The chapter 4 of the dissertation:Community dynamics of stabilized dune xerophytic shrubs (2016) reproduces entirely the manuscript of:Annals of Botany 119: 1157-1167 (2017).
El capítulo 4 de la tesis doctoral: Community dynamics of stabilized dune xerophytic shrubs (2016), reproduce íntegramente la información del artículo: Annals of Botany 119: 1157-1167 (2017).

Chapter 4

Environmental niche divergence among three dune shrub sister species with parapatric distributions

4 Environmental niche divergence among three dune shrub sister species with parapatric distributions

4.1 Abstract

The effects of environmental factors and biogeographical constraints on the diversification patterns of three dune shrub sister species with parapatric distributions were analysed. We studied the realized response of *Stauracanthus* species to environmental gradients, using their potential distributions and realized bioclimatic niche overlap to assess the geographical and environmental commonalities and differences between these species throughout their recent process of diversification. Four climate variables discriminate the distribution of all *Stauracanthus* species. While seasonality of precipitation, isothermality and mean temperature of the coldest quarter present higher values in the geographical distribution range of *Stauracanthus* species than the overall mean conditions of the Iberian Peninsula, they all show lower values of annual range of temperature. The three *Stauracanthus* species show remarkably similar responses to climatic conditions, with environmental niches of *S. boivinii* and *S. genistoides* being the most coincident, overlapping in average 67%, while overlapping between *S. spectabilis* and *S. boivinii was* 42% and between *S. spectabilis* and *S. genistoides* was 43%. Both the evolution and geographic distributions of *Stauracanthus* species were mainly constrained by their environmental requirements and historical events. Their occurrences are conditioned by the same climate variables, supporting common adaptations of this recently-diversified clade and explaining the existence of high levels of niche overlap. The diversification of *Stauracanthus* is largely consistent with a stochastic process of geographic range expansion and fragmentation coupled with niche evolution in the context of spatially complex environmental fluctuations.

4.2 Introduction

The geographic distributions of species are constrained by their ecological and environmental requirements. Current understanding of the spatial and temporal dynamics of species' ranges in space and time is tied to the Hutchinsonian niche concept (Colwell and Rangel 2009). Hutchinson's duality between ‘‘niche’’ and ‘‘biotope’’ (Hutchinson 1957; Hutchinson 1978) provides a conceptual framework that allows analysing environmental conditions, ecological interactions – i.e. the so-called Grinnelian and Eltonian niches (Soberón 2007) – and geographic distribution altogether (Colwell and Rangel 2009). For clarity and theoretical robustness we follow Hutchinson's (1978) conceptualization of the niche throughout the text (see Colwell and Rangel 2009). Further to these factors, historical events and biogeographical constraints (such as barriers to dispersal) also determine species distributions (Soberón 2007; Hortal *et al.* 2012), creating opportunities for diversification through isolation processes. The dynamic interaction between species' requirements, environmental dynamics, ecological processes and biogeographical events determine the evolutionary history of a given group (Yesson and Culham 2006; Wake *et al.* 2009). Therefore, the integration of statistical models of the distributions of phylogenetically related species with their phylogeographic patterns in an spatially-explicit framework may allow understanding the evolution of new traits and adaptations (Knowles 2003; Diniz-Filho *et al.* 2009).

Analyses combining information on species distributions, niche-mediated bioclimatic responses and species' functional traits with phylogeographic data may allow investigating their joint effects on diversification. Georeferenced data on species occurrences gathered from atlases, museum collections and databases can nowadays be combined with high-resolution climate data by using statistical techniques (commonly referred to as Ecological Niche Models or Species Distribution Models;

Guisan and Zimmermann 2000; Chefaoui *et al.* 2005; Hortal *et al.* 2012; Peterson and Soberón 2012) to predict species' distribution and describe climatic dimensions of a species' niche. Several plant functional traits would in turn reflect species ecological strategies (Pérez-Harguindeguy *et al.* 2013), providing insights about their environmental requirements. And species-level phylogenies are estimated from DNA sequence data (e.g. Pardo *et al.* 2008), being possible to date speciation events via relaxed molecular clock methods (Lepage *et al.* 2007).

In this paper we examine the environmental response of the three species of the Mediterranean thorny shrub genus *Stauracanthus*. The species of this small genus present parapatric distribution – they occupy separate but contiguous areas (Bull 1991) – in the South-Western Iberian Peninsula, a region characterized by the Iberian-African plate boundary, with high habitat heterogeneity and a complex paleoclimatic history. This makes this genus appropriate for analysing the effects of environmental conditions, ecological interactions, historical events and biogeographical constraints on diversification. However, apart from Pardo *et al.* (2008) work on the phylogeographic relationship between an array of *Stauracanthus* populations, little is known on the evolutionary patterns of this genus, and the shape of its diversification in space and time remains unclear. Here we study whether the geographical and environmental differences between these three taxa are the direct result of their diversification patterns. More specifically, we gather and review the available information on the distribution of *Stauracanthus* species in the Iberian Peninsula to then: (i) measure their response to the environmental gradients, (ii) map their potential distribution, and (iii) determine the bioclimatic niche overlap between them. Finally, according to this information and published analyses on their genetic differentiation (Pardo *et al.* 2008) we discuss the geographical and environmental commonalities and differences between these species in the light of their known evolutionary patterns.

4.3 Methods

Study system

Stauracanthus Link (Genisteae) is a genus of thorny shrubs, restricted to sandy soils in the South-West of the Iberian Peninsula and North-Western Africa (Morocco and Algeria; Paiva and Coutinho 1999). *Stauracanthus* taxonomy is not totally consensual, but all authors agree upon the existence of three main taxa (Guinea and Webb 1968; Díaz *et al.* 1990; Paiva and Coutinho 1999). Indeed, previous studies based on analysing chloroplast microsatellites markers provide support for the existence of three distinct clades (Pardo *et al.* 2008) that have been traditionally attributed to three species. After analysing 141 herbarium specimens of LISI and LISU (herbarium abbreviations are according to Holmgren *et al.* (1990) and using our taxonomic and ecological knowledge of the species (see Appendix S4.1), we decided to follow the more recent classification of Paiva and Coutinho (1999), that differentiates three species: *Stauracanthus boivinii* (Webb) Samp. – distributed throughout Western Iberia and North Western Africa on either sandy or gravelly soils (Guinea and Webb 1968); *S. genistoides* (Brot) Samp. and *S. spectabilis* Webb – both growing on coastal sandy soils in South-Western Iberia. An isolated population of *S. spectabilis* occurs on sandy soils in the Atlantic coast of Morocco near Rabat. We studied the distribution of the three species in the Iberian Peninsula. We referred environmental data and presence records of *Stauracanthus* species to the 6,171 cells of 10 km×10 km UTM grid squares that cover the 582,000 km^2 of mainland Iberia. Georeferenced records for the three *Stauracanthus* species were collected from herbaria (COI, SEV, LISI, LISU, MA, MACB and MAF), literature, the Anthos database (http://www.anthos.es/) and field work. In total, we compiled 740 presence records: 215 for *S. boivinii*, 394 for *S. genistoides,* and 131 for *S. spectabilis*, corresponding to 60, 125 and 24 10x10 km grid cells, respectively (Figure 4.1).

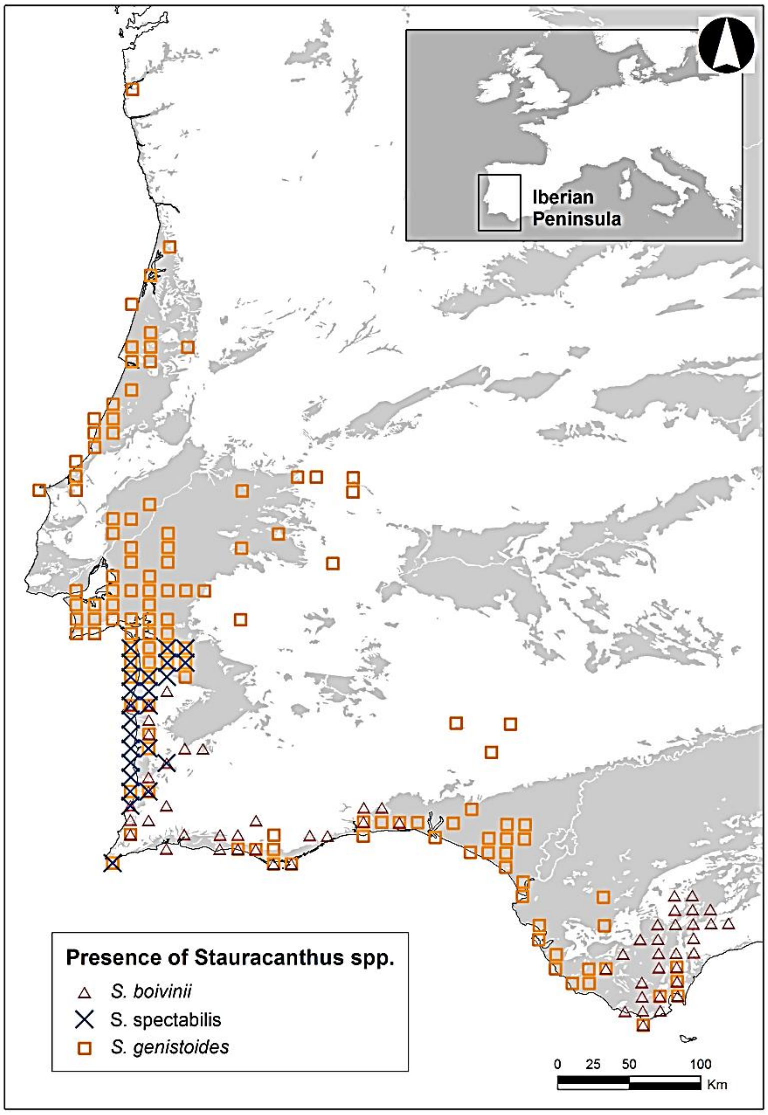


Figure 4.1 Distribution of *Stauracanthus* species in the Iberian Peninsula. Each symbol represents a 10x10 km UTM cell. Shaded area represents the suitable soils for the genus, namely sandy soils.

