 ± 13.6*	10.3 ± 14.8*
<i>Parapholis incurva</i> (L.) C.E.Hubb.	30,79	0.001	64.7 ± 41	-12.4 ± 16.9	11.7 ± 1.8*	4.2 ± 3	26.9 ± 2.3	6.1 ± 7.6*	37.2 ± 24.7	22 ± 27.7	19.8 ± 15.2*	18.7 ± 12	67.7 ± 14.3*	13.6 ± 16.8*
<i>Suaeda spicata</i> Moq.	30,73	0.003	48.7 ± 45.3	-9.6 ± 35.7	10.5 ± 2.4	5.9 ± 3.6*	47.1 ± 3*	9.7 ± 9.9	25.5 ± 18.3	16.1 ± 20.1	9.7 ± 8.9*	19.1 ± 11.9	50.2 ± 21*	30.6 ± 26.6
<i>Sagina maritima</i> Don	29,07	0.001	75.4 ± 40.4*	-19.7 ± 21.9	11.3 ± 2.1	2.4 ± 2.1*	18.4 ± 2.1*	12.3 ± 18.4	50.8 ± 34.3*	40.5 ± 38.7*	29.9 ± 21.7*	20.2 ± 13.6	65.4 ± 13.9*	14.5 ± 16.4*
<i>Polygogon maritimus</i> Kunze	27,5	0.031	71.1 ± 59.6*	-11.2 ± 40.2	11.4 ± 2.6	3.6 ± 3	24.5 ± 2.4	18.6 ± 23*	41.8 ± 36.2	33.5 ± 38*	21.3 ± 22.3*	22.4 ± 15.2	58.9 ± 17.8	18.7 ± 22.2
<i>Sphenopus divaricatus</i> Rehb.	17,34	0.005	86.2 ± 44.9*	-8.7 ± 12	12.6 ± 1.2*	4.5 ± 2.7	30.9 ± 1.9	6.3 ± 7.3	26.3 ± 15.9	12.2 ± 14.2	17.7 ± 12	25.2 ± 11.9*	70.5 ± 9.7*	4.3 ± 4.3*
<i>Limonium densissimum</i> Pignatti	10,94	0.005	124.1 ± 16.2*	-14.6 ± 8.1	12.9 ± 0.9*	4.7 ± 2.9	28.8 ± 2.3	10.7 ± 4.6	41.4 ± 35.4	27.1 ± 38.5	22.8 ± 17.3	30.6 ± 11.3*	68 ± 10.8*	1.4 ± 0.8*
<i>Limonium duriusculum</i> Fourr.	10,75	0.001	64.4 ± 39.8	-28.7 ± 32.4	10.8 ± 2.4	2.6 ± 1.6*	20.6 ± 1.7	3 ± 6.4*	33 ± 23.3	18 ± 21.8	19.8 ± 14.1	15.6 ± 10.2	70.8 ± 11.6*	13.6 ± 11.7*
Cluster ABSENCE of <i>Limonium girardianum</i>														
<i>Aetheorhiza bulbosa</i> (L.) Cass.	23,56	0.001	86.8 ± 60.1*	-35.9 ± 47.8*	9.4 ± 3.4*	1.2 ± 1.8*	12.8 ± 1.6*	24.3 ± 47.8*	80.8 ± 37.9*	78.6 ± 41.5*	51.7 ± 39.7*	15.5 ± 18.2	62.1 ± 26	22.4 ± 24.6
