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# Community dynamics of stabilized dune xerophytic shrubs

**Doutoramento em Biologia**

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Nota Prévia

A presente tese apresenta resultados de trabalhos já publicados ou em preparação para publicação (capítulos 2 a 5), de acordo com o previsto no nº 2 do artigo 25º do Regulamento de Estudos Pós-Graduados da Universidade de Lisboa, publicado no Diário da República II série nº 57 de 23 de março de 2015. Tendo os trabalhos sido realizados em colaboração, o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, janeiro de 2016

Sergio Chozas Vinuesa

*A Ssm*

*A mis padres*

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"Arenales que copas tan verdes
le dan al aire
¿Serán arenales?"
Francisco Pino (1910-2002)

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# Abstract

The overall goal of this thesis was to study the spatial and successional dynamics of plant communities at different scales. Stabilized dune xerophytic shrubs were selected since i) they are affected by severe environmental stress, and several biotic interactions are described for dune plant communities; ii) they are highly threatened habitats; and iii) a significant number of rare, endangered and endemic plant species occur in these communities.

First, in the General Background, the main concepts addressed in the thesis, namely ecological community, succession, biotic interactions, functional diversity and functional traits, and ecological niche are analysed. Since these concepts have already been reviewed by a significant number of authors, our objective was to outline the framework where our work was developed rather than do a deep analysis.

In the following chapters, the works where the different subjects related with the dynamics of xerophytic shrubs were addressed are presented. In Chapter 2 the main drivers acting on stabilized dune xerophytic shrubs in SW Portugal, namely *Juniperus navicularis*, *Stauracanthus genistoides* and *Ulex australis* communities, are analysed. Results indicate that these communities respond to edaphic site conditions, climate and human disturbance, confirming the existence of both Clementsian and Gleasonian processes. In addition, it is proposed a conceptual model of the inland dune community dynamics. In Chapter 3 the functional trait responses along the successions described in Chapter 2 are assessed. It was found that successional community changes in the studied system involve a turnover in key functional traits and imply variations in species richness and functional diversity. In Chapter 4, the effects of environmental factors and biogeographical limitations on the diversification patters of the genus *Stauracanthus* are studied. Finally, in Chapter 5 the successional models developed for a delimited

area in Chapter 2 are evaluated to nearly all the geographic range of these communities. A significant consistence in the succession between *S. genistoides* and *U. australis* communities throughout most of the area of co-occurrence of both species was found even though the factors driving this successional gradient changed from one region to another: in Setubal and Comporta regions soil organic matter content was the main driver, while in South/South-Western region temperature seasonality and the habitat suitability of *S. genistoides* explained the most of the gradient.

Finally, in the General Discussion, a synthesis of the major findings for the understanding of the xerophytic plant communities' dynamics system is presented. Additionally, and aiming to improve the conservation measures of these communities, it is proposed the implementation of dynamic conservation strategies to ensure the preservation of the natural functioning of xerophytic shrub communities guaranteeing the successional pathways between them.

**Key-words: biogeography, community ecology, ecological niche, functional diversity, succession**

# Resumo

Os matos xerofíticos que ocorrem em dunas estabilizadas, nomeadamente as comunidades dominadas por *Juniperus navicularis, Stauracanthus genistoides* e/ou *Ulex australis,* encontram-se sob um elevado grau de ameaça e possuem um considerável número de espécies endémicas, raras e em perigo. Estas comunidades encontram-se sujeitas a severos stresses ambientais e numerosas interações bióticas tem sido descritas nestes matos. Estes factores tornam estes habitats um objeto de estudo idóneo para analisar a dinâmica sucessional e espacial das comunidades vegetais, o que foi o principal objetivo desta tese.

O Capítulo 1 é uma introdução geral, onde os conceitos chave incluídos na tese foram analisados, assim como as teorias ecológicas onde se inserem. Neste contexto, conceitos relacionados com a ecologia de comunidades, sucessão, interações bióticas, diversidade funcional, características funcionais das plantas e nicho ecológico foram abordados. Estes conceitos têm sido sujeitos a numerosas revisões por parte de um elevado número de autores, pretendendo-se com o objetivo desta introdução não fazer uma análise aprofundada dos mesmos mas contribuir para o enquadramento dos trabalhos apresentados. Nos seguintes capítulos, analisam-se diferentes tópicos relacionados com a dinâmica ecológica destes matos xerofíticos de sistemas dunares interiores.

No Capítulo 2 são analisados os principais fatores que atuam sobre a composição e a distribuição das comunidades arbustivas xerofíticas no sudoeste de Portugal a diferentes escalas (local, da paisagem e regional). Paralelamente, avaliou-se se as dinâmicas ecológicas presentes nestas comunidades cumprem os paradigmas relativos à organização da comunidade propostos por Clements, que refere as interações locais desenvolvidas entre as espécies como determinantes da

composição da comunidade, e/ou por Gleason, que confere um papel preponderante às respostas individuais das espécies e aos processos que atuam a escala regional. Os resultados demostraram que os fatores ambientais locais e regionais atuam sobre estas comunidades e definem a distribuição em mosaico típica das mesmas. Encontrou-se um gradiente successional entre as comunidades de *Stauracanthus genistoides* e as de *Ulex australis*, que responde as condições edáficas presentes localmente. Foi ainda descrita uma segunda sucessão entre as comunidades de *S. genistoides* e *Juniperus navicularis* que responde aos gradientes de aridez e perturbação local de origem agrícola. Estes resultados confirmaram a existência de processos tanto de âmbito local como regional, tal como descrito anteriormente por Clements e por Gleason respetivamente.

O Capítulo 3 enquadra-se na perspetiva de que a análise das alterações na diversidade funcional, medida como a variação dos grupos funcionais das plantas ou como a variação das características funcionais das espécies, podem ampliar o conhecimento relativo aos processos relacionados com as dinâmicas successionais e espaciais das comunidades vegetais assim como aqueles ligados à constituição e organização da comunidade. Foram estudadas as variações na diversidade funcional ao longo das sucessões encontradas nos matos xerofíticos mediterrânicos que ocorrem sobre dunas estabilizadas previamente descritas no Capítulo 2. Concretamente foi estudada a relação entre as variações na diversidade funcional e os fatores ambientais e foi avaliada a presença de processos de convergência ou divergência sobre as características funcionais das espécies que ocorrem nestes matos xerofíticos. Os resultados confirmaram que as mudanças relacionadas com a evolução destas comunidades são acompanhadas por alterações no número de espécies (riqueza taxonómica) e na diversidade de grupos funcionais e características funcionais, tendo sido verificado ainda uma alteração nos valores de determinadas características funcionais chave ao longo das sucessões. No entanto, não foram encontrados fatores de convergência ou de divergência que explicassem os padrões de diversidade funcional ou de organização nestas comunidades. Confirmou-se ainda a ocorrência de variações funcionais ao longo dos gradientes de disponibilidade de nutrientes e de aridez, previamente descritos no Capítulo 2 a partir das variações na composição de espécies. Estas alterações permitiram a identificação de quatro estádios principais ao longo das sucessões descritas nos matos xerofíticos de dunas estabilizadas.

