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Chapter 2

Local and regional-scale factors drive xerophytic shrub community dynamics on Mediterranean stabilized dune

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2 Local and regional-scale factors drive xerophytic shrub community dynamics on Mediterranean stabilized dune

2.1 Abstract

The aim of this study was to analyse the main drivers of compositional and distributional changes of xerophytic shrub communities at different spatial scales. We also assess whether the ecological dynamics of these communities comply with the Clementsian and/or Gleasonian paradigms of community assembly. We study the influence of environmental variables and human impacts at different scales on three xerophytic scrub communities growing on inland sand dunes. In 70 plots we sampled shrub cover, herb presence, soil characteristics and human disturbance. PCA and NMS were used to describe environmental and species variations. The effects of main drivers were assessed through Mantel tests, taking spatial structure into account. GAMs were used to model the scrub dynamics across environmental gradients. We found that local and regional environmental factors drive the patchy distribution of the xerophytic scrub communities. The gradient found from *Stauracanthus genistoides* to *Ulex australis*-dominated communities depends on nutrient availability, probably through species interactions, namely facilitation and competition. In turn, the gradient from *S. genistoides* to *Juniperus navicularis*-dominated communities follows an aridity gradient associated with human disturbance, namely agriculture. We propose that the three studied scrub communities are the extremes of two successions. The *S. genistoides* to *U. australis*-dominated communities' succession is driven by local edaphic factors, following Clementsian principles while the *S. genistoides* to *Juniperus navicularis*-dominated communities' succession responds to local – disturbance – and regional – aridity – processes, following both Clementsian and Gleasonian principles.

This implies that only dynamic management approaches directed to ensure a natural functioning of this landscape can be successful for their long-time preservation.

2.2 Introduction

The dilemma of defining ecological communities as either dynamic or static entities has accompanied ecology since the beginning of the last century. Clements (1916) understood communities as closed structures, where local interactions between species play a major role in determining community composition. Contrasting with this organismal view, Gleason (1917) described communities as assemblages of species where local habitat selection and regional scale processes act by filtering the existing species pool. These two views represent the extremes of a gradient of increasing importance of species interactions in the structuring of the ecological systems, ranging from assemblages of merely co-occurring species to highly structured communities. Nowadays it is thought that by conciliating both concepts it is possible to get the whole picture of community composition, mainly integrating the effect of regional and local processes (Hortal *et al.* 2012). According to this view, community composition would be the result of macroecological constraints acting on a species pool with analogous environmental requirements and filtered by dispersal and ecological assembly rules (Guisan and Rahbek 2011).

Severe habitats such as deserts or sand dunes provide appropriate systems for studying the duality between assemblages and communities and factors determining communities' composition and distribution. On the one hand, they are characterized by the existence of physico-chemical stressors (Tobler 2008) that play an essential role by filtering the species pool, so that the harder the environmental conditions, the fewer the number of species available to make part of severe habitats' communities (Moser *et al.*

2005). On the other hand, several species interactions – in particular facilitation and competition – have been described as significant drivers of the dynamics of severe habitats (Armas and Pugnaire 2009; Muñoz-Vallés *et al.* 2011).

Stabilized sand dunes occur at the inland limit of coastal sand dunes. While the latter present a directional zonation of plant communities from the sea to inland due to the combination of biotic (e.g. plant cover and diversity, nitrogen availability, soil organic content) and abiotic (e.g. salt spray, high temperature, burial, sand transport) processes (Gilbert 2007, Rajaniemi and Allison, 2009; Carboni *et al.* 2011), the former are scarcely affected by coastal factors. Consequently, plant community zonation disappears, being frequently replaced by patchily distributed communities (Zunzunegui *et al.* 2005). Under a Mediterranean climate, several studies emphasize the role of water availability in explaining such patchiness. Díaz-Barradas *et al.* (1999) point to the depth of soil water table as the main factor determining the local establishment of either xerophytic or hygrophytic scrub communities in the stabilized dunes of Doñana National Park (Spain). At larger scales, Muñoz-Reinoso and García Novo (2005) propose that the distribution and composition of xerophytic and hygrophytic communities in the same area also responds to differences in water availability due to groundwater flow systems acting at different scales. Here, intermediate and regional discharges of the aquifer beneath Doñana National Park determine shrub composition on dunes depending on their topographic altitude. Although enlightening, these studies were mainly focused on discriminating between xerophytic and hygrophytic scrub distribution and they determined the crucial role of water in separating both types of communities. Other areas of the Iberian Peninsula also host scrub communities on stabilised sand dunes, although subject to a much more intensive regime of human disturbance (Neto *et al.* 2004) and where xerophytic shrub communities dominate due to water scarcity. These communities are home for a significant number of rare, endangered and endemic plant species and they are listed in Annex I of the EU

Habitats Directive due to their high interest for biodiversity (for details see EC 2007 and Costa *et al.* 2007). We propose that studies in these areas may allow a broader understanding of community dynamics on stabilized dunes, by signifying additional drivers other than water, such as edaphic, human disturbance and climate factors. These factors are also likely to determine the composition and distribution of these scrub communities.

Here, we study the xerophytic shrub communities inhabiting inland sand dunes across an environmental gradient in SW Portugal with the aim of determining which are the main drivers affecting their composition and distribution and evaluating at which scale they act (i.e. local, landscape or regional). Then, we examine if these processes follow Clementsian or Gleasonian principles, or both, considering the following alternative hypotheses: i) when Clementsian processes are preponderant, community diversity primarily responds to local conditions and species interactions, and variations in community composition is structured in a successional fashion, ii) if species assembly is determined by Gleasonian processes, landscape and regional-scale factors, such as climate and habitat selection, originate compositional variations; and finally, iii) a more complex picture with drivers acting at different scales will be expected if both types of processes are present.

2.3 Methods

Study system

The study area was located at Peninsula of Setúbal and Alentejo coast, South-West Portugal, on sandy soils between the left margin of Tagus River (38°53'N, 8°49'W) and Sines Cape (37°57'N, 8°52'W) in an area of about 1700 km² (Figure 2.1).