<i>Vulpia ciliata</i> Dumort.	18,02	0.005	90.9 ± 61.9*	-25.9 ± 26.7*	10.6 ± 2.9	1.4 ± 2.6*	12.4 ± 1.3*	26.2 ± 54.7*	81 ± 36.4*	77.5 ± 43.6*	62.7 ± 29.5*	21.5 ± 23.5*	67.5 ± 16.7*	11 ± 10.3*
<i>Phragmites australis</i> Trin.	17,82	0.020	86.3 ± 80.5*	-25.2 ± 37.9	11.3 ± 3	1.5 ± 2.4*	13.8 ± 2.1*	28.5 ± 79.6*	80.3 ± 43.7*	75.9 ± 54.3*	50.6 ± 42.5*	19.2 ± 19.3	66.8 ± 16.7	14 ± 19
<i>Hypochaeris glabra</i> L.	16,8	0.034	91.6 ± 56.9*	-33.3 ± 44.5*	10.1 ± 3.1	1.3 ± 1.8*	12.9 ± 1.5*	18.5 ± 30.4*	73.3 ± 26.8*	68.2 ± 32.6*	54.4 ± 36.4*	19.7 ± 17.5	64.4 ± 15.7	16 ± 13.5*
<i>Crepis sancta</i> (L.) Bab.	16,11	0.005	92.6 ± 38.9*	-20 ± 14.2	11.3 ± 1.8	1.1 ± 0.7*	12.1 ± 1.2*	27 ± 36*	87.4 ± 19.8*	83 ± 28.3*	64.3 ± 19.2*	21.8 ± 15	66.9 ± 10.7*	11.3 ± 9.4*
<i>Trifolium arvense</i> L.	13,64	0.001	89.6 ± 44.9*	-19.6 ± 10.2	11 ± 1.6	1.8 ± 2*	11.8 ± 1.2*	34.3 ± 41.5	90 ± 23.9*	88.6 ± 28.5*	63.8 ± 16.3*	21.6 ± 13.6	66.7 ± 9.7*	11.7 ± 9.8*
<i>Cerastium semi-decandrum</i> L.	12,11	0.003	86.7 ± 41.5*	-31.7 ± 22.6*	9.7 ± 2.4	1.1 ± 1.2*	11.4 ± 1.1*	20 ± 35	87.1 ± 22.1*	84.7 ± 25.1*	62.7 ± 28.5*	14.6 ± 10.4	67.7 ± 15.7	17.7 ± 16.5
<i>Crepis foetida</i> L.	11,9	0.008	86.4 ± 39.6*	-22.1 ± 13.2*	10.7 ± 1.9	1.5 ± 2.3*	11 ± 1.2*	21.3 ± 31.5	82.7 ± 20.7*	80 ± 23.7*	55.7 ± 24.5*	18.4 ± 14.3	63 ± 13	18.6 ± 17.1
<i>Vicia parviflora</i> Michx.	11,8	0.001	115 ± 31.3*	-15.5 ± 15.1	11 ± 2.7	1.5 ± 0.9*	12 ± 1.2*	57.6 ± 34.5*	97.6 ± 5.9*	97.6 ± 5.9*	76.3 ± 27.4*	30.6 ± 15.7*	62.5 ± 13.5	6.9 ± 8.6*
<i>Anagallis arvensis</i> L.	11,69	0.007	111.4 ± 31.5*	-19.8 ± 32.2	10.2 ± 2.8	1.8 ± 1*	13.4 ± 1.4*	43.5 ± 33.8*	83 ± 31.4*	80.5 ± 36.6*	65.1 ± 30.9*	35.1 ± 25.3*	57.8 ± 20.9	7.2 ± 11.7*