No Capítulo 4 é focada a importância dos fatores ambientas e das limitações biogeográficas nos padrões de diversificação encontrados nas três espécies que constituem o género *Stauracanthus* e que apresentam uma distribuição parapátrica (i.e. as espécies possuem distribuições adjacentes): *S. boivinii*, *S. genistoides* e *S. spectabilis*. Para tal, procedeu-se ao estudo da resposta das espécies de *Stauracanthus* aos gradientes ambientais. A partir das distribuições potenciais destas espécies e da sobreposição dos seus nichos bioclimáticos foram avaliadas as suas diferenças e semelhanças do ponto de vista da sua recente diversificação. Foram encontradas 4 variáveis climáticas que discriminam a distribuição das três espécies. A sasonalidade da precipitação, isotermalidade e a temperatura média do trimestre mais frio apresentam valores mais elevados em todo o gradiente de distribuição geográfica das espécies de *Stauracanthus*, bem como valores de amplitude da temperatura média anual menores do que no resto da área de estudo, a Península Ibérica. As três espécies mostraram uma marcada similaridade na resposta às condições climáticas, apresentando *S. boivinii* e *S. genistoides* uma sobreposição média de 67%, enquanto que a sobreposição entre *S. spectabilis* e *S. boivinii* foi em media 42% e a de *S. spectabilis* com *S. genistoides* foi de 43%. Estes resultados evidenciaram os fatores ambientais e os eventos históricos como os principais responsáveis pelos processos evolutivos e da distribuição geográfica apresentadas atualmente pelas espécies do género *Stauracanthus*. A ocorrência destas espécies é condicionada pelas mesmas variáveis climáticas o que aponta para a existência de adaptações comuns de um clado recentemente diversificado, explicando o elevado grau de sobreposição de nichos. Este trabalho permite concluir que a diversificação do género *Stauracanthus* é consistente com a ocorrência de processos estocásticos de expansão geográfica das espécies e uma posterior fragmentação acoplados à evolução do nicho num contexto de flutuações ambientais de elevada complexidade espacial.

No capítulo 5 é comparada a importância das respostas individuais das espécies ao ambiente e dos processos que atuam localmente na composição e organização das comunidades xerofíticas presentes nas sucessões ecológicas descritas nos capítulos 2 e 3. Para tal, foi analisada a coerência geográfica das sucessões entre as comunidades de *Stauracanthus genistoides* e de *Ulex australis* e entre as comunidades de *S. genistoides* e de *Juniperus navicularis* descritas anteriormente numa região delimitada, para uma área muito maior, incluindo a maior parte da área de coocorrência das três espécies indicadoras das comunidades, nomeadamente *J. navicularis, S. genistoides* e *Ulex australis*. Verificou-se uma consistência significativa da sucessão ao longo de toda a área geográfica, no entanto as comunidades responderam de forma distinta aos gradientes ambientais presentes nas diferentes regiões onde ocorrem. Assim, enquanto nas regiões de Setúbal e Comporta o conteúdo de matéria orgânica no solo foi o principal fator a condicionar a sucessão entre as comunidades de *S. genistoides* e de *U. australis*, na região sussudoeste as variáveis que condicionaram a sucessão foram a sazonalidade da temperatura anual média e a adequação ao habitat do *S. genistoides*. Analisando a área total de ocorrência das comunidades, foi o conjunto das três variáveis que melhor explicou o gradiente sucessional, tendo, no entanto, a matéria orgânica o papel predominante. Assim foi colocada a hipótese de que os principais fatores responsáveis pelas alterações registadas ao longo das sucessões podem variar dependendo dos diferentes processos históricos assim como do nível de adequação das condições ambientais presentes localmente para as espécies chave das comunidades, sendo simultaneamente condicionadas por mecanismos intrínsecos destas comunidades que se traduzem num elevado grau de homogeneidade entre os diferentes estádios sucessionais das várias regiões.

Para finalizar, na Discussão Geral é apresentada a síntese dos principais resultados obtidos ao longo dos capítulos anteriores, direcionados a uma maior compreensão das dinâmicas ecológicas dos matos xerofíticos mediterrânicos das dunas estabilizadas. Do ponto de vista da conservação, e com o intuito de complementar as medidas de proteção atualmente existentes, é proposta a implementação de estratégias de conservação dinâmicas que assegurem o funcionamento natural destas comunidades e garantam a existência dos vários estádios sucessionais assim como as dinâmicas entre eles.

**Palavras chave: biogeografia, diversidade funcional, ecologia de comunidades, nicho ecológico, sucessão**

# Chapter 1

## General Background

# 1 General Background

## 1.1 Organization of ecological communities. Successional and individualistic processes

The perception of an ecological community as a group of species interacting in a given space is intuitive to the human understanding of natural systems. Strongly linked to the broader concept of ecosystem, different cultures and languages have named communities highlighting their close relationship with men, mainly as a provider of different resources and services (Millennium Ecosystem Assessment 2005). Far from this utilitarian point of view, the origin and nature of ecological communities has been such a crucial question in ecology that it developed a branch devoted to the study of the communities themselves: community ecology. From its very beginnings, community ecology has studied communities from the dual perspective imposed by the long historical debate between Clementsian and Gleasonian principles as the main determinants of community composition and dynamics. That is, whether ecological communities should be defined as either fully coherent entities or random assortments of the species present in the regional pool. Here, Clements (1916) understood communities as organism-like entities with the capacity of replicating its structures, with local interactions between species determining community composition. Gleason (1917), on the other hand, considered communities as assemblages resulting from the mere coincidence of species in time and space, where local habitat selection and regional scale processes filter the existing species pool determining community composition. A large amount of evidence coming from biogeographical and macroecological research points to the major importance of large-scale evolutionary and biogeographical processes for the composition and structure of local communities, through the individualistic responses of species to environmental gradients and historical effects (Ricklefs 2007; Hawkins 2008). This has even led to the recent claim for the 'disintegration' of ecological communities, as a mere aggregate of their parts, i.e. the species that coincide in a particular time and space (Ricklefs 2008; but see Brooker *et al.* 2009).