Thirty-three topographic and climatic variables were extracted from the WorldClim interpolated map database (Hijmans *et al.* 2005, http://www.worldclim.org/) and from EDIT Geoplatform (http://edit.csic.es/GISdownloads.html), and reprocessed when necessary at 10 km^2 resolution using a standard UTM grid (Table S4.2). Additionally, shortest distance to the coast was calculated using ArcGIS 10 software (ESRI 2011). As *Stauracanthus* species mainly occur on sandy soils, we constructed a lithological map, with classes reclassified from the rock complexes described in the lithological maps of Portugal (APA 1992) and Spain (IGME 1994). The different origin of lithological data and the different resolutions (i.e. scales of 1:500,000 and 1:1,000,000 respectively) of these two maps made necessary to homogenize them. We therefore created five consistent lithological classes, particularly suited to study species growing in sandy soils: (i) Holocene and Pleistocene sedimentary rocks, (ii) Miocene and Pliocene sedimentary rocks, (iii) metamorphic and sedimentary rocks (excluding classes i and ii), (iv) plutonic rocks, and (v) volcanic rocks (Table S4.2).

Environmental niche modelling

To model the niche and obtain the potential distribution of the species, we used two different methods: ENFA (Ecological Niche Factor Analysis; Hirzel *et al.* 2002b), and Generalized Linear Models (GLMs; McCullagh and Nelder 1989) with stratified selection of pseudo-absences from non-suitable habitat. Though there are several modelling algorithms which may produce variability in the resulting predictions, it is beyond the scope of this study to analyse that. We chose ENFA and GLM as both provide statistical knowledge of the most relevant variables and do not produce overfitted models. Besides, the stratified selection of pseudo-absences contributes to obtaining a potential range of environmentally suitable habitats for the species (see Chefaoui and Lobo 2008). Both presence and Box-Cox transformed environmental data at 10 km^2 resolution were used to perform ENFA. ENFA analyses the position of the niche in the ecological space, computes suitability functions, and allows a quantification of the contribution of each variable to the marginality and the specialisation factors extracted. The marginality axis allows obtaining the direction of maximum difference between the species niche and the available conditions in the study area, while the specialisation factors measure the ratio of ecological variance of the species in relation to the mean habitat (Hirzel *et al.* 2002a). From our initial set of 39 variables, we first removed those that were highly correlated (Pearson correlation coefficients $\geq |0.80|$, $p < 0.001$) while exploring also their contribution to factors extracted by ENFA for each species. Those with high correlations and/or without contribution to ENFA´s factors were excluded (Table S4.2). After this first selection, ENFA models were performed using two subsets of variables: (i) the complete set of variables remaining after selection, and (ii) the coincident sets of relevant variables between the former ENFAs and GLMs for each species.

ENFA models were validated performing a 5-fold cross-validation and obtaining the absolute validation index (AVI), the contrast validation index (CVI), and continuous Boyce Index (BI) using a moving window width of 20 (see Hirzel *et al.* 2006). AVI measures the proportion of presences above HS = 0.5 and varies from 0 to 1. CVI is the difference between AVI and a random model; it oscillates from 0 to 0.5. The continuous BI is a modification from the original Boyce Index (Boyce *et al.* 2002), it varies from -1 to 1, and has shown a performance similar to AUC (Hirzel *et al.* 2006). ENFA computations were performed in Biomapper 4.0 (Hirzel *et al.* 2002b).

Presence and pseudo-absence data for each species were used to accomplish GLMs with binomial distribution and the logit link function. We selected 10 times more pseudoabsences than presences randomly from the non-suitable area (i.e. with habitat-suitability = 0) predefined by ENFA (Chefaoui and Lobo 2008) to be used in GLMs. After including all linear, quadratic and cubic terms of each variable, we performed a stepwise model selection by Akaike Information Criterion (AIC) in both directions using “MASS” package (Venables and Ripley 2002). To test whether the model terms were significant, we performed a Chi-squared ANOVA. We transformed the continuous predictions into a binary output adjusting the threshold value to the prevalence of our data (= 0.1), as suggested by Lobo *et al.* (2008) to map predicted distributions. Models were 5-fold cross-validated partitioning both presence and pseudo-absence data sets, and not using a higher number of folds due to the small data size. We calculated the area under the receiver operating characteristic (ROC) curve (AUC; Fielding and Bell 1997), sensitivity (presences correctly predicted), specificity (absences correctly predicted), and kappa statistics, using the maximum of the sum of the sensitivity and specificity as threshold value. All analyses were conducted in R (R Core Team 2013).

Niche overlap

We measured niche overlap among *Stauracanthus* species using two subsets of variables to account for differences in the interpretation of the niches: (a) all variables selected for at least one species, and (b) the best subset of variables found in ENFAs and GLMs for all species. We calculated environmental niche overlap using Schoener's index (D metric; Schoener 1970; Broennimann *et al.* 2012) which compares the occupancy of the environment between pairs of species. It allows an intuitive interpretation because it varies between 0 (no overlap) and 1 (identical niches). To calculate D, we chose PCA-env as ordination technique, a Principal Component Analysis (Pearson 1901) calibrated on the entire environmental space, which obtained the most accurate measures among other ordination techniques implemented in R by Broennimann *et al.* (2012). Further, we also explored the spatial niche overlap among the species by overlaying the habitat suitability (HS) maps obtained from ENFA. HS values were previously reclassified according to the same Boyce index used for validation, to discern among optimal, suitable, marginal and unsuitable HS areas (Hirzel *et al.* 2006).

4.4 Results

The number of variables considered after the initial selection procedure was reduced to less than half of the starting set: 9 for *S. boivinii*, 12 for *S. genistoides* and 12 for *S. spectabilis* (Table 4.1). The most important variables estimated by ENFA and GLMs were coincident for the three species. GLMs identified four statistically significant variables ($p < 0.001$) that were able to differentiate all *Stauracanthus* species distributions with respect to their less suitable climates: mean temperature of the coldest quarter, annual range of temperature, isothermality (i.e. mean diurnal temperature range/annual temperature range), and seasonality of precipitation. The same four variables contributed the most to the ENFA marginality factors, being precipitation seasonality and the mean temperature of the coldest quarter the most relevant (Table 4.1). The marginality scores were positive for isothermality, seasonality

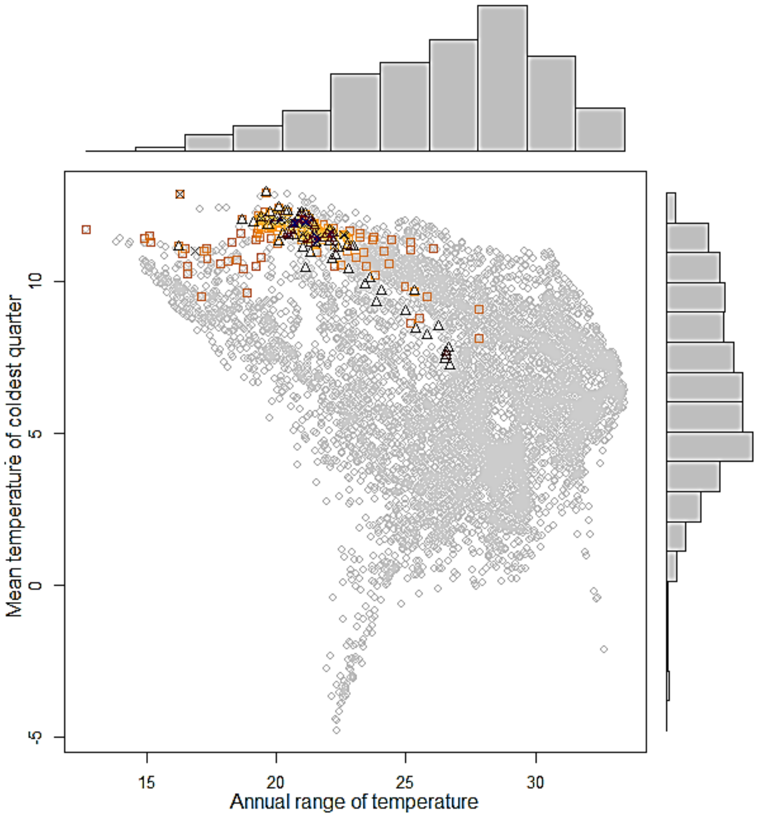
Table 4.1 Results of the ENFA analysis using all the variables, showing the contributions of each variable to the marginality // specificity factors of each species (SBO: *S. boivinii*; SGE: *S. genistoides*; SSP: *S. spectabilis*). Contributions for the marginality factor higher than 0.2 are in bold. The four variables with higher scores for the three species, that were also identified by GLMs and used in subsequent analyses, are highlighted with (*).