Table 2 – Results of Canonical Correspondence Analysis concerning the seven canonical axes only. Significance and F-ratio of axes were obtained by performing Monte Carlo row permutations (999 permutations).

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
Eigenvalue	0.646	0.395	0.247	0.226	0.187	0.165	0.136
Proportion explained	0.276	0.169	0.105	0.096	0.080	0.070	0.058
Cumulative proportion	0.276	0.444	0.550	0.646	0.727	0.797	0.855
Significance (<i>p</i> -value)	0.005	0.005	0.005	0.005	0.005	0.005	0.010
F-ratio	12.378	7.570	4.729	4.344	3.591	3.166	2.607

(table 1). Species indicative of the absence of *L. girardianum* showed wide differences in terms of habitat requirements, especially with regard to the summer soil moisture, soil salinity and vegetation cover (table 1).

The use of co-occurring plant species showed that the relationship between presence/absence and $\text{IndVal}_{\text{score}}$ was highly significant (adjusted $r^2 = 0.34$, $P < 0.001$, $\text{df} = 179$). For an $\text{IndVal}_{\text{score}}$ higher than 0.88, the probability of finding *L. girardianum* is greater than 0.5.

Concerning the characteristics of *L. girardianum* habitat, the main environmental variable that structures vegetation communities was summer soil moisture and salinity gradient along the topographical gradient. This ecological gradient corresponded to the first canonical axis of CCA that explained 27.6% of response table's variation (fig. 2A and table 2). The second ecological gradient corresponded to soil texture, winter soil moisture and flood level gradient on the second axis of CCA that explained 16.8% of variation (fig. 2A and table 2). Along the first gradient, *L. girardianum* response was unimodal and its habitat corresponded to the intermediate position between flooded habitats and higher

elevations such as dunes (on coarse soils) or grasslands (on fine soils). On the soil texture gradient, the response of *L. girardianum* was not unimodal. Plant communities in low and submersed habitat were dominated by *Arthrocnemum macrostachyum* K.Koch, *Sarcocornia fruticosa* (L.) A.J.Scott, *Spergularia salina* J.Presl. & C.Presl., and *Halimione portulacoides* (L.) Aellen. In contrast, in drier and less salty habitats at higher topographical locations, we observed two different vegetation communities. On the coarse sand of dunes, *Teucrium dunense* Sennen, *Saccharum ravennae* Bleb., *Lobularia maritima* Desv., and *Spartina versicolor* Fabre were the dominant species. On fine sands (i.e. grasslands), we observed *Veronica arvensis* L., *Geranium molle* G.Gaertn., B.Mey & Scherb., *Filago vulgaris* Lam., and *Lagurus ovatus* L. as dominant species.

Comparing the prediction capacity of co-occurring plant and environmental variables, we found that the difference of accuracy between the two models was not significant (ROC comparison test: $D = 0.5742$, $\text{df} = 355.238$, $P = 0.5662$). However, the vegetation model predicted less presence than the environmental variable model ($\text{Chi}^2 = 10$, $\text{df} = 1$, $P = 0.002$), i.e. 87 and 104 respectively. Furthermore, the vegeta-