Altitude varies from 0 to 180 m.a.s.l. The climate is Mediterranean, with ocean influences. During the period of 1950-2000, intra and inter-annual variations in mean monthly precipitation and mean monthly temperatures were considerable (SNIRH 2009). The dominant soil type is podzol, with some regosols and cambisols (with moderate and very weak soil development, respectively; APA 1992).

Figure 2.1 Study sites and potential area of occurrence of inland sandy xerophytic shrub communities in Alentejo coast and Peninsula of Setúbal, SW Portugal.

Vegetation is mainly dominated by semi-natural Maritime Pine (*Pinus pinaster* Aiton) forests of variable density, ranging from open to dense formations with a xerophytic shrub community understory (Neto *et al.* 2004). After the irruption of the pine wilt disease in 1999 caused by the pinewood nematode *Bursaphelenchus xylophilus*, to which Maritime Pine is very sensitive, Stone Pine (*Pinus pinea* L.) plantations and open

xerophytic shrub-dominated areas are progressively becoming more conspicuous in this area. The xerophytic shrub communities are characterized by the dominance or presence of *Juniperus navicularis* – a shrubby juniper endemic to the Iberian Peninsula – and *Stauracanthus genistoides* and/or *Ulex australis* subsp. *welwitschianus* – two thorny shrubs of the legume family (Fabaceae) endemic to Iberian Peninsula and Portugal respectively. For simplicity herein we use *J. navicularis*, *S. genistoides* or *U. australis* communities to refer to these three types of formations.

Community surveys

Plant communities were sampled at 70 sites after randomly selection with Hawth's Analysis Tools for ArcGIS (Beyer 2004), within the potential area of occurrence of sandy xerophytic shrub communities (Figure 2.1). This potential area was defined in ArcGIS version 10 using two layers depicting: i) sandy soils (extracted from the lithological map of Portugal; APA 1992); and ii) areas with forest and semi-natural land use cover (Caetano *et al.* 2009). On each study site, one 10x10 m plot was placed at random. The composition and cover of shrub species in the plot were estimated by using the line intercept method along four 10 m straight lines set at 2-m intervals, measuring height and crown diameter for each intercepted individual. Four 2x2 m quadrats were located within the 10x10 m plot, one in each corner. Composition and cover of all herbaceous species were visually estimated in each quadrat using a 50x50 cm quadrat grid with 10 cm squares. Plot slope and elevation were measured locally. Five sample soils, one in each 2x2 m quadrats and one in the centre of the 10x10 m plot, were collected from the top 20 cm and bulked to give one composite soil sample for each site.

Plant nomenclature follows the *Checklist da Flora de Portugal* (ALFA 2010), and species were determined using *Flora Iberica* (Castroviejo 1986-2012) and *Nova Flora de Portugal* (Franco 1971-1984; Franco and Afonso 1994-2003). Individual plants

in several study sites presented intermediate characters between *Stauracanthus genistoides* and *S. spectabilis*. Taking this into account, as well as the existence of some taxonomic discrepancies (see Pardo *et al.* 2008), both taxa were considered as *S. genistoides sensu lato* for our analyses.

A total of 70 sites were sampled, 53 in spring 2011 and another 17 in spring 2012. Since the study plots were sampled in different years (2011 and 2012), ten plots were surveyed both in 2011 and 2012. We used these plots to evaluate whether community composition varied between both years by using a non-metric multidimensional scaling (NMS) (Gaucherand and Lavorel 2007; McCune and Grace 2002). A Pearson regression test, using the scores of the first two axes of the NMS analysis, showed that community composition were correlated between both years (Pearson r values of 0.77/ 0.99 for shrub cover and 0.94/ 0.68 for the herb presence NMS axes; all correlations were significant at $p < 0.001$). So for all subsequent analyses we have used data from all 70 plots regardless of the year in which they were sampled. To avoid over-representation of the sites that were sampled in both years, we used only data from the 2011 survey to characterize them.

Environmental and disturbance factors

To study local and regional drivers, a broad set of climatic, topographical, soil, land use cover and disturbance variables were considered to account for the effects of the environmental and human disturbances on xerophytic shrub communities (see Table S2.1 for sources). Average altitude, average monthly temperature, maximum and minimum temperature, average monthly precipitation, and 19 other climate and altitude variables (Figure S2.1) were extracted from the WORLDCLIM interpolated map database with a 30 arc-seconds (~1 km) resolution (Hijmans *et al.* 2005). A PCA was performed with climate data and altitude to define the main climatic trends and to avoid collinearity (Dormann *et al.* 2012). Axis 1 (herein PC1) represented 50.36% of the

variance and reflects a gradient of aridity. Axis 2 (PC2) represented 32.26% of the variance and reproduces altitudinal and thermal gradients (Figure S2.1). Finally, Axis 3 represented only 10.83% of the variance, then, for simplicity, only the first two axes were included in the subsequent analyses.

The shortest distance from the coastline to each study site was used as a proxy for oceanic influence. Water table depth was estimated using Kriging interpolation (Desbarats *et al.* 2002). The annual average of water table altitude of 35 stations within the study area, expressed as meters above sea level, was calculated using the monthly measures from 2010-2012 (SNIRH 2009). Then, Geostatistical Analyst Extension from ArcGIS was used to map the estimated water table altitude of the study area. Water table depth in the 70 study sites was calculated as the difference between altitude and water table altitude (Figure S2.2).

Soil samples were collected only in 2011, so all analyses involving edaphic variables were restricted to the data collected that year (n=53). Also, three soil samples were excluded because of their unusual percentage of soil organic matter values (herein SOM) over 3%. Soil samples were analysed in the UIARN (Unidade de Investigação de Ambiente e Recursos Naturais) laboratory of the Faculdade de Ciências da Universidade de Lisboa for extractable phosphorus (P), potassium (K) and magnesium (Mg), SOM, total nitrogen (N), pH, and particle size (% of sand, silt, and clay). These analyses indicated that the soils of the study sites generally present low or very low fertility (all value references according to LQARS 2006). K and P values were very low (<24 mg/kg and <23mg/kg respectively), Mg values varied from very low to low (16 to 52 mg/kg), with SOM values from very low to low (0.24-2.15%), with acid and low acid pH values (5-6.5), and N values from very low to low (0.011-0.058%). Soil texture was classified as sandy (92.4-99.6% sand, silt 0.3-4.3% and 0-3.4% clay).