However, species do interact among them. A number of biotic mechanisms affect community structure (van Andel 2005) and provide the communities with emerging properties (Looijen and van Andel 1999). Different interactions are present in the communities resulting in positive, negative or indifferent effects (Table 1.1), forming more or less complex ecological networks that in turn generate ecosystem structure and functioning. These interactions determine the status of their populations locally (Chase and Leibold 2003), and have therefore an spatially-explicit component (Polis *et al.* 2004). As a result, species distributions are determined not only by their environmental requirements and species-specific spatial processes, but also by the interactions with other species (see Soberón 2007), in a scale-structured fashion towards more deterministic importance at landscape and local scales (Hortal *et al.* 2010) (Figure 1.1). Also, the functional characteristics of the species present locally determine the ecological structure of these communities and hence their functioning (see e.g. Naeem *et al.* 2002).

**Table 1.1** Possible types of interactions between two species: stimulation or positive (+), depression or negative (-) and no effect or indifferent (0) effects. Adapted from van Andel (2005)

| | **Species A** | **Species B** |
|---|---|---|
| **Competition** | - | - |
| **Allelopathy** | 0 | - |
| **Parasitism, Predation and Herbivory** | + | - |
| **Facilitation** | 0 | + |
| **Mutualism** | + | + |

Nonetheless, the neutral theory of biodiversity and biogeography formulated by Hubbell (2001) includes components from both perspectives. While it assumes that communities are highly determined by ecological interactions, as in the Clementsian paradigm, these interactions are unspecific within trophic levels, and are mainly the outcome of dispersal processes extrinsic to the community, more in line with the Gleasonian paradigm. This theory, and specifically the hypothesis of ecological equivalence, assumes that trophically similar species are ecologically equivalent, i.e. there is a significant amount of niche overlapping (see 1.4) which, together with the zero-sum ecological drift assumption, thereby results in that the presence of species is determined by random processes, at least in species-rich communities that are dispersal and recruitment limited (Hubbell 2006). Although Hubbel's hypothesis has been very criticized and some studies failed to find the predictions of neutral theory on some communities (e.g. Dornelas *et al.* 2006; Ricklefs 2006), other authors have successfully used it to describe species abundance patterns (e.g. Etienne and Olff 2004; Rosindell *et al.* 2010).

Regarding the concept of succession, ecologists have long observed that plant communities often experience similar patterns of change in species abundances, distribution and structure after disturbances or changes in the environment. These changes frequently involve the dominance of species with similar characteristic at different stages (Table 1.2), with progressively larger size, age, and shade tolerance, and progressively lower growth rates and dispersal abilities (Huston and Smith 1987). These generalizations are recognized and accepted by most plant ecologists, although real situations vary enormously (McCook 1994). Nevertheless, the determination of which are the main processes and interactions driving these successional changes, and if they act at individual- or population-based level, the predictability of successional changes and the existence of a climax community are still subject of discussion.

**Table 1.2** Physiological, life history and ecosystem characteristics of early and late-successional stages of succession. Adapted from Huston and Smith, 1987

| Characteristic | Early stages | Late stages |
|---|---|---|
| **Photosynthesis** | | |
| Light-saturation intensity | high | low |
| Light compensation point | high | low |
| Efficiency at low light | low | high |
| Photosynthetic rate | high | low |
| Respiration rate | high | low |
| **Water-use efficiency** | | |
| Transpiration rate | high | low |
| Mesophyll resistance | low | high |
| **Seed** | | |
| Number | many | few |
| Size | small | large |
| Dispersal distance | large | small |
| Dispersal mechanism | wind, birds, bats | gravity, mammals |
| Longevity | long | short |
| Induced dormancy | common | uncommon? |
| **Resource-acquisition rate** | high | low? |
| **Recovery from nutrient stress** | fast | slow |
| **Root-to-shoot ratio** | low | high |
| **Mature size** | small | large |
| **Structural strength** | low | high |
| **Growth rate** | rapid | slow |
| **Maximum life span** | short | long |
| **Ecosystem properties** | | |
| Site quality | extreme | mesic |
| Stability | low | high |
| Resilience | high | low |
| Importance of macro-environment | great | moderate, dampened, less |
| Plant diversity | low | high |
| Species life history | r*/R** | K*/S** |

* According the theory of r- and K selection of MacArthur and Wilson (1967) and ** the C-S-R strategy model of Grime (1977; 2001)

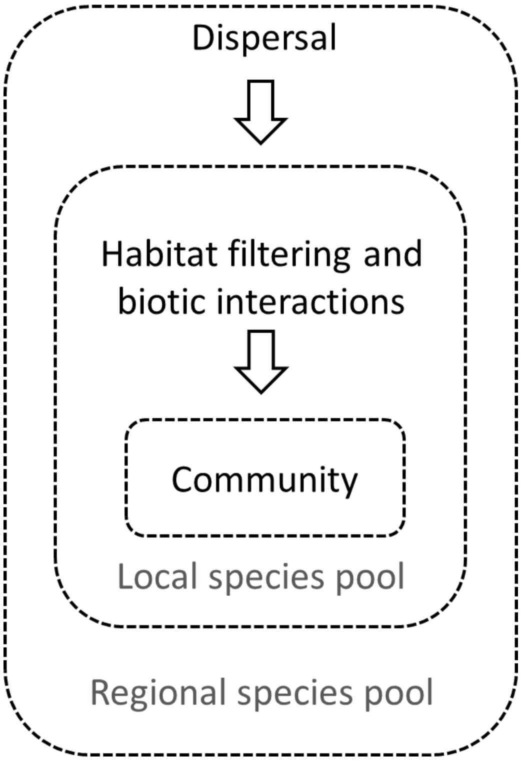


**Figure 1.1** At a given local site, the regional species pool is constituted by the species that are present regionally and are therefore able to disperse there (dispersal assembly). Within the locality, habitat filtering and biotic interactions define the actual assemblage of species that are present in each site (ecological assembly). Adapted from Götzenberger *et al.* (2012).

Primary succession is often considered a likely candidate for 'facilitatory' successional interactions (McCook 1994; Walker and del Moral 2003), and where earlier species improve the establishment or growth of later species. However, other processes seem to play additional roles in secondary successions, and quite certainly in primary too, as well as in the regeneration or maintaining of mature vegetation (following Tilman 1985 and Walker and Chapin 1987 terminology).