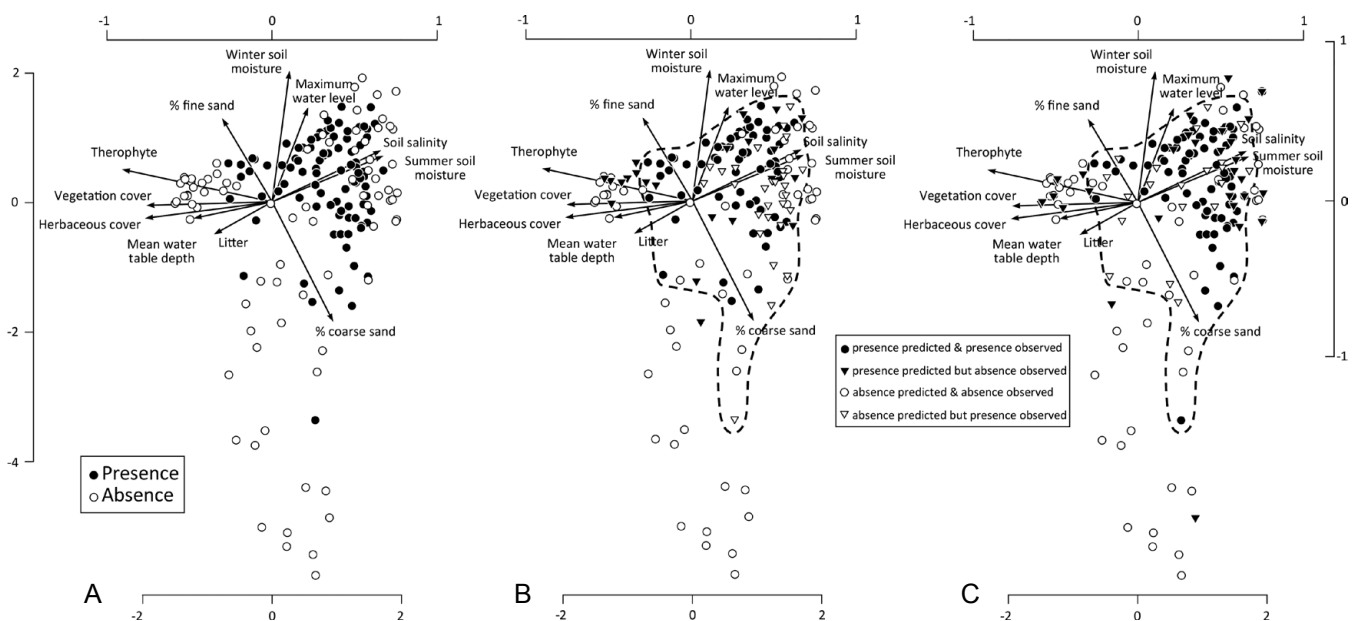


Figure 2 – CCA ordination biplots of species-environment relationship. Only quadrats (dots) and environmental variables (arrows) are shown. A, observed presence and absence of *Limonium girardianum*; B, probability of presence estimated by plant species composition using $\text{IndVal}_{\text{score}}$; C, probability of presence estimated by environmental variables. The two first canonical axes are significant and explain 27.6% and 16.8% of the response table's variation, respectively. For B and C, predictions are given based on probability classes with a range of 0.2 units in five grey levels. Dashed line corresponds to the envelope of observed presence.

tion model predicted less FP than the environmental variable model ($\text{Chi}^2 = 11.98$, $\text{df} = 1$, $P < 0.001$). $\text{Misratio}_{\text{plant}}$ was equal to 27.6% (fig. 2) with good classification accuracy ($\text{AUC} = 0.838$). Missed predictions were characterized by 44% of overestimation of the probability of presence (FP) of *L. girardianum*, and 56% of underestimation of the probability of presence (FN). Environmental variables had a $\text{Misratio}_{\text{env}}$ of 28% but presented similar accuracy ($\text{AUC} = 0.813$). The model overestimated the presence of *L. girardianum* with 61% of overestimation of presence (FP) compared to 39% of underestimation (FN).

DISCUSSION

Our results show that *L. virgatum*, *Hymenolobus procumbens*, and *Frankenia pulverulenta* are the best indicator species of the presence of *Limonium girardianum*. These species grow at the upper limit of temporarily flooded areas where salt and soil anoxia are moderate and where vegetation cover is not too dense (Pennings & Callaway 1992, Álvarez-Rogel et al. 2006). In the lower parts of salt marshes, we essentially found *Arthrocnemum macrostachyum*, *Sarcocornia fruticosa*, and *Halimione portulacoides* which are typically adapted to high soil anoxia and long flood duration (Colmer & Flowers 2008). At higher topographical elevations, we observed two different plant communities according to soil texture. On coarse sand, we recorded *Teucrium dunense*, *Saccharum ravennae*, and *Lobularia maritima* that tolerate dry summers (Álvarez-Rogel et al. 2007). On fine soil, we recorded grassland dominated by *Veronica arvensis*, *Lagurus ovatus*, and *Geranium molle*. In these habitats, vegetation cover is dense and induces high competition pressure that does not allow non-competitive but stress tolerant species such as *L. girardianum* (Bertness et al. 1992). The habitat of *L. girardianum* corresponds to an intermediate position along the gradient of salinity and soil moisture that our sampling encompassed. *Limonium girardianum* responded indifferently on soil texture gradient.

We found that indicator species are good predictors of the presence of *L. girardianum*. The predictive model of the presence of *L. girardianum*, constructed on the base of vegetation composition and indicator species, and the model constructed on the base of abiotic factors, showed similar predictive power (72.4% and 72% of good predictions respectively). Furthermore, results showed that the model based on abiotic factors overestimated the presence of *L. girardianum*, i.e. high FP mostly at the periphery of the niche (fig. 2), whereas the model based on plant species showed less FP. This supports the observation that while the model based on abiotic factors defines fundamental niche, the model based on plant species defines a niche close to realized niche as plants integrate both local abiotic conditions and biotic interactions (Meier et al. 2010).

Through the case of *L. girardianum*, our results suggest that it is possible to construct a simple predictive model of suitable habitats for such rare species.

However, in order to validate the relevance of such models for any targeted plant species, the application will have to be tested on species with different ecological requirements and living in different ecosystems. Since extensive and nu-

merous vegetation databases are available throughout the world and especially in Europe (Schaminée et al. 2011), this simple method could be used to predict the presence of several species with low abundance. We suggest conservation managers to use this simple method for plant conservation as their actions are mainly based on vegetation inventories.