ENFA results	**SBO**	**SGE**	**SSP**
Marginality	1.587	1.757	1.936
Specialisation	7.822	3.991	9.257
Marginality factor (% explained)	40	32	69
1st Specialisation factor (% explained)	50	33	15
Environmental variables			
Mean Temperature of Coldest Quarter (*)	**0.47**//175.8	**0.47**//55.34	**0.48**//452.28
Annual Temperature Range (*)	**-0.36**//98.52	**-0.40**//73.59	**-0.36**//330.34
Isothermality (*)	**0.37**//85.34	**0.34**//28.19	**0.41**//302.94
Seasonality of Precipitation (*)	**0.59**//255.03	**0.43**//83.18	**0.44**//443.95
Mean Temperature of Warmest Quarter	-	0.14//72.17	-
Mean Temperature of Wettest Quarter	0.13//77.10	0.16//29.26	0.19//245.62
Hydric balance	-0.14//204.6	-	**-0.22**//189.7
Altitude Range	-	**-0.32**//36.82	**-0.33**//276.66
Average Monthly Radiation	-	0.05//54.27	0.04//186.33
Precipitation of Coldest Quarter	**0.29**//286.6	**0.23**//21.52	-
Holocene and Pleistocene sedimentary rocks	-	0.18//16.33	0.11//89.80
Metamorphic and sedimentary rocks	-	**-0.22**//18.70	**-0.21**//166.47
Miocene and Pliocene sedimentary rocks	0.15//36.72	0.11//12.59	0.11//93.92
Plutonic rocks	-0.11//30.12	-	-0.13//110.55

of precipitation and the mean temperature of the coldest quarter, indicating that the species are present in locations with higher values of each of these variables than the overall mean conditions of the study area. However, *Stauracanthus* is found in habitats with lower annual range of temperature in comparison to the rest of the Iberian Peninsula (Table 4.1 and Figure 4.2). The specialisation scores were in general higher for *S. spectabilis*, indicating a more restricted range of the species on most of the variables within the studied region.

GLM results allow differentiating the importance of these variables: seasonality of precipitation was the most powerful explanatory variable for GLMs, indicating the preference of all species for habitats with a higher difference of precipitations among seasons than in the rest of the Iberian Peninsula (Figure S4.3). Together with this common variable, GLMs found other relevant climatic conditions different for each of the species: *S. boivinii* is conditioned by lower annual range of temperature; most favourable areas for *S. genistoides* are found where mean temperature of coldest quarter is above 7.5 ºC; and *S. spectabilis* prefers isothermal regions (Figure S4.3).

None of the categories of sandy soils were highly significant in the configuration of the models. Among these, the presence of metamorphic and sedimentary rocks was identified by ENFAs as slightly relevant for *S. genistoides* and *S. spectabilis*, but the others were considered less relevant (Table 4.1). However, as these species have been found exclusively on these types of soils, we think lithological variables show a lower predictive power in relation to climatic ones due to their widespread distribution throughout the peninsula. Thus, rather than including them in the models, we used soil conditions afterwards to filter model predictions.



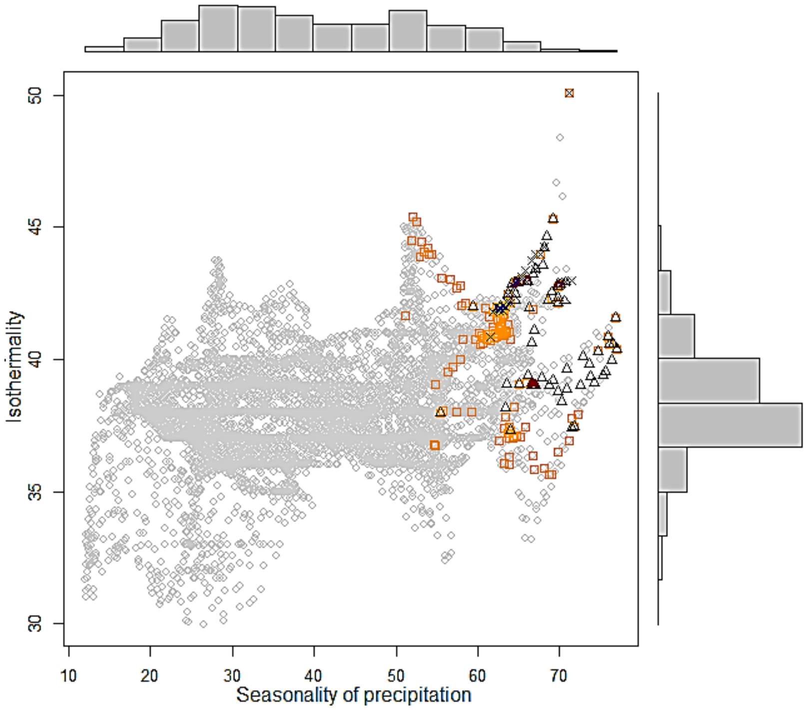


Figure 4.2 Responses to the most significant bioclimatic variables determining the three *Stauracanthus* species according to the Ecological Niche Factor Analysis (ENFA) and Generalized Linear Models (GLM). Circles = cells without presences, triangles = *S. boivinii*, squares = *S. genistoides*, crosses = *S. spectabilis*.

After using (i) all the variables selected, and (ii) only the four most relevant variables mentioned above, to perform ENFA models, the worst evaluation results were obtained for *S. spectabilis* using all the variables (Table S4.4). This result can be explained by the fewer presences available for this species. On the other hand, GLMs were quite parsimonious, showing low AIC values (6-8) and high percentage of total *deviance explained* (D^2 = 100%). Cross-validation results were also optimal Table S4.3), but these overoptimistic results often occur when using pseudo-absences from non-suitable area (Chefaoui and Lobo 2008), as it creates a complete separation between presences and absences regarding good predictors. Thus, to prevent this statistical phenomenon in our predictive models, we decided to discard GLM outputs and not use them to create maps nor for the niche overlap analyses. We preferred the ENFAs performed with the concurring four variables to predict suitable habitats, as we considered the match of results as a sign of robustness in the analyses. After filtering with lithological data, predicted suitable habitat was reduced by 54 % in average (Figure 4.3).

The assessment of environmental niche overlap between pairs of species using the two subsets of variables is shown in Table 4.2. The three *Stauracanthus* species showed remarkably similar responses to the climatic conditions in the Iberian Peninsula. The total value of D was similar between the two subsets of variables (total $D_{\text{all variables}} = 1.538$; total $D_{\text{four variables}} = 1.517$), and the niche overlap obtained an average value of 0.51 among all species. Considering the two subsets, environmental niches of *S. boivinii* and *S. genistoides* were the most coincident, overlapping 67% in average. Despite the slight differences in D measures, PCA-env ordinations were coincident for all pairs in each subset of variables (Figure 4.4).