To assess disturbance at the local scale, tree cover, 13 land use class areas and 8 potential sources of impact variables were quantified in a radius of 250 meters around each study site plot, based on field work combined with photointerpretation (Table S2.2). These variables include accessibility (i.e. proximity to roads or inhabited places), forest management and time since the last (forestry) management action (Table S2.3), grazing, presence of rabbits or anthropogenic litter, and abundance of both invasive alien plants and species with floristic conservation value. Tree cover, land use and all disturbance variables with geographic expression were measured using ArcGIS. Two study sites had no graphical information and therefore were discarded for all analyses using these data.

For assessing and comparing the influence on community composition of land use cover at local and landscape scales, following Hortal *et al.* 2010, the areas of seven land use classes derived from Corine 2006 – Agricultural areas (AGR), Artificial areas (ART), Coniferous forests (CON), Cork oak *Montado*, open savannah-like landscape with cork oak (*Quercus suber*) (MON), Scrubs (SCR), Sea (SEA) and Water courses and bodies (WAT) – were calculated on concentric buffers with radii 25, 50, 100, 250, 500, 1000, 2500 and 5000 m around the study sites.

Data Analysis

Previous to all analyses, shrub cover values were squared-rooted to reduce the influence of large values, and herb cover values were transformed to presence/absence data because of their high dependence on inter-annual weather patterns in Mediterranean ecosystems (Espigares and Peco 1993; Fernández-Moya *et al.* 2011). To avoid an excessive influence of rare species, shrubs and herbs with less than four occurrences (5%) were excluded from the ordination analyses, which resulted in maintaining 18 (out of 40) shrubs and 46 (out of 121) herbs (Table S2.4).

Vegetation gradients

The main gradients of vegetation composition were described with a NMS ordination of shrub cover data and the presence/absence of herbaceous species, with the function metaMDS of R Package “vegan”. Square root transformed data were submitted to Wisconsin double standardization (species are first standardized by maxima and then sites by site totals). The Bray and Curtis method was used to measure the distance/similarity between plots. Goodness of fit of the ordination was assessed through the percentage of variance represented (see McCune and Grace 2002 for details). NMS axes resulting from these analyses are herein denominated “community NMS axes” for short.

Selection of explanatory variables

To select the main drivers affecting xerophytic shrub communities, firstly Spearman correlations between all the environmental and disturbance variables and community NMS axes were performed to examine the relationships between those variables and the shrub and herbaceous composition. This resulted in a first set of potential explanatory variables (Table 2.1); then, in order to select the most meaningful land use cover variables, Spearman correlations between community NMS axes and land use cover at all buffer sizes (from 25 to 5000m radius) were performed. When significant correlations were found, for each land use and for both local (<250m) and landscape (>250m) scales, the buffer distances with the largest Spearman r value were selected for inclusion in the set of potential explanatory variables. Multicollinearity among potential explanatory variables was handled by dropping collinear covariates (Graham 2003; Zuur *et al.* 2010) when correlated at $|\text{Spearman } r| > 0.7$ (Dormann *et al.* 2012). This selection resulted in a second set of potential explanatory variables each community NMS axes (Table 2.2).

To separate truly causal processes acting on xerophytic shrub communities from those that merely reflect spatial covariation (Legendre and Troussellier 1988; Legendre and Legendre 1998), Simple Mantel Tests (SMT) and Multiple Regression on distance Matrices (MRM) were performed by using the “ecodist” software package (Goslee and Urban 2007). Firstly, SMT between geographic distances and community NMS axes indicated if shrub and herbaceous communities were spatially structured (Borcard *et al.* 2004). Then we used MRM, a multiple regression of a response distance matrix on any number of explanatory distance matrices, to characterise the relationship between each community NMS axis-based distance matrix and the distance matrices based on all the explanatory variables including space (Table 2.2), as well as the contribution of each explanatory variable to the composition of the shrub and herbaceous communities (Legendre and Legendre 1998; Lichstein 2007). The MRM formula is $Y = X_1 + X_2 + \dots + X_n$, where Y is the dependent distance matrix and $X_1, \dots, X_n$ are the n independent distance matrices. A backward selection method was used for selecting the best subset of predictors, where all predictor matrices were initially included, and the non-significant ones were subsequently deleted (Legendre *et al.* 1994). Because soil analyses were available only for 50 sites and we lacked management value for one of them, MRM was performed only for 49 study sites. Bonferroni correction was used to adjust the p-values to multivariate analyses. Standard Mantel tests only indicate the existence of a relationship but not its direction. Hence, information of the sign of the correlation was obtained from Spearman r values (Table 2.1 and Figure 2.2).

Community gradients characterisation

We also performed Generalized Additive Models (GAMs) to characterise the relationships of the most important species composition gradients identified from NMS analyses with the cover of the dominant shrub species using the “mgcv” software package (Wood 2006). Although this author indicates that the proportion of null

deviance explained is “probably more appropriate for non-normal errors”, the models’ adjusted r-squared values are also indicated for clarity. All analyses except kriging and diversity index calculation were performed on R statistical software V.2.15.2 (R Development Core Team 2011) using the R Studio V 0.97.312 interface.

2.4 Results

The main gradients in plot species composition were described for the first two axes of a three axis non-metric multidimensional scaling ordination of both shrub cover and the presence/absence of herbaceous species, with final stress values of 0.15 and 0.18 respectively (Figure 2.2). The first two axes accounted for most variance in both cases (43% out of 50% for shrubs and 69% out of 82% for herbs), so we only present the results for these axes. The first axis of the shrub cover NMS ordination (NMS1; Figure 2.2a) identified a gradient between sites dominated by *S. genistoides* (negative values) and sites dominated by *U. australis*. The second NMS axis (herein NMS2) discriminated between sites with or without *J. navicularis*. In the case of herbs, the NMS ordination identified the same gradient between sites dominated by *S. genistoides* and those dominated by *U. australis* (Figure 2.2b), although here this gradient was expressed along a combination of both NMS axes (herein hNMS1 and hNMS2).