The concept of succession has followed a similar trajectory to that of community with, again, high implications for the dichotomy between the i) holistic and interaction-based Clementsian and the ii) reductionist and individualistic Gleasonian theories. Clements (1916, 1936) presented a highly deterministic concept of succession linked to the idea of a progressive convergence of communities into a stable climax. In his works, species interactions played the main role in successional changes. On the other hand, Gleason (1917, 1926) referred succession as an unpredictable and largely random process. Different models have been developed aiming to explain successions and to evaluate the processes involved in them. The early model for successional changes proposed by Clements (1916) emphasized the role of facilitation as a driver of ecological succession. Later Connell and Slatyer (1977) proposed three alternative models of succession: i) facilitation ii) tolerance and iii) inhibition. In the facilitation model, processes of facilitation by early pioneer species “facilitate” the colonization by later successional species first and then competition determine succession. In this model, early successional species disappear as they make the environment less suitable for themselves and more suitable for others species. In the tolerance model, life history traits of the species are the main drivers and later successional species are those tolerant of environmental conditions early in succession, and finally, in the inhibition model competition and life history traits condition successional stages. Within this context, (Grime 1977; 2001) underlined the role of plant strategies in succession and emphasized disturbance, stress and competitive interactions as selective forces that change over the course of plant succession. He viewed succession as a shift in the dominance of three plant strategies C-S-R (competitive, stress tolerant and ruderal), in response to changing environmental conditions. Changes in plant strategy dominance result of autogenic changes in resource availability, mainly light, nutrients and water. These changes are a direct result of resource consumption by the plants, with resource abundance decreasing as succession progress. He proposed that disturbance-adapted species dominate early successional stages, and then good competitor and stress-adapted species dominate later stages. The resource-ratio model proposed by Tilman (1985; 1988) explained the general patterns observed in succession stressing the main role of competition and resource limitation (nutrients and light). Tilman also underlined the importance of life history traits, mainly height and growth rates, in determining alternative successional pathways. Both Grime's and Tilman's models of succession predict changes in the resource supply and resulting shifts in species adapted to the changing environmental conditions. In both models these changes are autogenic, however these models differ in the nature of environmental change and in their views of competition (Smith and Smith 2001). Between these two works, MacMahon (1980) proposed a successional model where environmental drivers, migration capacity and "residuals" (i.e. remaining from the period previous to the disturbance, namely propagules and local chemical and physical properties) conditioned early stages of the succession. Then, after ecesis processes (the establishment and growth of a given species in the successional stage), the "reaction" (i.e. the effect of initial community) together with biotic interactions determined successional pathways and later stages. MacMahon maintained that succession can be predicted with certain accuracy on a regional basis, while it is nearly impossible to predict at local scale. After analysing the proposal of Connell and Slatyer (1977), Walker and Chapin (1987) argued that no single processes can explain successional changes; rather, these changes would be the result of complex interactions among several of these processes. They assigned different processes and interactions to Connell and Slatyer's models, mainly life history traits (arrival time, longevity and growth rate), competition and facilitation. They found that those processes and interactions often occur simultaneously and therefore, these models cannot always be considered as mutually exclusive (Figure 1.2). In the same way, Huston and Smith (1987) argued that those processes can occur concurrently, with different levels of importance, along the entire successional sequence.

Then, the conciliation of holistic and reductionist approaches represents the current state of thinking among community ecologists (van Andel 2005), no matter whether they study species assembly, community structure or ecological successions. Both approaches alternate in importance depending on the type of the questions addressed and at the scale at which those questions are formulated (Guisan and Rahbek 2011; Hortal *et al.* 2012).

## 1.2 Biotic interactions and succession of species and traits

Biotic interactions structure communities both in space and time, creating patterns along geographic gradients and successional processes. Regarding to space, it is generally accepted that biotic interactions shape species' spatial distributions at local and landscape scales (Pearson and Dawson 2003; Lortie *et al.* 2004; Hortal *et al.* 2010; Wisz *et al.* 2013). Nevertheless, their impact on succession is more controversial. Walker and Chapin (1987) proposed that biotic interactions probably were more important in determining the rate of succession than its final outcome, and pointed out to life history traits as indicators of both the temporal patterns of species replacement and the endpoint of successional changes (Figure 1.2). They also indicated a main importance of facilitation along succession in severe environments and in early stages than in favourable and intermediate and final stages (Figure 1.2). It is therefore likely that biotic interactions are irrelevant only in early stages of primary succession, when individuals just accumulate in a largely free environment; however, at some point facilitation processes that allow the establishment of intermediate successional species dominate, allowing to reach a moment where density is so important that produces a shift to competition as the main driver of temporal change (del Moral *et al.* 2005). In fact, the intensity of a particular interaction frequently varies along the succession, and different interactions often work simultaneously shaping up community composition and structure ( e.g., Callaway and Walker 1997).

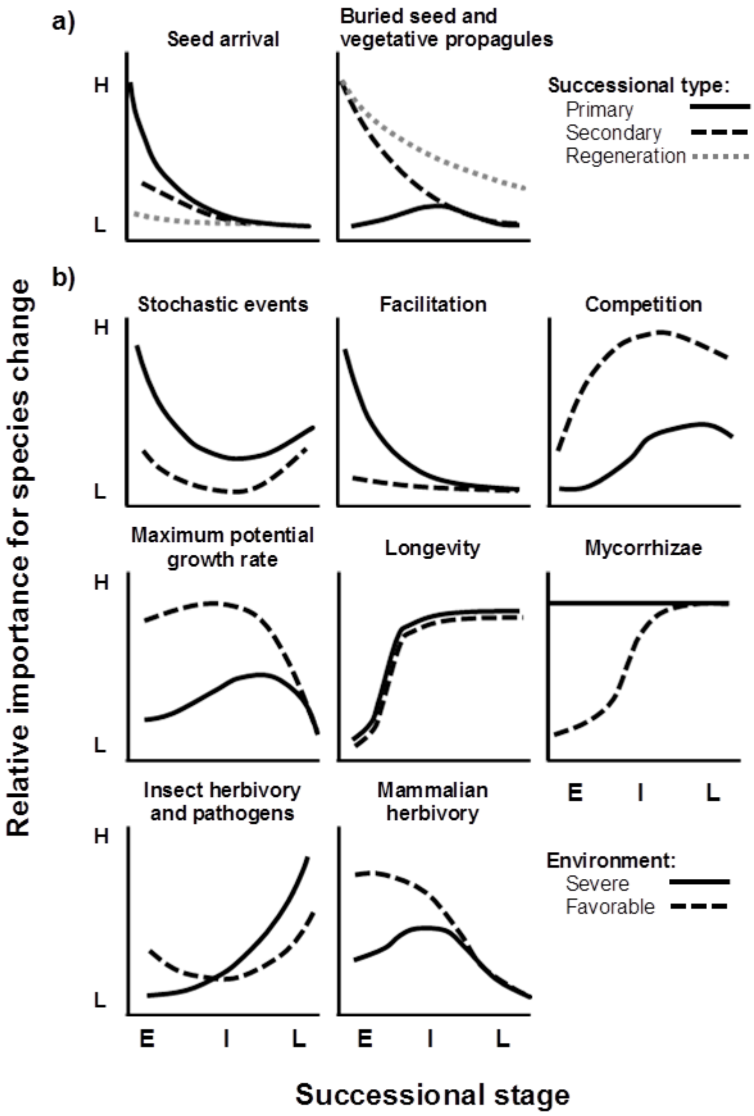


**Figure 1.2** Influence of a) type of succession and b) environmental severity upon major successional processes determining changes in species composition during colonization. Early (E), Intermediate (I) and Late (L) successional stages. High (H) and Low (L) relative importance of processes. Adapted from Walker and Chapin (1987).