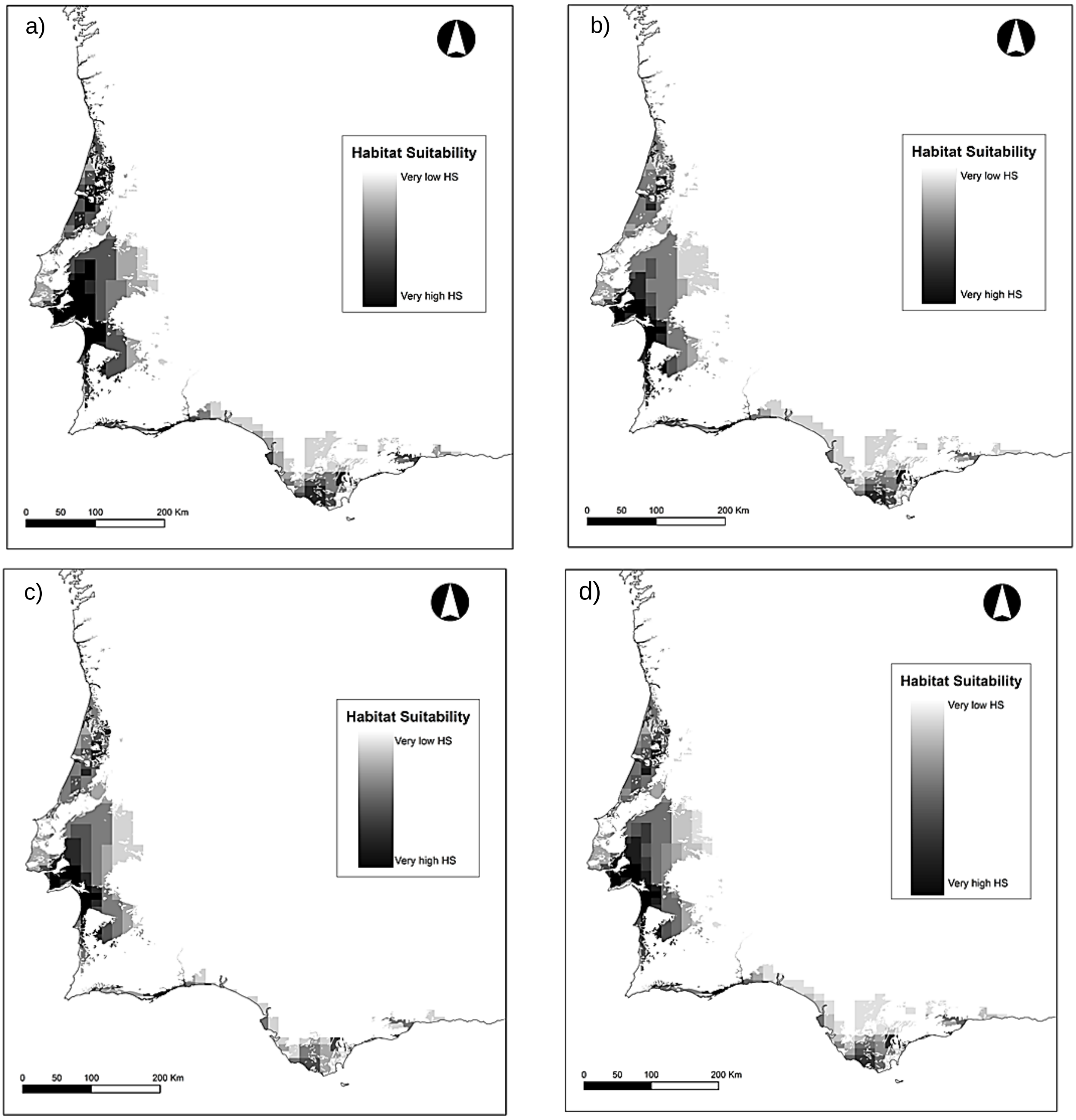


Figure 4.3 Overlap of the habitat suitability (HS) maps obtained with Ecological Niche Factor Analysis (ENFA) using the set of four variables which coincided in relevance both in ENFAs and Generalized Linear Models (GLM) for the three species. Overlap of HS maps between *S. boivinii* and *S. genistoides* (a), *S. boivinii* and *S. spectabilis* (b), *S. genistoides* and *S. spectabilis* (c) and the three species (d), once reclassified using the continuous Boyce index.

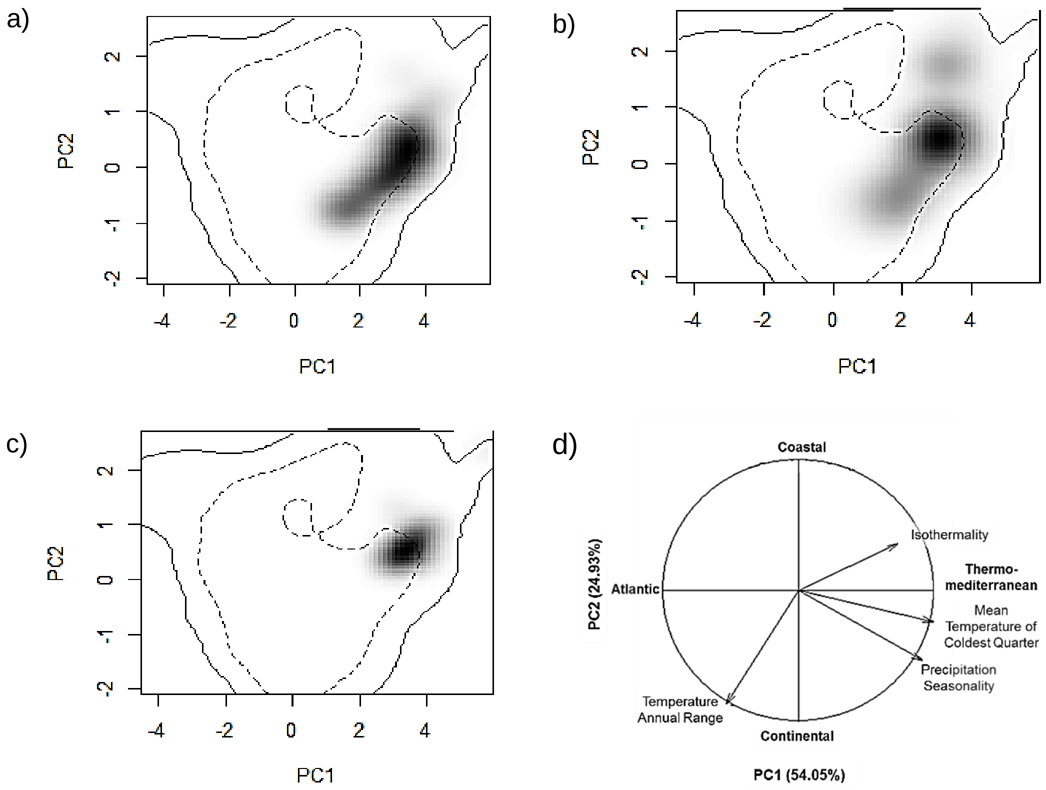


Figure 4.4 Realized niches of the *Stauracanthus* species in the climatic space available in the Iberian Peninsula: (a) represents the niche of *S. boivinii*, (b) the niche of *S. genistoides* and (c) the niche of *S. spectabilis* along the two first axes of the PCA in the Iberian Peninsula. Grey shading gradient shows the density of the occurrences of each species by grid cell. The solid and dashed contour lines illustrate, respectively, 100% and 50% of the available (background) environment. The pie (d) represents the contribution of the climatic variables on the two axes of the PCA. PC1 (X axis) reflects a gradient between Mediterranean and Atlantic conditions in the Iberian Peninsula. Y Axis (PC2) reproduces a gradient of continentality.

Ordination analysis of the four most relevant variables indicated the existence of a climatic maximal variance direction in which temperature and precipitation fit firstly Thermo-Mediterranean versus Atlantic vegetation zones and secondly coastal versus continental conditions.

Using the four-variables subset, we found a correspondence between D and the geographical extent of the areas with HS defined as optimal for each pair of species, e.g. *S. boivinii* and *S. genistoides*, the species that showed greater environmental overlap, also revealed a greater area using this subset (Table 4.2). However, there is no such correspondence using all the variables.

Table 4.2 Description of the overlapping areas between pairs of species of *Stauracanthus* found using all variables selected, and only the four most relevant. D stands for Schoener's D, a measure of niche overlap over the whole environmental space of the study area. HS area is the extension in which both species were found to have an optimum HS value. SBO: *S. boivinii*; SGE: *S. genistoides*; SSP: *S. spectabilis*.

	All variables		**Four variables**	
	D	**HS area** (km^2)	**D**	**HS area** (km^2)
SBO-SGE	0.726	1239	0.612	3894
SBO-SSP	0.395	1947	0.468	1593
SGE-SSP	0.417	1770	0.437	1593

Another interesting observation is that the marginality factors of the three species are highly correlated. There was a significant positive Pearson correlation among the marginality factors of all the species using the four variables subset ($0.995 \leq r \leq 0.998$), and also using all the variables ($0.882 \leq r \leq 0.965$). The first specialisation factors using all the variables were correlated only for *S. spectabilis* and *S. genistoides* ($r = -0.943$).

4.5 Discussion

Our analysis of the realized niche of the *Stauracanthus* species in the Iberian Peninsula has shown that the distributions of these three species are largely constrained by yearly and daily climatic variability and winter temperatures. Despite the differences in their geographic distributions, all three species inhabit similar conditions and their occurrences are discriminated by the same variables, a similarity that evidences the common adaptations of this recently-diversified clade (see Pardo *et al.* 2008). *Stauracanthus* species occur on sandy soils of, mainly, coastal areas and in some mountains with high difference of precipitations among seasons, relatively mild winters, and with moderately low variations between both daily and annual temperatures, conditions that characterize the Thermo-Mediterranean bioclimate with Atlantic influence (according to Barbero and Quezel, 1982). However, each species shows particular requirements that determine its distribution within these bioclimatic conditions. Currently *S. boivinii* occurs on coarse-texture sandy and gravelly soils in both coastal areas and mountains in the South-Western Iberian Peninsula, but always with oceanic influence (Figure 4.1). *S. genistoides* mostly occupies the hot-summer Mediterranean climate coastal areas in South-Western Iberian Peninsula – temperate climate areas with dry and hot summers, “Csa” type according to the Köppen-Geig climate classification (AEMET-IM 2011) – and the coastal area of warm-summer Mediterranean climate in North-Western Iberian Peninsula. *S. spectabilis* distribution area mostly coincides with the area of warm-summer Mediterranean climate – temperate climate areas with dry and warm summers (Köppen-Geiger “Csb” type) (AEMET-IM 2011) – in South-Western Iberian Peninsula.