REFERENCES

- Álvarez-Rogel J., Carrasco L., Marín C.M., Martínez-Sánchez J.J. (2007) Soils of a dune coastal salt marsh system in relation to groundwater level, micro-topography and vegetation under a semiarid Mediterranean climate in SE Spain. *Catena* 69: 111–121. <http://dx.doi.org/10.1016/j.catena.2006.04.024>
- Álvarez-Rogel J., Martínez-Sánchez J.J., Blázquez L.C., Semitiel C.M.M. (2006) A conceptual model of salt marsh plant distribution in coastal dunes of southeastern Spain. *Wetlands* 26: 703–717. [http://dx.doi.org/10.1672/0277-5212\(2006\)26\[703:ACMO SM\]2.0.CO;2](http://dx.doi.org/10.1672/0277-5212(2006)26[703:ACMO SM]2.0.CO;2)
- Arnold T.W. (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178. <http://dx.doi.org/10.2193/2009-367>
- Austin M. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157: 101–118. [http://dx.doi.org/10.1016/S0304-3800\(02\)00205-3](http://dx.doi.org/10.1016/S0304-3800(02)00205-3)
- Bertness M.D., Gough L., Shumway S.W. (1992) Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 73: 1842–1851. <http://dx.doi.org/10.2307/1940035>
- Bissardon M., Guibal L., Rameau J.-C. (1997) CORINE Biotopes, types d'habitats français. Nancy, ENGREF.
- Carboni M., Thuiller W., Izzi F., Acosta A. (2010) Disentangling the relative effects of environmental versus human factors on the abundance of native and alien plant species in Mediterranean sandy shores. *Diversity and Distributions* 16: 537–546. <http://dx.doi.org/10.1111/j.1472-4642.2010.00677.x>
- Chapman V.J. (1974) Salt marshes and salt deserts of the world. 2nd Ed. Bremerhaven, Verlag von J. Cramer Ed.
- Colmer T.D., Flowers T.J. (2008) Flooding tolerance in halophytes. *New Phytologist* 179: 964–974. <http://dx.doi.org/10.1111/j.1469-8137.2008.02483.x>
- Corre J.-J. (1975) Etude phyto-écologique des milieux littoraux salés en Languedoc et en Camargue. Montpellier, Université des Sciences et techniques du Languedoc.
- Danton P., Baffray M. (2005) Inventaire des plantes protégées en France. Paris, Nathan/AFCEV/Yves Rocher.
- De Cáceres M., Legendre P., Moretti M. (2010) Improving indicator species analysis by combining groups of sites. *Oikos* 119: 1674–1684. <http://dx.doi.org/10.1111/j.1600-0706.2010.18334.x>
- Duboul-Ravazet C., Gadel F., Martin R., Barusseau J.-P. (1982) Evolution holocène du milieu margino-littoral du Languedoc-Rousillon: un stade ultime de comblement, l'étang de Canet-Saint-Nazaire. *Mémoires géologiques de l'Université de Dijon* 7: 73–80.
- Dufrêne M., Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366. <http://dx.doi.org/10.2307/2963459>
- Erben M. (1993) *Limonium*. In: Castroviejo S., Aedo C., Cirujano S., Lainz M., Montserrat P., Morales R., Muñoz Garmienda F., Navarro C., Paiva J., Soriano C. (eds) *Flora Iberica*. Plan-