The relationship between community NMS axes and the environmental and disturbance variables and land use cover buffers performed with Spearman correlations identified 41 significant correlates including 16 environmental predictors, 10 local land use descriptors, 6 disturbance variables and 9 land use cover buffers (Table 2.1, Figure S2.3). After analysing multicollinearity among candidate explanatory variables (Table S2.5) and dropping covariates for each axis, a set of predictor

variables accounting for variations in each community NMS axis were selected (Table 2.2). The relationship between community NMS axes for shrubs and herbaceous species and space (i.e. geographical position) performed with the Simple Mantel test correlations (r) indicated that NMS2, hNMS1 and hNMS2 presented some spatial structure ($r=0.15^{***}$, 0.12^{***} and $r=0.15^{***}$, respectively), while NMS1 did not correlate with space, so space was included as a potential explanatory variable only for the former three axes.

The results of multiple regression on distance matrices (MRM) with all explanatory variables confirmed the correlation of NMS1 with soil organic matter (SOM) content (Table 2.3). MRM also allows relating the spatial structure in NMS2 with an aridity gradient and the local presence of agricultural areas. MRM results also confirmed the correlation between hNMS1 and NMS1, as well as with aridity (PC1) and soil sand content. This highlights the importance of edaphic gradients and climate in the determination of the structure of both herbaceous and shrub communities. Finally, MRM also detected a minimum effect of the presence of *Pinus pinaster* forests on community hNMS2 axis (Table 2.3). No landscape effect of land use cover emerged for the 4 community axes. MRM results did not show any association between the gradient between *S. genistoides* and *U. australis*-dominated communities (defined by NMS1 axis) and land use, either at local or landscape scale. Nevertheless NMS2 is significantly and positively correlated with the local presence of agricultural areas.

Table 2.1 Spearman R correlations between shrub and herbaceous NMS axes and the studied predictors. Only predictors with at least one significant correlation are shown.

	Shrub		Herbs	
	NMS1	NMS2	hNMS1	hNMS2
Geographical variables				
x	-0.24*	-0.51***	-0.43***	ns
y	ns	0.27*	0.42***	-0.43***
Elevation	ns	ns	ns	0.25*
Distance to the sea	ns	ns	ns	ns
Water table level	ns	ns	ns	0.26*
Soil variables				
Clay	ns	0.51***	0.63***	ns
Sand	-0.28*	-0.42**	-0.68***	ns
Silt	0.29*	ns	0.40**	ns
Mg	0.59***	ns	0.48***	0.36*
N	0.65***	ns	0.35*	ns
SOM - Soil organic matter	0.55***	0.28*	0.44**	ns
pH	ns	0.37**	0.34*	ns
Plant cover				
Herb cover	ns	0.40***	0.25*	-0.35**
Shrub cover	0.35**	ns	0.37**	ns
Tree cover	0.25*	0.26*	0.34**	ns
Herbaceous NMS				
hNMS1	0.36**	ns	-	-
hNMS2	0.32**	ns	-	-
Shrub NMS				
NMS1	-	-	0.36**	0.32**
NMS2	-	-	ns	ns
Climate variables (PCA axes)				
PC1 - Aridity gradient	ns	0.47***	0.52***	ns
PC2 – Thermal and altitudinal gradient	ns	ns	ns	0.24*
Disturbance variables				
Accessibility	ns	0.26*	0.44***	ns
Invasive-spp	ns	0.36**	ns	ns
Litter	ns	0.35**	ns	ns
Time-Mng	-0.27*	ns	-0.31*	ns
Rabbits	-0.24*	ns	ns	-0.27*
Relape-spp	ns	-0.36**	ns	ns
Land use class				
Agriculture	ns	0.29*	ns	ns
Eucalyptus	ns	0.25*	ns	ns
Firebreaks	0.29*	-0.39***	ns	0.24*
Grasslands	ns	0.33**	ns	ns
Mixed forest	ns	0.38**	0.31**	-0.25*
Montado	ns	ns	ns	-0.29*
<i>P. pinaster</i>	0.40***	ns	ns	0.35**
Roads	ns	0.25*	0.34**	ns
Ruderal	ns	0.24*	ns	-0.27*
Urban	ns	0.34**	0.32**	ns

n=70 in all cases except Time-Mng (n=68) and soil variables (n=50); ns = non significant, *p<0.05, **p<0.01, ***p<0.001.

Figure 2.2 Axes 1 and 2 of the 3-dimensional non-metric multidimensional scaling ordinations of study sites based on a) shrub cover (NMS1 and NMS2) and b) herbaceous presence and absence (hNMS1 and hNMS2). Final stress values for the 3-dimensional configuration were 0.15 and 0.18 for shrubs and herbs, respectively. Diamonds and dots represent study sites with and without *Juniperus navicularis*, respectively. Full black symbols are study sites without *S. genistoides* (SGE), empty symbols without *U. australis* (UAU), and full grey symbols represent study sites with both species. Arrows reflect the main gradients identified by the ordinations and confirmed by multiple regression on distance matrices (MRM). Species codes according to Table S2.4.

Figure 2.3 Relationship between the first axes of the ordination based on scrub cover (NMS1) and percentage of soil organic matter (SOM). Solid and dashed lines represent the main trend and 95 % confidence intervals of a Generalized Additive Model (GAM); $n=50$, $k=1.326$, percentage variance explained= 39.3% and $\text{adj.r}^2 = 0.38$ ($p < 0.001$). Black circles are study sites without *S. genistoides* (SGE), open circles without *U. australis* (UAU), and grey circles those with both species

The Generalized Additive Models (GAM) between the community NMS axes with the cover of dominant shrubs showed a remarkable relationship between the gradients of nutrient availability – inferred from the gradient of soil organic matter (SOM) – and aridity with the community composition gradients identified by NMS1 and NMS2 respectively. The fit between NMS1 and SOM reflects the gradient from *S. genistoides* to *U. australis* communities (Figure 2.3). The relationship between the covers of these two species identified by GAM evidences a clear replacement throughout the soil organic matter gradient defined by NMS1. Here, *S. genistoides* is substituted by *U. australis* in habitats with progressively higher nutrient availability (Figure 2.4a). The change in cover between *J. navicularis* and *S. genistoides* along NMS2 reflects also a spatial gradient fostered by the aridity and agricultural disturbance gradient (Figure 2.4b).