Several functional characteristics (i.e. functional traits) of *Stauracanthus* species are key adaptations that determine their environmental tolerances and, therefore, their geographic distribution. Their spininess and leaf reduction to phyllodes allow them to endure the summer droughts that are characteristic of Mediterranean climate (Díaz-Barradas *et al.* 1999), and may have prevented herbivory since the ancient establishment of livestock in this region (Vallejo *et al.* 2006). Several spiny legumes, including *Stauracanthus genistoides* (Zunzunegui *et al.* 2010) and probably the other two *Stauracanthus* species, are drought avoiders – a plant functional type of species with high stomatal control that enables them to avoid cellular dehydration for long periods of drought (Levitt 1980) – presenting no photoinhibition in winter. This unique combination allows *Stauracanthus* species to surmount precipitation seasonality by maintaining stable carbon assimilation throughout the year, even in winter when low temperatures reduce photosynthetic efficiency but there is high water availability (Ain-Lhout *et al.* 2004). In addition, *Stauracanthus boivinii* is a withering resprouter (Andrés and Ojeda 2002), growing and flowering vigorously for a number of years after which their above-ground biomass progressively wither in long disturbance periods; after disturbance, they resprout again in a cyclic phenological pattern (Ojeda 2001). A similar behaviour was described for *S. genistoides* by García-Novo (1977). Further, *S. genistoides* and *S. boivinii* (and probably *S. spectabilis*) also present seeder behaviour, i.e. their seeds are stored in the soil and they constitute another source of regeneration of plant populations after fire (Herrera 1987; Ojeda *et al.* 1996). These resprouting and seedling capacities provide this genus with a competitive advantage to inhabit fire-prone and frequently disturbed habitats such as the Mediterranean sandy habitats.

The combination of all these response traits defines a common set of adaptations to the conditions of a region of the environmental space that is consistent with the largely-overlapping realized Grinnellian niches of the three *Stauracanthus* species identified by our analyses. They share key functional traits and, in consequence, similar environmental responses and geographic distributions in relation to the entire Iberian Peninsula. However, these three species show parapatric distributions within a relatively small, although climatically and lithologically diverse, region (South-Western Iberian Peninsula). Our results indicate that such spatial segregation is, at least in part, determined by differences in bioclimatic requirements that go beyond the common adaptations determined by their common traits, as evidenced by their different levels of niche overlap. *S. boivinii* and *S. genistoides* show the higher niche overlap and hold the larger distribution ranges but *S. boivinii's* edaphic requirements are differentiated, as it occurs on more coarse-texture sandy soils or on gravelly soils (Guinea and Webb 1968). However, *S. spectabilis* shows much larger divergences in the response to climate compared with these two species. In fact, it shows a low niche amplitude in the four climatic variables analysed (Figure 4.2), thus it is likely that this species has undergone a process of specialisation, becoming well adapted to a very particular climatic domain (i.e. areas with smaller daily variations in temperature). In addition, *S. spectabilis* and *S. genistoides*, which share edaphic requirements (Neto, 2002), form a distinct clade, clearly separated from *S. boivinii* since, at least, the Early Miocene (see Cubas *et al.* 2005; Pardo *et al.* 2008).

Edaphic conditions seem to play a major role in determining the parapatry between *S. boivinii* and the *spectabilis-genistoides* clade (note, however, that the spatial resolution of our lithological maps did not allow distinguishing between different sand and gravel textures). It is therefore likely that they were involved in the diversification of the two main *Stauracanthus* clades. Being the differences in the responses of *S. genistoides* and *S. spectabilis* to climate clearly behind their parapatry in the Iberian Peninsula, it could be argued that the process of speciation within this clade involved some new physioclimatic adaptations for one of the taxa. Following the most parsimonious explanation, *S. genistoides* would have retained the main ancestral adaptations to climate of the genus that are largely shared by *S. boivinii*. We should however point to the differences in their realized bioclimatic niches: *S. boivinii* is restricted to the areas with annual range of temperature below 27 ºC and the most favourable areas for *S. genistoides* are those with mean winter temperature above 7.5 ºC (Figure S4.3).

The diversification of Stauracanthus is largely consistent with a stochastic process of geographic range expansion and fragmentation coupled with niche evolution in the context of spatially complex environmental fluctuations (see Rangel *et al.* 2007; Colwell and Rangel, 2009). The current distribution (Figure 4.5) of Stauracanthus is thought to be largely conditioned by the Messinian Salinity Crisis (MSC) in late Miocene, and the opening of the Strait of Gibraltar in the Early Pliocene (Pardo *et al.* 2008).

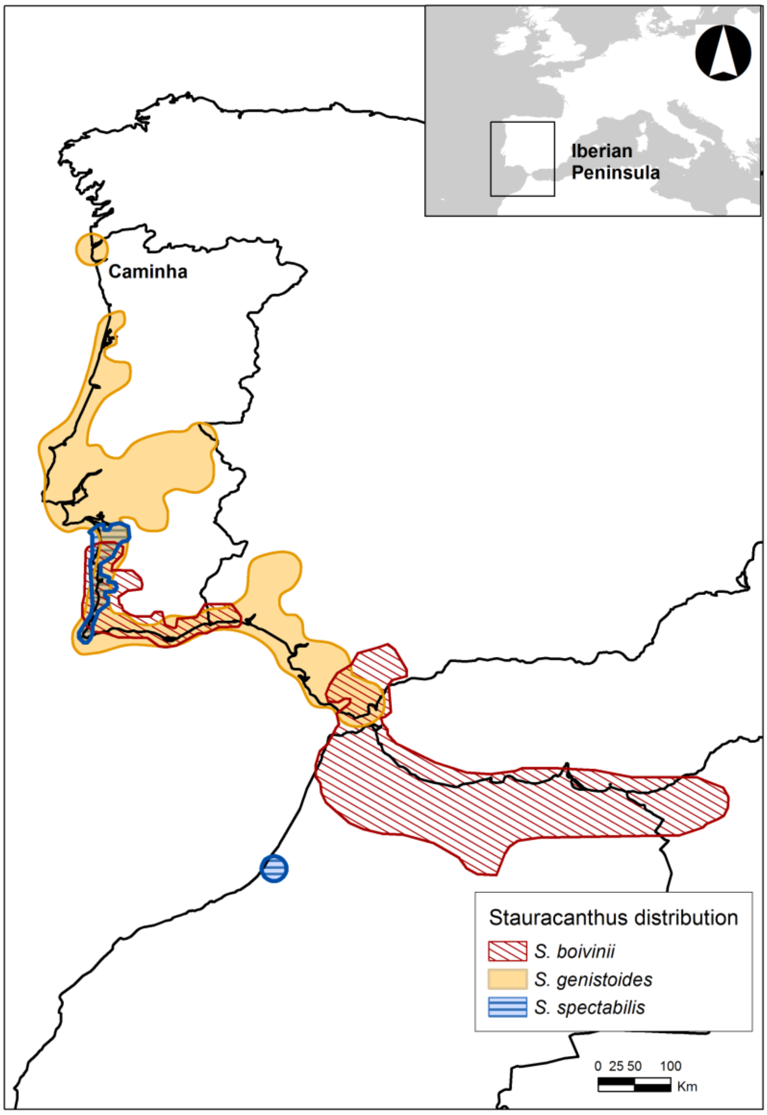


Figure 4.5 Current known distribution of *Stauracanthus* species.

The genus may have appeared before the end of the Paleogene (Pardo *et al.* 2008), so *Stauracanthus* could have been distributed along the Betic-Rif mountain belt formed during the African-Iberian collision (Early Miocene) as it has been hypothesized for *Ulex* genus (Cubas *et al.* 2005). Firstly, the formation of the Alboran Sea by the Middle Miocene, and then the dryer climate conditions of MSC reduced and fragmented the geographic ranges of *Stauracanthus* species (probably at that moment *S. boivinii* and *S. spectabilis-genistoides)*, though the former event reduced the gene flow while the latter also allowed the recolonization of new suitable areas. According to

Pardo *et al.* (2008), some *S. spectabilis* populations (or related ones) located in or near its current distribution area, diversified into the more resilient *S. genistoides*, undergoing niche evolution processes, and enlarging its distribution area to more Northern and Southern locations, although they do not preclude the existence of an ancestral, i.e. previous to the MSC event, *S. genistoides* taxon already separated from *S. spectabilis*. Our analyses of *Stauracanthus'* realized responses to climate point to the second hypothesis as the more likely and parsimonious process of niche evolution. Although we agree in that *S. genistoides* expansion after the Miocene may be related with its wider response to climate, including larger variations in daily temperatures, it is unlikely that these adaptations correspond to an enlargement of its niche compared to that of *S. spectabilis.* Rather, its large similarity with that of *S. boivinii* would point to both species retaining in large part the ancestral adaptations of the ancestral *Stauracanthus* lineage. According to this scenario, the populations that originated current *S. spectabilis,* genetically more basal according to Pardo *et al.* (2008), would have undergone a process of adaptation to the climatic conditions occurring in the fragmented landscape of the West Mediterranean during MSC. These particular conditions have been less prevalent during the Pleistocene, so the distribution of *S. spectabilis* has been progressively reduced to a few pockets of fixed dunes of the Iberian Peninsula and NW Morocco. In contrast, the populations of *S. genistoides* show a wider response to climate, that could be explained because is genetically more heterogeneous (see Figure 3 in Pardo *et al.* 2008), so *S. genistoides* could be a complex of monophyletic but distantly related populations that show diverging responses to climate, and therefore an apparently wide bioclimatic niche, close to that of *S. boivinii*. However, the large overlap (D value) found between *S. genistoides* and *S. boivinii* provide support for the ancestral character of its current response to climate. In any case, the expansion of the *genistoides* lineage in the Iberian Peninsula since MSC (Pardo *et al.* 2008) would have been facilitated by the increase of sandy coastal areas created during the lowering of sea level associated with Pleistocene glaciations

(Zazo and Goy 1989). These sea-level changes could explain the existence of isolated populations such as those located in Caminha, in the border between Portugal and Spain (Figure 4.5).