Plant functional traits are any morphological, physiological or phenological attribute measurable at the individual level that affects the fitness of organisms and/or their influence on other organisms and on ecosystem functions (Violle *et al.* 2007). They therefore constitute indicators of the processes governing ecological assembly processes and ecosystem functioning (Suding *et al.* 2008; Freschet *et al.* 2011; Pérez-Harguindeguy *et al.* 2013). The selection of certain plant traits in a community can be the consequence of the filtering effect of climatic disturbance and biotic interactions.

These filters determine which components of a species pool are assembled into local communities. Several authors point to the relationship between plant traits and succession-related mechanisms (e.g. Huston and Smith 1987, see Table 1.2). While dispersal and establishment traits are related with colonization (del Moral *et al.* 2005; Dölle *et al.* 2008), the capacity of becoming dominant is related with the established and regenerative strategies related with life traits, pollination mode and immigration status traits (Prach and Pyšek 1999). It is therefore clear that the analysis of trait turnover along successions may give us key insights about the species' environmental requirements and biotic interactions that ultimately determine their capacity to first establish and survive in any particular environment, and then dominate it. The Chapter 3 of this thesis was moved by this hypothesis.

## 1.3 Community composition and functional diversity

Searching for universal rules associating species and environment has been a goal for community ecologists (Lavorel and Garnier 2002). Here, functional diversity can be defined as the diversity of species traits in ecosystems or communities (Schleuter *et al.* 2010). The relevance of this area of research has grown exponentially in the last two decades (Tilman 1997; Díaz and Cabido 2001; Petchey and Gaston 2006). Although some authors found that both taxonomic and functional diversity often perform similarly in relation to community composition (Petchey and Gaston 2002), it is frequently argued that trait diversity is better in detecting truly functional changes in both communities and ecosystems (McGill *et al.* 2006), to the point that species are sometimes considered as mere assemblages of traits (Cadotte *et al.* 2011). Several indices have been proposed to measure the functional diversity of a given community, following two strategies (see Ricotta and Moretti 2011). While some authors propose indices aiming to capture all the different components of functional diversity (Mason *et al.* 2005; Villéger *et al.* 2008; Etienne and Legendre 2010), others argue that by analysing single trait variations it is possible to link community structure and ecosystem functioning (Garnier *et al.* 2004; Lepš *et al.* 2006). Aiming to conciliate both points of view, in this thesis we used three functional indices described by Villéger *et al.* (2008), namely functional richness, functional evenness and functional divergence, Rao's quadratic entropy (Rao, Botta-Dukát 2005), and the community-weighted mean trait value (CWM, Garnier *et al.* 2004). Villéger's indices link diversity and ecosystem function via niche complementarity, by measuring species distribution in niche space (Mason *et al.* 2005). Functional richness measures the volume of functional space occupied by the community, functional evenness assesses the regularity of the distribution of abundance in that volume, functional divergence measures the divergence in the distribution of abundance in this volume, and Rao's quadratic entropy represents a mix between functional richness and functional divergence (Mouchet *et al.* 2010). Further, we also measure the community weighted mean of each trait (CWM), that is, the mean of the trait values present in the community weighted by the relative abundance of the species bearing each value (Garnier *et al.* 2004; Lavorel *et al.* 2007). This metric provides insights about the dominant traits within a community, and supports the mass-ratio hypothesis by considering that the traits of the most abundant species regulate the main ecosystem processes (Ricotta and Moretti 2011).

## 1.4 Ecological niche and species geographic distributions

The niche is another fundamental concept for ecology. As community and succession, it has received numerous definitions and interpretations (Chase and Leibold 2003). The duality between habitat and effect is the principal origin of these misunderstandings, dating back to the seminal works of Grinnell (1917) and Elton (1927), where Grinnell identified niche with the habitat where species occur and Elton with the effect of those species on the habitat. Hutchinson (1957) provided a first synthesis, defining the niche as the n-dimensional hypervolume delimiting the environmental conditions and resources needed for a given species to survive. In this definition, Hutchinson adds a quantitative component to the concept and also identified niche as an attribute of a given species or population rather than a characteristic of the habitat (see also Hutchinson 1978). Currently, most niche definitions include components of both requirements and impacts; for example Peterson *et al.* (2011) define niche as the ecological conditions that a species requires to maintain populations in a given region (i.e. the Grinnellian niche), together with the impact that species has on its resources, other interacting species, habitat, and environment (i.e. the Eltonian niche) (see also Soberón 2007).

The duality between biotope and niche underlined by Hutchinson (1957; 1978) allows the establishment of a direct link between environment and geography (Soberón 2007; Soberón and Nakamura 2009) and provides the framework necessary to analyse species distributions in relation to the spatial variations in environmental conditions and biogeographical processes (Colwell and Rangel 2009). Several methods try to identify places suitable for the survival of populations of a species *via* the identification of their environmental requirements. These methods relate ‘‘niches’’ to ‘‘areas of distribution’’ (Soberón and Nakamura 2009) and they are traditionally called species distribution models (SDM), habitat modelling or ecological niche modelling (ENM) (Guisan and Zimmermann 2000; Chefaoui *et al.* 2005; Jiménez-Valverde *et al.* 2008; Peterson and Soberón 2012). By collecting species occurrence records and environmental variables data these models are capable of characterize the ecological niche, or as claimed by Peterson *et al.* (2011) “the existing fundamental niche”.

## 1.5 Study system

Severe habitats such as deserts, salt marshes or sand dunes provide unique systems for studying the duality between Gleasonian and Clementsian principles. They are characterized by the existence of physio-chemical stressors (Tobler 2008) that play an essential role by filtering the species pool (Guisan and Rahbek 2011; de Bello *et al.* 2013), so that the harsher the environmental conditions, the fewer the number of species are able to survive and thrive to make part of the communities from severe habitats (Moser *et al.* 2005). Additionally, several species interactions, in particular facilitation, symbiosis and competition have been described as significant drivers of the dynamics of these communities (Walker and Chapin 1987; Armas and Pugnaire 2005; Butterfield 2009; Muñoz Vallés *et al.* 2011). The poor communities, low resources and reliance on interactions among a few species make severe habitats particularly sensible to human activities, particularly in areas where they compete with agricultural, farming, forestry or touristic land uses. Within this context, dune habitats are among the most threatened habitats in Europe. The extension of these habitats in Portugal provides this country with an enormous value for the preservation of dune ecosystems within the broader European context (DG Environment and ETC/BD Report 2001-2006). Taking this into account, xerophytic scrubs communities growing on stabilized dunes in South-Western Portugal were selected as our model system.