Table 2.2 Set of potential predictors accounting for variations in each NMS shrub and herbaceous (hNMS) community axis. In bold, selected response variables after dropping collinear covariates (see Table S2.5). Space (i.e. geographical position) was added after performing Simple Mantel tests between NMS axes and space (see text). Agricultural (AGR), Artificial (ART) and Coniferous forests (CON) areas and respective radii (25-5000m). See text for details.

Shrubs		Herbs	
NMS1	NMS2	hNMS1	hNMS2
ART2500	Accessibility	Accessibility	AGR2500
CON50	Agriculture	AGR5000	CON25
Firebreaks	AGR100	ART5000	CON500
Mg	AGR5000	Clay	Elevation
Time-Mng	ART5000	Herb cover	Firebreaks
N	Clay	Mg	Mg
<i>P pinaster</i>	Con5000	Mixed forest	Mixed forest
Rabbits	Eucalyptus	Time-Mng	Montado
Relape-spp	Firebreaks	N	NMS1
Sand	Grasslands	NMS1	PC2
Shrub cover	Invasive-spp	PC1	<i>P pinaster</i>
Silt	Litter	pH	Rabbits
SOM	Mixed forest	Roads	Ruderal
Tree cover	PC1	Sand	Space
	pH	Shrub cover	Water table level
	Relape-spp	Silt	
	Roads	SOM	
	Ruderal	Space	
	Sand	Tree cover	
	SOM	Urban	
	Space		
	Tree cover		
	Urban		

Table 2.3 Regression coefficients and regression R^2 of the Multiple Regression on distance Matrices between each NMS axis and the predictors obtained by backward selection method. p-values were adjusted using Bonferroni correction.

Variables	NMS1	Variables	NMS2	Variables	hNMS1	Variables	hNMS2
SOM	0.32***	Agriculture	0.26***	NMS1	0.23***	<i>P pinaster</i>	0.16**
		PC1	0.26**	PC1	0.22***		
				Sand	0.29***		
R^2	0.10***	R^2	0.13***	R^2	0.21***	R^2	0.02**

n=49; ns = non significant, *p<0.05, **p<0.01, ***p<0.001.

2.5 Discussion

Our results show that both local and regional factors drive the distribution of xerophytic shrub and herbaceous communities on the inland dunes of SW Portugal. We have identified some clear relationships between these communities and edaphic and climatic gradients and human disturbance in this region. Species composition and abundance vary mainly according to changes in soil organic matter (shrubs and herbs), aridity (shrubs and herbs), sand content (herbs), shrub cover (herbs) and presence of agricultural areas (shrubs). These drivers shape up a spatial mosaic of communities mainly determined by differences in nutrient availability and aridity. While *Ulex australis*-dominated communities occur in areas with higher nutrient availability, those dominated by *Stauracanthus genistoides* do so in sites with very low to low nutrient availability. Furthermore, variations in aridity discriminate between sites with or without *J. navicularis*. This species is known to dominate the dry tops of stabilized old dunes in this region of Portugal (Neto 2002), where available water is scarce. The other extreme of this gradient is characterised by the presence of *Cistus salviifolius* and *Asparagus aphyllus*, two species characteristic of the psammophilous (i.e. living in or frequenting sandy places) *Montado* (Pérez Latorre 1993) and with higher hydric requirements. Finally, the variations in the shrub stratum also determine to a large extent the distribution of herbaceous communities, together with additional effects of aridity and the proportion of sand in the soil.

Figure 2.4 Relationships identified by Generalized Additive Models of the binomial family between: a) *S. genistoides* (in grey) and *U. australis* (in black) cover and the first axis of the ordination based on scrub cover (NMS1), $n=70$. Effective degrees of freedom $k= 1.99$ and 2 , percentages of variance explained= 51.8% and 65.9% , and $\text{adj.}r^2 = 0.45$ and 0.64 respectively; and b) *J. navicularis* (in black) and *S. genistoides* (in grey) square rooted covers and the second axis of the ordination based on scrub cover (NMS2). $n=70$ Effective degrees of freedom $k= 1.99$ and 1.99 , percentages of variance explained= 16.8% and 35.8% , and $\text{adj.}r^2 = 0.16$ and 0.26 respectively. Cover values are square root transformed. Black circles represent *U. australis* cover, open circles *S. genistoides* cover and black diamonds *J. navicularis* cover. All p values < 0.001 .

Human disturbances did not show any direct local effect on the gradient between the *Ulex australis* and *Stauracanthus genistoides* communities. These results suggest that these communities are quite indifferent to their surrounding land use, also pointing to a high resistance of their species. Nevertheless *Juniperus navicularis* communities' occurrence were negatively affected by the presence of agriculture areas, probably because management practices associated to agriculture are incompatible with the presence of this community and also because less arid areas are more suitable for agriculture.

A conceptual model of inland dune community dynamics

Composition and distribution of xerophytic communities on the studied inland dunes respond, on the one hand, to edaphic site conditions (SOM and sand content) and local human disturbance, pointing to the existence of Clementsian processes acting at local scale on these communities. On the other hand the influence of climate (aridity) on community composition is consistent with the Gleasonian view.

The presence of Clementsian processes driving these communities implies that the adaptation of early colonizers to local conditions and their interaction with more demanding species ultimately determine the composition and structure of the communities, and that those variations in community composition will be structured in a successional fashion. Considering succession as the sequential replacement of species following a disturbance (Prach and Walker, 2011) where facilitation and competition mechanisms play the key role (Pickett *et al.* 1987), the communities dominated by the legume *S. genistoides* would improve soil conditions by introducing organic matter and nitrogen symbiotically fixed into the system. In addition to facilitation processes involving the improvement of soil nutrient content, *S. genistoides* may be increasing the recruitment of the less stress-tolerant species of *U. australis* and