- tas vasculares de la Península Ibérica e Islas Baleares. Vol. 3: 2–143. Madrid, CSIC Real Jardín Botánico de Madrid.
- Fielding A.H., Bell J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49. <http://dx.doi.org/10.1017/S0376892997000088>
- Gedan K.B., Silliman B.R., Bertness M.D. (2009) Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science* 1: 117–141. <http://dx.doi.org/10.1146/annurev.marine.010908.163930>
- Guisan A., Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009. <http://dx.doi.org/10.1111/j.1461-0248.2005.00792.x>
- Guisan A., Zimmermann N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186. [http://dx.doi.org/10.1016/S0304-3800\(00\)00354-9](http://dx.doi.org/10.1016/S0304-3800(00)00354-9)
- Hirzel A., Guisan A. (2002) Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling* 157: 331–341. [http://dx.doi.org/10.1016/S0304-3800\(02\)00203-X](http://dx.doi.org/10.1016/S0304-3800(02)00203-X)
- Legendre P., Legendre L. (1998) *Numerical Ecology*. 2nd Ed. Amsterdam, Elsevier Science BV.
- Lomba A., Pellissier L., Randin C., Vicente J., Moreira F., Honrado J., Guisan A. (2010) Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. *Biological Conservation* 143: 2647–2657. <http://dx.doi.org/10.1016/j.biocon.2010.07.007>
- Maschinski J., Ross M., Liu H., O'Brien J., von Wettberg E., Haskins K. (2011) Sinking ships: conservation options for endemic taxa threatened by sea level rise. *Climatic Change* 107: 147–167. <http://dx.doi.org/10.1007/s10584-011-0083-z>
- Meier E.S., Kienast F., Pearman P.B., Svenning J.C., Thuiller W., Araújo M.B., Guisan A., Zimmermann N.E. (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33: 1038–1048. <http://dx.doi.org/10.1111/j.1600-0587.2010.06229.x>
- Molinier R., Viano J., Leforestier C., Devaux J.P. (1964) Etudes phytosociologiques et écologiques en Camargue et sur le Plan du Bourg. *Annales de la Faculté des Sciences de Marseille* 36: 1–100.
- Odum W.E. (1988) Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics* 19: 147–176. <http://dx.doi.org/10.1146/annurev.es.19.110188.001051>
- Oostermeijer J.G.B., Vantveer R., Dennijs J.C.M. (1994) Population-structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of Applied Ecology* 31: 428–438. <http://dx.doi.org/10.2307/2404440>
- Pavon D. (2005) Note sur le genre *Limonium* Miller dans le département des Bouches-du-Rhône. *Bulletin de la Société Linéenne de Provence* 56: 135–139. [Available at http://perso.numericable.fr/daniel.pavon/Telechargements/PAVON-2005_Limonium-Bouches-du-Rhone.pdf]
- Pennings S.C., Callaway R.M. (1992) Salt-marsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73: 681–690. <http://dx.doi.org/10.2307/1940774>
- Pinder D.A., Witherick M.E. (1990) Port industrialization, urbanization and wetland loss. In: Williams M. (ed.) *Wetlands: A Threatened Landscape*: 234–266. Oxford, Basil Blackwell Ltd.
- Pulliam H.R. (2000) On the relationship between niche and distribution. *Ecology Letters* 3: 349–361. <http://dx.doi.org/10.1046/j.1461-0248.2000.00143.x>
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. Vienna, R Foundation for Statistical Computing.
- Schaminée J., Janssen J., Hennekens S., Ozinga W. (2011) Large vegetation databases and information systems: new instruments for ecological research, nature conservation, and policy making. *Plant Biosystems* 145: 85–90. <http://dx.doi.org/10.1080/11263504.2011.602744>
- Schröter D., Cramer W., Leemans R., Prentice I.C., Araújo M.B., Arnell N.W., Bondeau A., Bugmann H., Carter T.R., Gracia C.A. et al. (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science* 310: 1333–1337. <http://dx.doi.org/10.1126/science.1115233>
- Somoza L., Barnolas A., Arasa A., Maestro A., Rees J.G., Hernandez-Molina F.J. (1998) Architectural stacking patterns of the Ebro delta controlled by Holocene high-frequency eustatic fluctuations, delta-lobe switching and subsidence processes. *Sedimentary Geology* 117: 11–32. [http://dx.doi.org/10.1016/S0037-0738\(97\)00121-8](http://dx.doi.org/10.1016/S0037-0738(97)00121-8)
- Swets J.A. (1988) Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293. <http://dx.doi.org/10.1126/science.3287615>
- Wolters M., Garbutt A., Bekker R.M., Bakker J.P., Carey P.D. (2008) Restoration of salt-marsh vegetation in relation to site suitability, species pool and dispersal traits. *Journal of Applied Ecology* 45: 904–912. <http://dx.doi.org/10.1111/j.1365-2664.2008.01453.x>

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