Stabilized dunes occur at the inland limit of coastal sand dunes. This limit is highly determined by the interaction between wind power and vegetation cover (Yizhaq *et al.* 2007). While coastal dunes present a directional zonation of plant communities from the sea to inland due to the combination of biotic (e.g. plant cover and diversity) and abiotic (e.g. salt spray, high temperature, burial, sand transport) factors (Gilbert 2007; Rajaniemi and Allison 2009; Carboni *et al.* 2011), stabilized dunes 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, such patchiness can be mainly driven by water availability, which determines the distribution of xerophytic and hygrophytic scrubs within the landscape, thereby resulting in two largely different types of communities (Díaz Barradas *et al.* 1999). However, stabilized dunes in South-Western Portugal are mainly occupied by xerophytic shrub communities due to water scarcity (Neto *et al.* 2004). They are home for a significant number of rare, endangered and endemic plant species, being listed in Annex I of the EU Habitats Directive 92/43/EEC due to their high interest for biodiversity (Costa *et al.* 2007; EC 2007). The study of these systems can help highlight additional drivers other than water, thereby reaching a broader understanding of community dynamics on stabilized dunes and, in general, on severe habitats.

For the selection of the study area, the potential area of occurrence of inland dune xerophytic shrub communities was defined in ArcGIS version 10 using three layers depicting: i) sandy soils (extracted from the lithological map of Portugal; APA 1992); ii) areas with forest and semi-natural land use cover (Caetano *et al.* 2009) and iii) the known distribution of the main shrub indicators of the main scrubs occurring on stabilized dunes in SW Portugal (Figure 1.3). The study area for Chapters 2 and 3 was located at 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), mainly occupying the Peninsula of Setúbal and Comporta regions, in an area of about 1700 km² (Figure 1.4). For Chapter 5, the area between Sines Cape and the Guadiana River Estuary (37°10’N, 7°24′W) was also included. This new area occupies the coastal areas of both SW Alentejo and Algarve, totalling an area of about 2900 km² (Figure1.4), aiming to evaluate the consistency of the successional dynamics beyond the original studied area defined in Chapters 2 and 3. Finally, the study area of Chapter 4 was the whole

Iberian Peninsula (Figure 1.5), due to the presence of populations of *Stauracanthus genistoides* and *S. boivinii* in South-Western Spain.

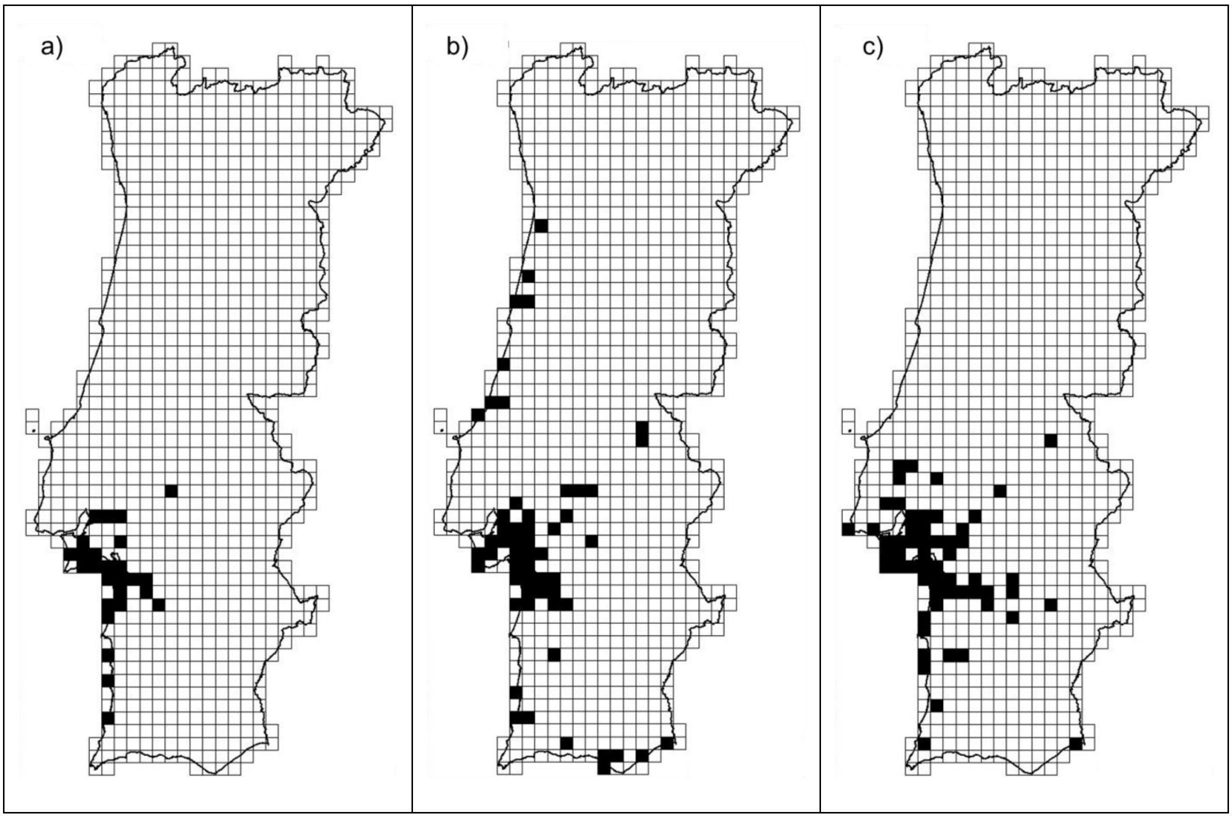


**Figure 1.3** Maps of known presences of a) *J. navicularis* (Carapeto *et al.* 2015), b) *S.* genistoides (Chozas *et al.* 2015a) and c) *U.* australis (Chozas *et al.* 2015b) in Portugal

For all chapters but Chapter 4, altitude varies from 0 to 180 m a.s.l. The climate is mild Mediterranean, presenting ocean influences, with a dry summer period. Precipitation exhibits strong seasonal and inter-annual variability. Under the Köppen-Geig climate classification, "Mediterranean" climates are classified as Csa and Csb types. According to this classification (AEMET-IM 2011), most of the study area is included in the Csa type: temperate climate region with dry and hot summers, except the SW Alentejo coast, coinciding with the Csb: temperate climate areas with dry and warm summers. Mean annual precipitation ranges from 509.1 mm in Faro (Algarve region) to 715.9 mm in Setúbal (Setúbal Peninsula), and mean annual air temperature ranges from 16.2 ºC in Setúbal and 17.3 ºC in Faro (SNIRH 2009).