Figure 2.5 Conceptual scheme of the xerophytic shrub community dynamics on stabilized dunes of the South-Western Iberian Peninsula. The relationships identified by our results, where scrub dynamics in Alentejo coast and Peninsula of Setúbal are mainly determined by soil organic matter and aridity, are included in a broader context, defined by the presence of improved humid edaphic conditions or the existence of consolidated soils. Letters indicate the relationships that have been described in the literature: the presence of communities co-dominated by *U. australis* and heaths is caused by a) the presence of a hardpan layer in soil – Neto *et al.* (2004) or b) to the existence of close to surface water table – Díaz-Barradas *et al.* (1999). c) Neto (2002) described the incorporation or exclusion of sand avoider or psammophilous species in stabilized sandy soils or consolidated soil respectively. d) Our results supported the successional processes between *J. navicularis* and *S. genistoides* and *U. australis* communities described by García Novo (1977) and Neto (2002). Finally, e) the psammophilous understory of cork oak (*Quercus suber*) Montado in South Spain described by Pérez Latorre *et al.* (1993) is analogous to scrub communities found in our work. Dashed arrows denote the impact of disturbance, solid arrows identify successional processes. JNA: *J. navicularis*, SGE, *S. genistoides*, UAU: *U. australis*.

J. navicularis communities by the so-called ‘nurse plant syndrome’ in which adult plants of one species facilitate the establishment of seedlings of another species (Armas and Pugnaire 2005). Surprisingly, seedlings of several species but none of *S. genistoides* were found under *S. genistoides* adult individuals (authors' pers. obs.). Preliminary and unpublished data obtained by the authors (see Chapter 3) have shown that weighted mean height of *U. australis* communities is significantly greater than *S. genistoides* communities, favouring a higher performance of the former under an eventual competition for light (Olf *et al.* 1993). These results would imply that the pattern of succession between *S. genistoides* and *U. australis* communities follows the resource-ratio hypothesis of plant succession (Tilman, 1985) that predicts a gradual change from

nutrient competition in nutrient-poor successional stages toward light competition in nutrient-rich stages. However, this hypothesis needs further corroboration from experimental studies.

We propose a conceptual model (Figure 2.5) where *S. genistoides* communities increase soil organic matter enabling colonisation by the more demanding species conforming *U. australis* and *J. navicularis* communities, which in turn will also produce a positive feedback of nutrient incorporation into the soil and they will enhance light competition eliminating colonizer species. In soils with low nutrient availability, *Stauracanthus genistoides* is accompanied by psammophilous dwarf shrubs such as *Armeria rouyana* and *Helichrysum italicum*. This community also dominates regularly disturbed habitats, such as semi-natural pine forest under forestry management, mainly due to the resprouting capacity of *S. genistoides*. In turn, *Ulex australis* would be restricted to soils with higher nutrient content (Figure 2.5). Arguably, *S. genistoides* and *Ulex australis* communities would arise as a result of soil disturbances that impede the maintenance of the climax *Juniperus navicularis* formations (García Novo 1977; Neto 2002; Neto *et al.* 2004). Our data had little power to better characterise this gradient, due to the limitations on the spatially-explicit analyses imposed by the geographically restricted distribution of *J. navicularis*. Thus, although our results point to a neat effect of soil disturbance associated with agricultural areas in the replacement of *J. navicularis* by either *S. genistoides* or *U. australis*, the localised distribution of the former community within the study area and the small number of sites occupied by this late successional stage (Neto *et al.* 2004) did not allow us to separate the effects of micro-environmental gradients from the possibility of a mere spatial bias.

In any case, our model is consistent with others proposed for communities in sandy soils of the Iberian Peninsula, contributing to the explanation of the patchy distribution of these communities. Neto *et al.* (2004) suggested that the presence of a hardpan layer (i.e. a sub superficial layer of sand cemented by iron oxides) in the past

improved humid edaphic conditions in sandy soils of the Sado and Galé areas (located within our study area). This would have facilitated the preservation of a relict and more humidity-demanding community in these areas, characterised by the co-dominance of *U. australis* and heaths (mainly *Erica umbellata* and *E. scoparia*). Historical agricultural practices destroyed most of that cemented sandy layer and therefore most of those communities have already disappeared. Nowadays this type of community is restricted to sandy soils with high available water capacity, either because they possess a water table close to the surface or because they retain an undestroyed hardpan layer. This community dominated by *U. australis* and heaths is analogous to the hygrophytic scrub communities inhabiting the stabilized dunes of Doñana National Park (Díaz-Barradas *et al.* 1999). A similar community, but with no psammophilous co-dominant species (mainly *Cistus crispus*, *C. ladanifer* and *Quercus lusitanica*) occurs in consolidated soils surrounding our study area (Figure 2.5).

Concluding remarks

A direct consequence of the complex dynamics of the vegetation reflected in our conceptual model is that *J. navicularis*, *Stauracanthus genistoides* and *Ulex australis*-dominated communities, which are identified by the EU Directive Habitats as separate entities, could in fact be continuous successional stages of a single plant formation (see Figure 2.5). This would imply that a paradigm shift is necessary in the management of these habitats for conservation. While our results support that all three types of communities are the extremes of two successions – and therefore three “natural” habitats of similar conservation value – the Directive Habitats assigns them to three different categories (EC, 2007). However, for the preservation of the formations characterized by both *U. australis* and *J. navicularis* it is necessary to ensure that the dynamics of *S. genistoides*-dominated communities are preserved in a way that guarantees the succession towards the other two communities. Therefore, only dynamic management approaches directed to ensure a natural functioning of this

landscape can be successful if the aim is the long-time preservation of the stabilized dune habitats in Peninsula of Setúbal and Alentejo coast.

To summarise, the patchy distribution of xerophytic plant communities on inland sandy habitats in SW Portugal responds to edaphic site conditions, climate and human disturbance, confirming the existence of both Clementsian and Gleasonian processes. However, our data does not allow ruling out the existence of other large scale processes other than climate that would filter the regional flora into a smaller pool of colonizers. Further work, encompassing both surveys at larger geographical extents and local experiments to characterise and measure facilitation and competition processes, is needed to determine the relative importance of environmental gradients and community-level interactions for the structure of these Iberian endemic xerophytic shrub communities over their whole distribution.