To summarise, the evolution and current distribution of *Stauracanthus* species has been strongly conditioned by their soil and climatic requirements and, probably, it has been conditioned by the complex history of the Western Mediterranean region during the Miocene and the Pleistocene. Consequently, the current distributions of the three species that can now be recognized are shaped by climatic and edaphic requirements, as well as by historical events and biogeographical constraints. Further analyses, including northern populations of *S. genistoides,* on the evolutionary relationships between the Iberian populations of *S. spectabilis* and *S. genistoides* are required to ascertain whether the genetic heterogeneity of this latter species corresponds to a rapid expansion from a restricted number of populations, or to a series of relatively less connected populations that are occupying different parts of the bioclimatic niche space.

Acknowledgements

We thank to Juan Carlos Moreno who pointed us to study the distribution of *Stauracanthus* species. This work was partly funded by the Portuguese FCT project COMDUNES (EXPL/BIA-BIC/2311/2013). S.C was supported by the FCT PhD grant SFRH/BD/65659/2009 and afterwards by a FCT BI grant funded by the project COMDUNES, R.C. was supported by the FCT postdoctoral fellowship SFRH/BPD/85040/2012, and J.H. by a Spanish DGCyT Ramón y Cajal grant.

References

AEMET-IM (2011) Iberian climate atlas. AEMET-IM, Madrid

Ain-Lhout F, Barradas MCD, Zunzunegui M, *et al.* (2004) Seasonal differences in photochemical efficiency and chlorophyll and carotenoid contents in six Mediterranean shrub species under field conditions. Photosynthetica 42:399–407. doi: 10.1023/B:PHOT.0000046159.96228.49

Andrés C, Ojeda F (2002) Effects of afforestation with pines on woody plant diversity of Mediterranean heathlands in southern Spain. Biodivers Conserv 11:1511–1520. doi: 10.1023/A:1016850708890

APA (1992) Atlas do ambiente. Agência Portuguesa do Ambiente. Lisbon.

Barbero M, Quezel P (1982) Classifying Mediterranean Ecosystems in the Mediterranean Rim Countries and in Southwestern U.S.A. USDA Forest Service general technical report PSW United States, Pacific Southwest Forest and Range Experiment Station.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. (2002). Evaluating resource selection functions. *Ecological modelling*, *157*(2), 281-300.

Broennimann O, Fitzpatrick MC, Pearman PB, *et al.* (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr 21:481–497. doi: 10.1111/j.1466-8238.2011.00698.x

Bull CM (1991) Ecology of Parapatric Distributions. Annu Rev Ecol Syst 22:9–36.

Chefaoui RM, Hortal J, Lobo JM (2005) Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian *Copris* species. Biol Conserv 122:327–338. doi: 10.1016/j.biocon.2004.08.005

Chefaoui RM, Lobo JM (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. Ecol Modell 210:478–486. doi: 10.1016/j.ecolmodel.2007.08.010

Colwell RK, Rangel TF (2009) Hutchinson' s duality : The once and future niche. PNAS 106:19651–19658.

Cubas P, Pardo C, Tahiri H (2005) Genetic variation and relationships among *Ulex* (Fabaceae) species in Southern Spain and Northern Morocco assessed by chloroplast microsatellite (cpSSR) markers. Am J Bot 92:2031–2043.

Díaz-Barradas MC, Zunzunegui M, Tirado R, *et al.* (1999) Plant functional types and ecosystem function in Mediterranean shrubland. J Veg Sci 10:709–716.

Díaz TE, Rivas Martínez S, Fernández González F (1990) Stauracan*t*hus Link (Leguminosae) en la Península Ibérica. Itinera Geobot 3:131–135.

Diniz-Filho JAF, Nabout JC, Bini LM, *et al.* (2009) Niche modelling and landscape genetics of *Caryocar brasiliense* (“Pequi” tree: Caryocaraceae) in Brazilian Cerrado: an integrative approach for evaluating central–peripheral population patterns. Tree Genet Genomes 5:617–627. doi: 10.1007/s11295-009-0214-0

ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49.

García-Novo F (1977) The effects of fire on the vegetation of Donana National Park, Spain. Symp. Environ. Consequences Fire Fuel Manag. Mediterr. Ecosyst. USDA For. Serv. Gen. Tech. Rep. WO-3 US Department of Agriculture California, pp 318–325

Guinea E, Webb DA (1968) *Stauracanthus* Link. In: Tutin TG, Heywood VH, Burges NA, *et al.* (eds) Flora Eur. vol. 2. Cambridge University Press, Cambridge, pp 103–104.

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Modell 135:147–186. doi: 10.1016/S0304-3800(00)00354-9

Herrera J (1987) Flower and fruit biology in southern Spanish Mediterranean shrublands. Ann MISSOURI Bot Gard 74:69–78. doi: 10.2307/2399263

Hijmans RJ, Cameron SE, Parra JL, *et al.* (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978.

Hirzel A, Hausser J, Chessel D, Perrin N (2002a) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83:2027–2036.

Hirzel AH, Hausser J, Perrin N (2002b) Biomapper 4.0 Lausanne, Lab. for Conservation Biology. http://www.unil.ch/biomapper.

Hirzel AH, Le Lay G, Helfer V, *et al.* (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Modell 199:142–152.

Holmgren PK, Holmgren NH, Barnett LC (1990) Index Herbariorum, edition 8, Part I. The Herbaria of the World. Regnum Veg 120:1–693.

Hortal J, De Marco Jr P, Santos AMC, Diniz-Filho JAF (2012) Integrating biogeographical processes and local community assembly. J Biogeogr 39:627–628. doi: 10.1111/j.1365-2699.2012.02684.x

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symp. Quant Biol 22:415–427.

Hutchinson GE (1978) An introduction to population ecology. Yale University Press, New Haven.

IGME (1994) Mapa geológico de España. Instituto Geológico y Minero de España. Madrid.

Knowles LL (2003) The burgeoning field of statistical phylogeography. J Evol Biol 17:1–10. doi: 10.1046/j.1420-9101.2003.00644.x

Lepage T, Bryant D, Philippe H, Lartillot N (2007) A general comparison of relaxed molecular clock models. Mol Biol Evol 24:2669–80. doi: 10.1093/molbev/msm193

Levitt J (1980) Responses of plants to environmental stresses. Academic Press, New York.

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17:145–151. doi: 10.1111/j.1466-8238.2007.00358.x

McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

Neto C (2002) A flora e a vegetaçao do superdistrito Sadense (Portugal). Guineana 8:1–269.

Ojeda F (2001) El fuego como factor clave en la evolución de plantas mediterráneas. In: Zamora R, Pugnaire FI (eds) Ecosistemas Mediterráneos. Análisis Funcional. CSIC-AEET, Madrid, pp 319– 349.

Ojeda F, Marañon T, Arroyo J (1996) Postfire regeneration of a Mediterranean heathland in southern Spain. Int J Wildl Fire 6:191. doi: 10.1071/WF9960191

Paiva J, Coutinho AXP (1999) *Stauracanthus* Link. In: Talavera S, Aedo C, Castroviejo S, *et al.* (eds) Flora Ibérica 7(II). Real Jardín Botánico, CSIC, Madrid, pp 240–245.

Pardo C, Cubas P, Tahiri H (2008) Genetic variation and phylogeography of *Stauracanthus* (Fabaceae, Genisteae) from the Iberian Peninsula and northern Morocco assessed by chloroplast microsatellite (cpSSR) markers. Am J Bot 95:98–109.

Pearson K (1901) On lines and planes of closest fit to systems of points in space. Philos Mag 2:559–572.

Pérez-Harguindeguy N, Díaz S, Garnier E, *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234. doi: 10.1071/BT12225

Peterson AT, Soberón J (2012) Species Distribution Modeling and Ecological Niche Modeling: Getting the concepts right. Nat Conserv – Brazilian J Nat Conserv 10:102–107.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org/

Rangel TFLVB, Diniz-Filho JAF, Colwell RK (2007) Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. Am Nat 170:602–16. doi: 10.1086/521315

Rothmaler W (1941) Revision der Genisteen. I. Monographien der gattungen um Ulex. 72 : 69 – 116. Bot Jahrbücher für Syst 72:69–116.

Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10:1115–23. doi: 10.1111/j.1461-0248.2007.01107.x

Vallejo R, Aronson J, Pausas JG, Cortina J (2006) Restoration of Mediterranean woodlands. In: van Andel J, Aronson J (eds) Restor. Ecol. new Front. Blackwell, Oxford.