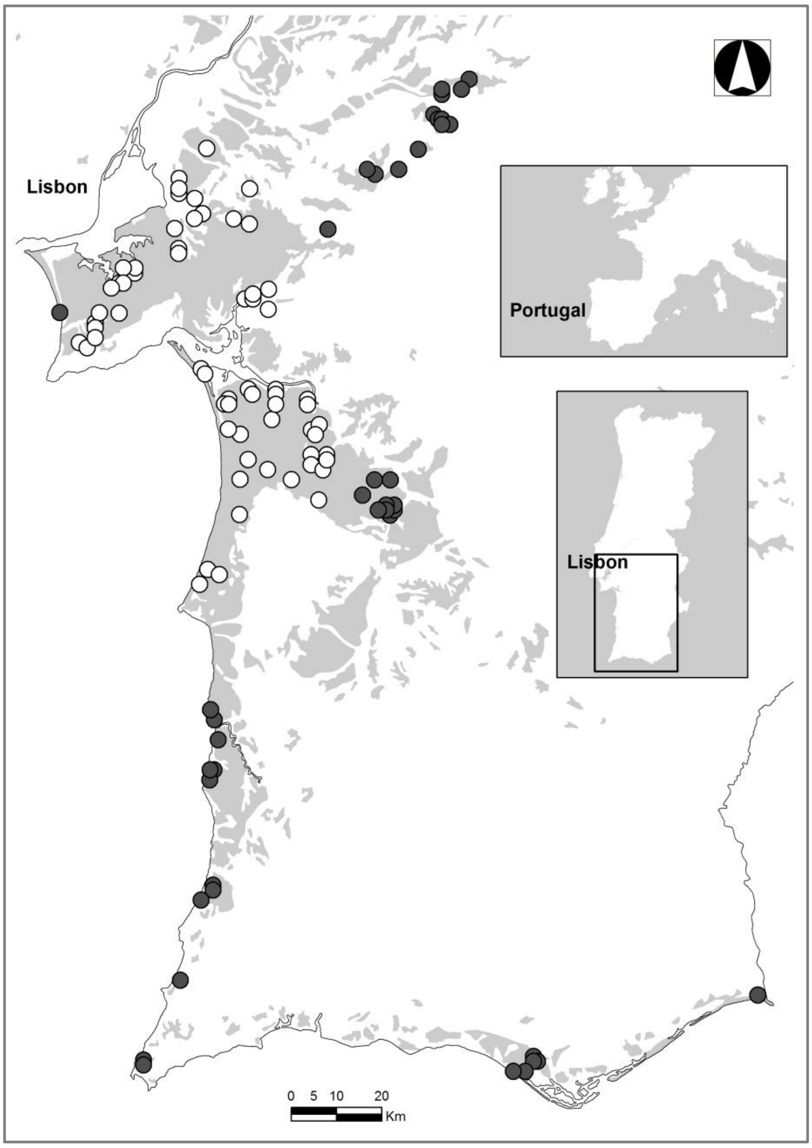


**Figure 1.4** Study sites and potential area of occurrence of inland sandy xerophytic shrub communities (in grey) in South-Western Portugal. Empty circles correspond to study sites in Chapter 2 and 3. Both empty and full circles correspond to study sites in Chapter 5.

The dominant soil type is podzol, with some regosols and cambisols, with moderate and very weak soil development, respectively (APA 1992). 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). The xerophytic shrub communities are characterized by the dominance or presence of *Stauracanthus genistoides* (Brot.) Samp. and/or *Ulex australis* Clemente – two thorny shrubs of the legume family (Fabaceae) endemic to Iberian Peninsula – and *Juniperus navicularis* Gand., a shrubby juniper endemic to the Iberian Peninsula. For simplicity we use *J. navicularis*, *S. genistoides* or *U. australis* communities to refer to these three types of formations throughout the whole text.

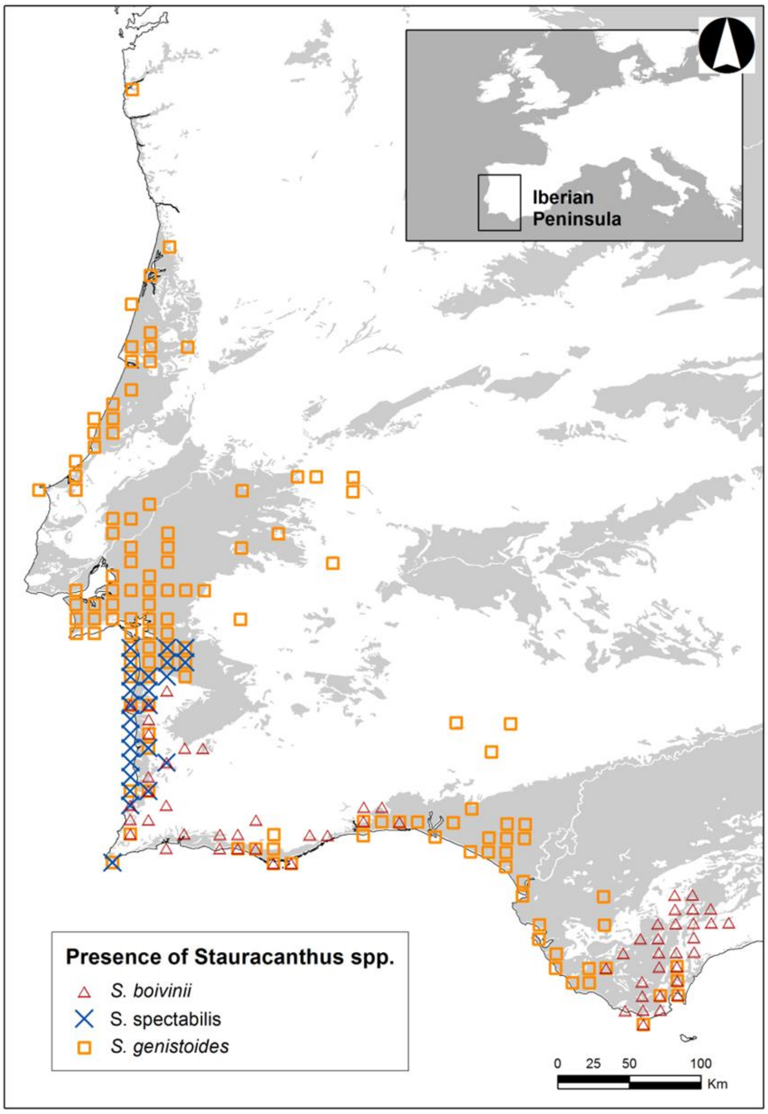


**Figure 1.5** Distribution map of *Stauracanthus* species in the Iberian Peninsula. Each symbol represents a 10x10km UTM cell. Shaded area represents the suitable soils for the genus, namely sandy soils.