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Supporting Information

Climate and altitude variables	Code	Climate and altitude variables	Code
Mean Altitude	Alt	Min Temperature of Coldest Month	mTCM
Annual Mean Temp.	AnMnT	Temperature Annual Range	TARg
Average Monthly Maximum Temp.	TM1-12	Temperature Seasonality	TSn
Average Monthly Mean Temp.	Tm1-12	Annual Precipitation	AnP
Average Monthly Minimum Temp.	Tm1-12	Average Monthly Precipitation	P1-12
Isothermality	Isso	Precipitation of Coldest Quarter	PCQ
Max Temp. of Warmest Month	MTWM	Precipitation of Driest Month	PDM
Mean Diurnal Range	MnDRg	Precipitation of Driest Quarter	PDQ
Mean Temp. of Coldest Quarter	MnTCQ	Precipitation of Warmest Quarter	PWQ
Mean Temp. of Driest Quarter	MnTDQ	Precipitation of Wettest Month	PWeM
Mean Temp. of Warmest Quarter	MnTWQ	Precipitation of Wettest Quarter	PWeQ
Mean Temp. of Wettest Quarter	MnTWeQ	Precipitation Seasonality	PSn

Figure S2.1 Results from the PCA of climate variables and altitude. The first axis (PC1) explains 50.36% of the variance and reflects a gradient of aridity, while the second one (PC2) explains 32.26% and reproduces a thermicity gradient. Codes of climate and altitude variables used in the PCA to define principal climate trends are listed below the scatterplot. The codes for monthly average temperatures and precipitation are followed by the number of the given month (i.e, 1 for January, 2 for February, etc.).

Figure S2.2 Water table altitude, measured as meters above sea level. This GIS layer was constructed by kriging interpolation from the sites with piezometric data.

Figure S2.3 Results of the Spearman R correlations between shrub and herbaceous NMS axes, (a) NMS1, (b) NMS2, (c) hNMS1 and (d) hNMS2), and land use cover along at different scales (calculated around each plot for concentric radii ranging from 25 to 5000m). Agricultural areas (AGR), Artificial areas (ART) and Coniferous forests (CON).

Table S2.1 Description and source of environmental and perturbation factors evaluated. Worldclim variables come from Hijmans *et al.* (2005), Portuguese altimetry, lithological and hypsometric maps from APA (1992), Corine Land Cover 2006 from Caetano *et al.* (2009) and hydrometric records from SNIRH (2013).

Variable	Data source
<i>Ecological requirements</i>	
Soil characteristics	Field work samples
Mean Altitude	WorldClim
Climate (23 variables)	WorldClim
Distance to sea	Portuguese hypsometric map
Forest and semi-natural areas	Corine Land Cover 2006
Lithological classes (5)	Portuguese lithological map
Water table depth	Portuguese hypsometric map and hydrometric records
<i>Disturbance</i>	
Sources of impact (8 variables; 250m radius)	Field work and photointerpretation. Time since the last (forestry) management action was estimated by photointerpretation using Google Earth images and digital orthophotos from Portuguese DGT – Direção Geral do Território 1995, 1999 and 2005 flights
Land use variables (13 variables; 250m radius)	Field work and photointerpretation
Land use variables (7 variables; 50–5000m radii)	Corine Land Cover 2006
Tree coverage (250m radius)	Field work and photointerpretation

Table S2.2 Variables and land use classes considered for assessing local habitat perturbation. All variables were estimated within a 250m radius around each study site. Land use classes are measured as the total area at each buffer, in ha.

Name	Description	Classes
Variables		
Accessibility	Accessibility	None: 0; Low: 1 Moderate 2; High: 3; Very High: 4; Intensive 5
Forest-Mng	Forest management	None: 0; Low: 1 Moderate 2; High: 3; Very High: 4; Intensive 5
Grazing	Grazing	None: 0; Low: 1 Moderate 2; High: 3; Very High: 4; Intensive 5
Invasive-spp	Abundance of invasive species	Presence:1; 2:<5%; 3:6-25%; 4: 26-50%; 5: 51-75% ; 6: 76-100
Litter	Anthropogenic Litter	None: 0; Low: 1 Moderate 2; High: 3; Very High: 4; Intensive 5
Time-Mng	Time since (forest) management	0-5 years: 1; 6-10 years: 2; 11-25 years: 3; >16: 4
Rabbits	Presence of rabbits	None: 0; Low: 1; Moderate 2; High: 3; Very High: 4; Intensive 5
Relape-spp	Abundance of RELAPE (Rare, Endemic, Localised, Endangered or Threatened with Extinction) species	Presence:1, 2:<5%; 3:6-25%; 4: 26-50%; 5: 51-75% ; 6: 76-100
Land use classes		
Agricultural	Agricultural areas	
Eucalyptus	<i>Eucalyptus</i> plantations	
Firebreaks	Firebreaks	
Grasslands	Grasslands	
Mixed forest	Mixed forest (coniferous and cork oaks)	
Montado	Cork oak <i>Montado</i> , open savannah-like landscape with cork oak (<i>Quercus suber</i>)	
Ppinea	Stone Pine forests	
Ppinaster	Maritime Pine forests	
Roads	Road and rail networks	
Ruderal	Ruderal vegetation	
Scrubs	Scrubs	
Urban	Urban areas	
Water	Water courses and bodies	

Table S2.3 Years (or period of years) since last forestry management in the study sites calculated by photointerpretation. When it was not possible to assess management practices for a single year, the mean of the period was calculated. There were two study sites with no available information

Time since management (years)	Count of Study Sites	Mean value (years)	Classes
1	2	1	1
2	1	2	1
2 to 4	1	3	1
1 to 6	17	3.5	1
4 to 6	4	4	1
2 to 7	7	4.5	1
4 to 5	4	4.5	1
5	1	5	1
5 to 6	1	5.5	2
6	1	6	2
5 to 7	2	6	2
7	1	7	2
8	2	8	2
7 to 9	6	8	2
7 to 11	1	9	2
7 to 12	2	9.5	2
8 to 11	1	9.5	2
8 to 12	1	10	3
9 to 12	1	10.5	3
6 to 16	3	11	3
12 to 16	2	14	3
12 to 17	1	14.5	3
13 to 17	1	15	3
>16	2	17	4
>18	1	19	4
>20	2	21	4
No data	2	NA	NA

Table S2.4 Surveyed plants. Species with “Code” were used to calculate community NMS axes. RELAPE (Rare, Endemic, Localized, Endangered or Threatened with Extinction species) and invasive species were used to calculate disturbance NMS axes.