Venables WN, Ripley BD (2002) Modern Applied Statistics with S. Springer, New York

Wake DB, Hadly EA, Ackerly DD (2009) Biogeography, changing climates, and niche evolution. PNAS 106:19631–19636.

Yesson C, Culham A (2006) Phyloclimatic modeling: combining phylogenetics and bioclimatic modeling. Syst Biol 55:785–802. doi: 10.1080/1063515060081570

Zapata F, Jiménez. I (2012) Species delimitation: inferring gaps in morphology across geography. Syst Biol 61:179–194.

Zazo C, Goy JL (1989) Sea-level changes in the Iberian Peninsula during the last 200,000 years. Late Quat. Sea-level Correl. Appl. Springer Netherlands, pp 27–39

Zunzunegui M, Díaz-Barradas MC, Ain-Lhout F, *et al.* (2010) Seasonal physiological plasticity and recovery capacity after summer stress in Mediterranean scrub communities. Plant Ecol 212:127–142. doi: 10.1007/s11258-010-9809-7

Supporting Information

Appendix S4.1: Note on the taxonomy of *Stauracanthus* Link.

Stauracanthus taxonomy is not totally consensual but all authors coincide in the existence of three main taxa. Rothmaler (1941) described *S. genistoides* and *S. boivinii*, dividing the former into three sub-species: *S. genistoides* ssp. *genistoides*, *S. genistoides* ssp. *spectabilis* and *S. genistoides* ssp. *vicentinus*. Díaz *et al.* (1990) described three species, namely *S. boivinii* (Webb) Samp, *S. genistoides* (Brot) Samp. and *S. spectabilis* Webb, the latter divided into two sub-species: *S. spectabilis* ssp. *spectabilis* Webb and *S. spectabilis* ssp. *vicentinus* (Devaux ex Coutinho) T.E. Díaz, S. Rivas-Martínez and F. Fernández-González. Finally, Paiva and Coutinho (1999) maintained only three species: *S. boivinii* (Webb) Samp, *S. genistoides* (Brot) Samp. and *S. spectabilis* Webb. The existence of the taxa *S. boivinii* and S. *genistoides* are consensual for all authors, being the discrepancies at the taxonomic level of *S. spectabilis* sensu lato (as species or as a *S. genistoides* subspecies) and the recognition of S. *genistoides*/*spectabilis* ssp. *vicentinus* as a different taxon. Morphological characters used for separating the three taxa are size and shape of the bracteoles, standard petal indumentum, and calyx size (Table S4.1).

In an effort to validate the classification for later analyses, we analysed the 112 specimens of *S. genistoides* and *S. spectabilis sensu lato* deposited in LISI and LISU herbaria. This collection is classified following the taxonomy proposed by Díaz *et al.* (1990) (i.e. accepting the existence of *S. spectabilis* ssp. *spectabilis* and ssp. *vicentinus*). Because the morphological characters used for separating these taxa are floral, we selected only the 75 specimens with flowers: 42 identified as *S. genistoides*, 21 as *S. spectabilis* ssp. *spectabilis* and 12 as *S. spectabilis* ssp. *vicentinus*

(Figure S4.2). We calculated the average length and width of 5 bracteoles per specimen. Non-metric multidimentional analyses (NMS) (McCune and Grace 2002) was used to characterise the relationship between the bracteole sizes with the four climate variables selected by ENFA and GLM (see main text) able to differentiate all *Stauracanthus* species distributions with respect to the less suitable habitat: seasonality of precipitation, isothermality, annual range of temperature, and mean temperature of the coldest quarter (Figure S4.1). Climate variables were extracted from WorldClim interpolated map database (Hijmans *et al.* 2005) at 1 km^2 resolution.

Relationship between bracteole width and climate variables clearly separates *S. genistoides* and *S. spectabilis sensu lato* (see confidence ellipses in Figure S4.2). Nevertheless they failed to discriminate between *S. spectabilis* subspecies. Since in taxonomy species are typically recognized by gaps in the patterns of variation in morphological characters of individuals (Zapata and Jiménez. 2012), the existence of a continuous gradient in bracteoles width values in studied specimens indicates the existence of a single taxon presenting continuous bracteole morphological variation. Similar results were obtained by using the bracteole length/width ratio (figures not included) that take into account both size and shape. These results are consistent with other reports that show that size, mainly width, and shape of bracteoles are the main taxonomical characters for separating *S. genistoides* and *S. spectabilis* (Guinea and Webb 1968; Díaz *et al.* 1990; Paiva and Coutinho 1999). In the same way, comparison among requirements with respect to the climate variables distinguishes between *S. genistoides* and *S. spectabilis sensu lato* but it fails to separate *S. spectabilis* subspecies (Figure S4.2).

Overall, our findings support Paiva and Coutinho (1999) taxonomy, which also reject the recognition of the taxa *S. spectabilis* ssp. *vicentinus* based on the existence of individuals with intermediate floral character states between the type forms of both *S. spectabilis* ssp *spectabilis* and ssp. *vicentinus*.

Table S4.1 Size of the principal morphological characters used for separating *S. genistoides*, *S. spectabilis* ssp. *spectabilis* and ssp. *vicentinus* showing divergences in literature, namely bracteole and calyx sizes. W: width, L. length. Values in mm.

	S. genistoides		***S. spectabilis***			***S. spectabilis ssp. vicentinus***		
	Bracteole	**Calyx**	**Bracteole**		**Calyx**	**Bracteole**		**Calyx**
	W	**L**	**W**	**L**	**L**	**W**	**L**	**L**
Díaz *et al.* 1990	<1	-	3-5	4-5(6)	14-16	(1) 2 (3)	(1) 2 (3)	12-14
Paiva and Coutinho 1999	0.4-0.7	9-11	(1) 2.5-4 (5)	-	12-14 (15)	-	-	-

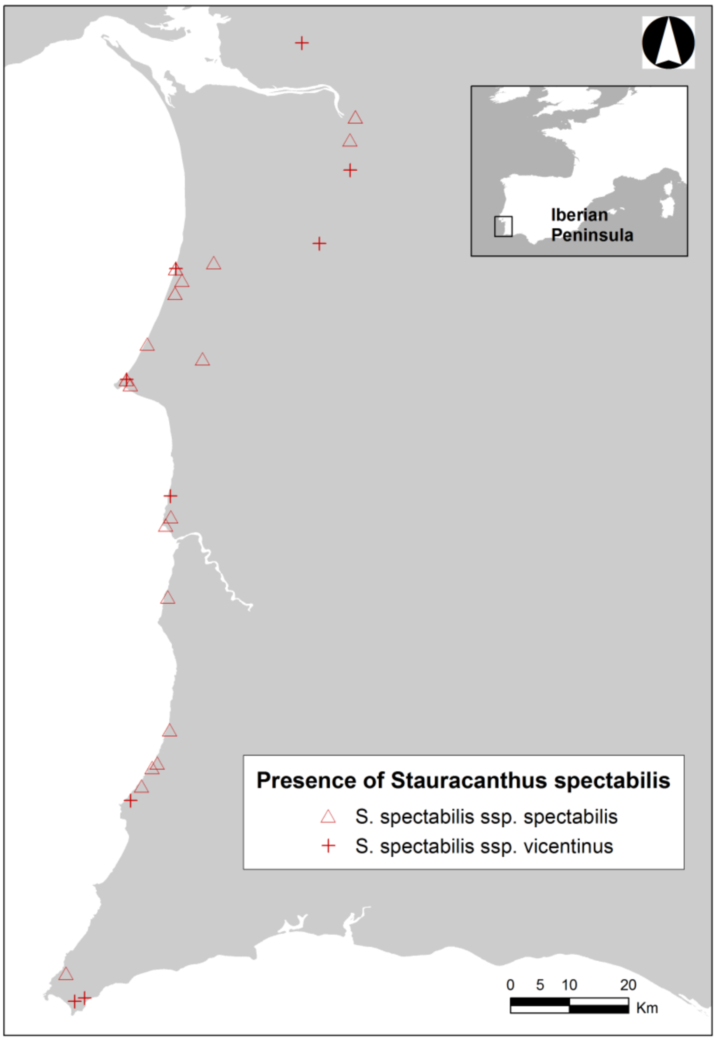


Figure S4.1 Map showing the location of S. spectabilis ssp. spectabilis and S. spectabilis ssp. vicentinus. Note that each symbol corresponds to a single 1x1 km UTM grid square, corresponding to, at least, one presence record of S. spectabilis subspecies.