Shrub species	Code	Shrub species	Code
<i>Armeria rouyana</i> Daveau	ARO	<i>Juniperus navicularis</i> Gand.	JNA
<i>Asparagus aphyllus</i> L.	AAP	<i>Lavandula pedunculata</i> (Mill.) Cav. subsp. <i>pedunculata</i>	LPE
<i>Calluna vulgaris</i> (L.) Hull	CVU	<i>Lithodora prostrata</i> (Loisel.) Griseb. subsp. <i>lusitanica</i> (Samp.) Valdés	LPR
<i>Cistus salviifolius</i> L.	CSA	<i>Phillyrea angustifolia</i> L.	PAN
<i>Corema album</i> (L.) D.Don	CAL	<i>Rosmarinus officinalis</i> L.	ROF
<i>Daphne gnidium</i> L.	DGN	<i>Santolina impressa</i> Hoffmanns. & Link	SIM
<i>Halimium calycinum</i> (L.) K.Koch	HCA	<i>Stauracanthus genistoides</i> (Brot.) Samp.	SGE
<i>Halimium halimifolium</i> (L.) Willk.	HHa	<i>Thymus capitellatus</i> Hoffmanns. & Link	TCA
<i>Helichrysum italicum</i> (Roth) G. Don subsp. <i>picardi</i> (Boiss. & Reut.) Franco	HPI	<i>Ulex australis</i> Clemente subsp. <i>welwitschianus</i> (Planch.) Esp.Santo, Cubas, Lousã, C.Pardo & J.C.C	UAU
Herbaceous species	Code	Herbaceous species	Code
<i>Arrhenatherum album</i> (Vahl) Clayton	Aal	<i>Margotia gummiifera</i> (Desf.) Lange	Mgu
<i>Andryala arenaria</i> (DC.) Boiss. & Reut.	Aar	<i>Micropyrum tenellum</i> (L.) Link	Mte
<i>Avena barbata</i> Link	Aba	<i>Ononis broteriana</i> DC.	Obr
<i>Anarrhinum bellidifolium</i> (L.) Willd.	Abe	<i>Plantago bellardii</i> All.	Pbe
<i>Aira caryophyllea</i> L.	Aca	<i>Pterocephalidium diandrum</i> (Lag.) G.López	Pdi
<i>Asterolinon linum-stellatum</i> (L.) Duby	Ali	<i>Polycarpon tetraphyllum</i> (L.) L.	Pte
<i>Agrostis tenerrima</i> Trin.	Ate	<i>Rumex acetosella</i> L. subsp. <i>angiocarpus</i> (Murb.) Murb.	Rac
<i>Briza maxima</i> L.	Bma	<i>Sesamoides purpurascens</i> (L.) G.López.	Sep
<i>Corynephorus canescens</i> (L.) P.Beauv	Cca	<i>Silene colorata</i> Poir.	Sco
<i>Crepis capillaris</i> (L.) Wallr.	Ccap	<i>Senecio gallicus</i> Vill.	Sga
<i>Carlina hispanica</i> Lam.	Chi	<i>Stipa gigantea</i> Link	Sgi
<i>Chaetonymchia cymosa</i> (L.) Sweet	Ccy	<i>Scilla monophyllos</i> Link	Smo
<i>Chamaemelum mixtum</i> (L.) All.	Cmi	<i>Silene portensis</i> L. subsp. <i>portensis</i>	Spo
<i>Dipcadi serotinum</i> (L.) Medik. subsp. <i>serotinum</i>	Dse	<i>Spergularia purpurea</i> (Pers.) G.Don	Spu
<i>Erodium cicutarium</i> (L.) L'Hér.	Eci	<i>Silene scabriflora</i> Brot. subsp. <i>scabriflora</i>	Ssc
<i>Euphorbia exigua</i> L.	Eex	<i>Solidago virgaurea</i> L.	Svi
<i>Euphorbia segetalis</i> L.	Ese	<i>Tolpis barbata</i> (L.) Gaertn.	Tba
<i>Hypochaeris glabra</i> L.	Hgl	<i>Teesdalia coronopifolia</i> (J.P.Bergeret) Thell.	Tco
<i>Jasione montana</i> L.	Jmo	<i>Thapsia villosa</i> L.	Tvi
<i>Loeflingia baetica</i> Lag.	Lba	<i>Urginea maritima</i> (L.) Baker	Uma
<i>Logfia gallica</i> (L.) Coss. & Germ.	Lga	<i>Vulpia alopecuros</i> (Schousb.) Dumort.	Val
<i>Logfia minima</i> (Sm.) Dumort.	Lmi	<i>Vulpia myuros</i> (L.) C.C.Gmel.	Vmy
<i>Linaria spartea</i> (L.) Chaz.	Lsp	<i>Xolantha guttata</i> (L.) Raf.	Xgu

RELAPE Species

Armeria pinifolia (Brot.) Hoffmanns. & Link
Armeria rouyana Daveau
Cladina spp.
Drosophyllum lusitanicum (L.) Link

Euphorbia transtagana Boiss.
Santolina impressa Hoffmanns. & Link
Thymus capitellatus Hoffmanns. & Link

Invasive Species

Acacia dealbata Link
Acacia longifolia (Andrews) Willd.
Acacia melanoxylon R.Br.
Ailanthus altissima (Mill.) Swingle
Arctotheca calendula (L.) Levyns
Arundo donax L.

Carpobrotus edulis (L.) N.E.Br.
Cortaderia selloana (Schult. & Schult.f.)
 Asch. & Graebn.
Hakea sericea Schrad.
Nicotiana glauca Graham
Opuntia ficus-indica (L.) Miller
Robinia pseudoacacia L.

Table S2.5 Spearman r correlations between shrub and herb NMS axes correlates. Variables were defined as covariates when correlated at |Spearman r| > 0.7.

Sand		SOM	
Silt	-0.75***	Mg	0.76***
Clay	-0.84***	N	0.94***
CON25		PC2	
CON500	-0.78***	Elevation	0.83***
		Water table level	0.73***

***p<0.001