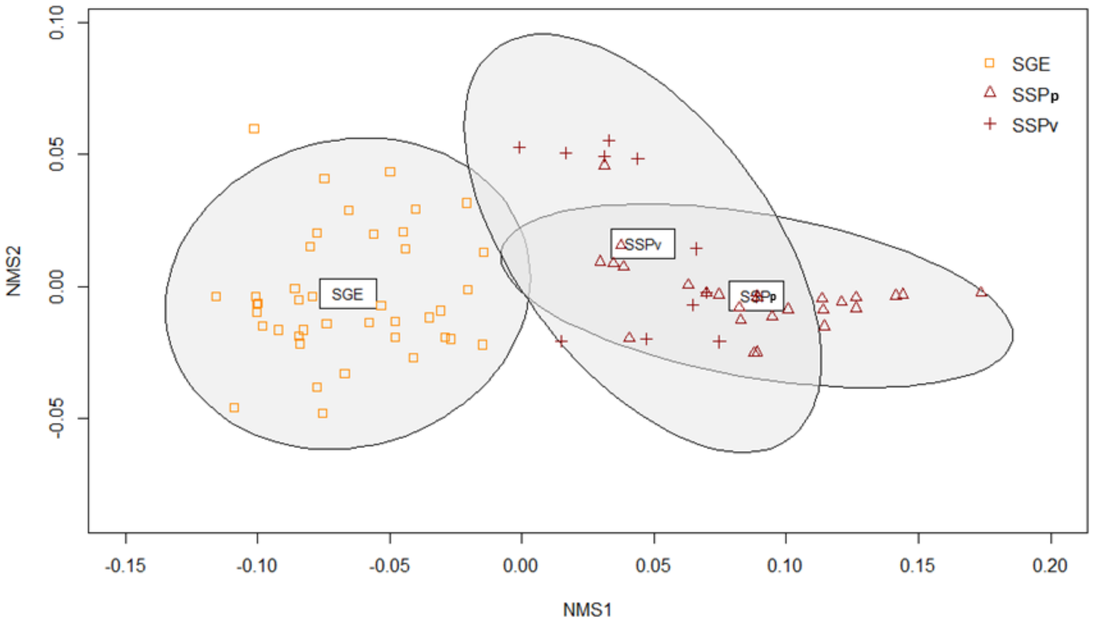


Figure S4.2 Axes 1 and 2 of the 2-dimensional nonmetric multidimensional scaling ordinations of specimens based on bracteole sizes and the four climate variables most relevant to characterise *Stauracanthus* species distribution: seasonality of precipitation, isothermality, annual range of temperature, and mean temperature of the coldest quarter. Final stress value for the 2-dimensional configuration was 0.04. For each taxon confidence ellipses ($P < 0.05$) are shown (SGE = S. genistoides, SSPp = S. spectabilis ssp. spectabilis, SSPv = S. spectabilis ssp. vicentinus).

References

Díaz TE, Rivas-Martínez S, Fernández-González F (1990) *Stauracanthus* Link (Leguminosae) en la Península Ibérica. Itinera Geobot 3:131–135.

Guinea E, Webb DA (1968) *Stauracanthus* Link. In: Tutin TG, Heywood VH, Burges NA, *et al.* (eds) Flora Eur. vol. 2. Cambridge University Press, Cambridge, pp 103–104.

Hijmans RJ, Cameron SE, Parra JL, *et al.* (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978.

McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

Paiva J, Coutinho AXP (1999) *Stauracanthus* Link. In: Talavera S, Aedo C, Castroviejo S, *et al.* (eds) Flora Ibérica 7(II). Real Jardín Botánico, CSIC, Madrid, pp 240–245

Rothmaler W (1941) Revision der Genisteen. I. Monographien der gattungen um *Ulex*. Botanische Jahrbücher für Systematik 72:69–116.

Zapata F, Jiménez I (2012) Species delimitation: inferring gaps in morphology across geography. Systematic Biology 61:179–194.

Table S4.2 Climatic, topographic and lithological variables initially available.

Climatic and topographic variables	
Mean Altitude	Temperature Seasonality
Max Altitude	Annual Precipitation
Min Altitude	Average Monthly Precipitation
Altitude Range (*)	Precipitation of Coldest Quarter (*)
Annual Mean Temperature	Precipitation of Driest Month
Average Monthly Maximum Temperature	Precipitation of Driest Quarter
Average Monthly Mean Temperature	Precipitation of Warmest Quarter
Average Monthly Minimum Temperature	Precipitation of Wettest Month
Isothermality (*)	Precipitation of Wettest Quarter
Max Temperature of Warmest Month	Precipitation Seasonality (*)
Mean Diurnal Range	Average Monthly Radiation (*)
Mean Temperature of Coldest Quarter (*)	Aridity Index
Mean Temperature of Driest Quarter	Real evapotranspiration
Mean Temperature of Warmest Quarter (*)	Actual evapotranspiration
Mean Temperature of Wettest Quarter (*)	Hydric balance (*)
Min Temperature of Coldest Month	Distance to Pyrenees
Temperature Annual Range (*)	Distance to coast
Lithological variables	
Holocene and Pleistocene sedimentary rocks (*)	Miocene and Pliocene sedimentary rocks (*)
Metamorphic and sedimentary rocks (excluding prior classes) (*)	Plutonic rocks (*)
Volcanic rocks	

Those used in the analyses after selection are marked with (*).

Table S4.3 Results of Generalized Linear Models (GLM). Five-fold cross-validation for GLMs results summarized as mean ± SD scores**.**

	Models	AUC	Sensitivity	Specificity	Kappa
Stauracanthus genistoides	Mean Temperature Coldest Quarter + Precipitation seasonality	1±0	1±0	1±0	1±0
Stauracanthus spectabilis	Isothermality + Precipitation seasonality	1±0	1±0	0.992±0.010	0.959±0.050
Stauracanthus boivinii	(Temperature Annual Range)2 + (Precipitation seasonality)3	1±0	1±0	0.998±0.003	0.991±0.018

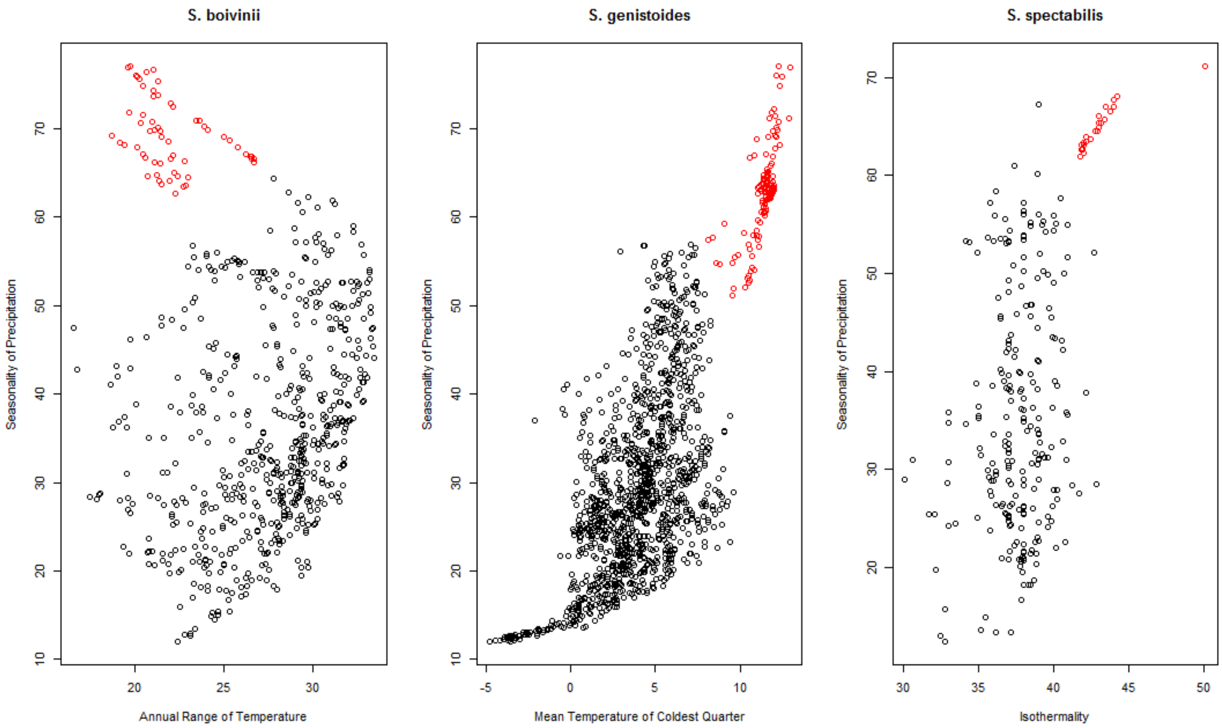


Figure S4.3 Environmental response of *Stauracanthus* species in relation to GLM significant variables. Contrasting conditions of presence locations (in red), with respect to the less suitable locations (pseudo-absences; black), show the power of these variables as predictors.

Table S4.4 Validation of ENFA analyses obtained after a 5-fold cross-validation using presence only measures: Boyce index (BI), the absolute validation index (AVI), and the contrast validation index (CVI). SBO: *S. boivinii*; SGE: *S. genistoides*; SSP: *S. spectabilis*.

	BI	AVI	CVI
SGE all variables	0.567 ± 0.342	0.478 ± 0.254	0.451 ± 0.250
SBO all variables	0.157 ± 0.576	0.504 ± 0.303	0.449 ± 0.278
SSP all variables	-0.074 ± 0.109	0.425 ± 0.190	0.396 ± 0.183
SGE 4 variables	0.286 ± 0.810	0.457 ± 0.405	0.415 ± 0.391
SBO 4 variables	0.338 ± 0.658	0.477 ± 0.310	0.436 ± 0.293
SSP 4 variables	0.338 ± 0.781	0.575 ± 0.429	0.551 ± 0.423