The *J. navicularis* communities (Figure 1.6a) correspond to the Portuguese *J. navicularis*, dominated subtype of the Annex I "Coastal dunes with *Juniperus spp*." habitat defined in the European Habitats Directive with the code 2250. It is characterized by the presence of *J. navicularis* and it is considered as the climax community of paleo-sand dunes in Mediterranean Portugal (Neto 2002). Forestry practices have seriously disturbed these communities, resulting in open psammophilous shrub formations with sparse junipers. The higher the disturbance, the larger the number of species belonging to *S. genistoides* communities (see next paragraph for details) and the lower the shrub cover. Nevertheless, dense *J. navicularis* formations, frequently with *Phillyrea angustifolia* and *Daphne gnidium,* occur under low disturbance levels.

The *S. genistoides* communities (Figure 1.6b) are open formations inhabiting stabilized dunes and other sand deposits dominated by *S. genistoides*, with a floristic composition including *Halimium halimifolium*, H. calycinum, *Helichrysum* subsp. *picardi*, *Armeria rouyana*, *Lavandula pedunculata* subsp. *pedunculata*. These communities are classified within the Portuguese and Andalusian "*Cisto-Lavenduletalia* dune sclerophyllous scrubs" habitat described in the Annex I of the Habitats Directive with the code 2260. This formation is traditionally considered as the result of the destruction of *J. navicularis* communities and it constitutes an early stage of succession of the psammophilous cork oak (*Quercus suber*) *montado* understory (Rivas-Martínez *et al.* 2001; Neto 2002).

a)

b)

c)

**Figure 1.6** General aspects of the communities under study; a) Dense *J. navicularis* community located on a very steep face of a paleo-dune. Although forestry management was present in the area, dune inclination prevented this formation of the impacts of more destructive practices; b) *S. genistoides* community, dominated by adult individuals flowering, occurring in a maritime pine forest clearing; c) *U. australis* community co-dominated by *U. australis* and *Halimium halimifolium* occurring in the clearing of a stone pine plantation with some cork oak individuals.

The *Ulex australis* communities (Figure 1.6c) occurring on stabilizes dunes correspond to the Portuguese and Andalusian *U*. *australis*-dominated subtype of the Annex I “Atlantic decalcified fixed dunes (*Calluno-Ulicetea*)” habitat of the EU Habitats Directive with the code 2150. They constitute dense formations dominated by either *U*. *australis ssp*. *welwitschianus* (in Mediterranean Portugal) or *U*. *australis ssp*. *australis* (in Andalusia), together with *Calluna vulgaris* (in both regions). This formation often results from the destruction of *J. navicularis* communities, and constitutes an early/intermediate stage (see Chapter 2) of succession of the psammophilous cork oak *Montado* understory (Rivas-Martínez *et al.* 2001; Neto 2002). This community shares some psammophilous species with *S. genistoides* communities: namely *H*. *halimifolium*. However, when these communities occur on soils with a hardpan layer (i.e. a sub superficial layer of sand cemented by iron oxides) in the study area, sand avoider or edaphically indifferent species such as *Cistus ladanifer*, *Erica scoparia*, *E*. *umbellate* or *Genista triacanthos* also become established (Neto *et al.* 2004).

As mentioned above, these three types of habitats are home for a significant number of rare, endangered and endemic plant species (e.g. *Armeria rouyana* Daveau, *A. pinifolia* (Brot.) Hoffmanns. & Link, *Thymus capitellatus* Hoffmanns. & Link, *Santolina impressa* Hoffmanns. & Link). The three communities are listed in the Annex I of the Habitats Directive due to their high interest for biodiversity (for details see EC 2007 and Costa *et al.* 2007), being *J*. *navicularis* and *U*. *australis* communities labelled as priority habitats, i.e. in danger of disappearance. They are also protected under the Portuguese Decreto-Lei 49/2005, the law transposing the Habitats Directive in Portugal.

## 1.6 Objectives and structure of the Thesis

The overall goal of this thesis was to study spatial and successional dynamics of xerophytic shrub communities from inland stabilized sand dunes at different scales. The analysis of the role of environmental requirements and biotic interactions on the organization and distribution of these communities aimed to conciliate the individualistic and holistic paradigms dominating the community ecology and to determine the different importance of those agents at local, landscape and regional scales. Stabilized dune xerophytic shrubs were selected since i) they are affected by severe environmental stresses and several biotic interactions are described for dune habitats; ii) they are highly threatened habitats; and iii) a significant number of rare, endangered and endemic plant species occur in these communities.

These studies are particularly important for the conservation and management of habitats involving several successional stages and presenting a geographical distribution highly coincident with human interests (mainly tourism but also forestry and agriculture). On the one hand, only dynamic management approaches can guaranty the long-time preservation of all successional stages of a given set of communities. On the other hand, it is necessary to conciliate economic development with conservation. Therefore, exhaustive and detailed studies of the factors involved in the ecological dynamics of these communities are strongly needed to proportionate the elements necessary to conciliate both requirements.

First, the main drivers acting on stabilized dune xerophytic shrubs were analysed, proposing a conceptual model for the successional dynamics in these communities (Chapter 2). Secondly, the key functional traits associated to the change in these communities were identified and their responses along the successions previously described were assessed (Chapter 3). In Chapter 4 the effects of environmental factors and biogeographical limitations on the distribution of the genus *Stauracanthus* in the Iberian Peninsula were studied. At the end in Chapter 5, the impact of the suitability of environmental conditions for *Stauracanthus genistoides* and *Ulex australis* on the succession between the communities dominated by these two species were evaluated, also validating the successional models developed in the original study area of the Tejo Estuary to the whole geographic area of these xerophytic shrub communities in Iberian Peninsula.

The specific objectives and main methodological approaches of each chapter are described below:

**Chapter 2. Local and regional-scale factors drive xerophytic shrub community dynamics on Mediterranean stabilized dunes.** The main objective of this chapter was to 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). We also examined if these processes follow Clementsian or Gleasonian principles. Shrub cover, herb presence, soil characteristics and human disturbance were sampled in 70 plots to study the influence of environmental variables and human impacts at different scales on the xerophytic scrub communities. 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. This study has been already published as Chozas *et al.* (2015) *Plant and Soil* **391(1):** 413–426.

**Chapter 3. Dynamics of functional and trait structure during succession in xerophytic shrub communities on Mediterranean stabilized dunes.** In this chapter we evaluated the hypothesis that community changes in the species composition of xerophytic shrub communities imply concurrent changes in functional structure involving a turnover in functional traits. We further analysed how this trait turnover responds to environmental factors. Finally we studied if the trait turnover in successional community evolution follows a random or a non-random pathway, testing the hypothesis that functional trait diversity, particularly of those traits directly involved in the succession, will be linked to the factors that drive successional dynamics. This chapter is in preparation for publication.

**Chapter 4. Environmental niche divergence among three dune shrub sister species with parapatric distributions.** In this chapter we analysed the effects of environmental factors and biogeographical constraints on the distribution and diversification patterns of three dune shrub sister species with parapatric distributions in the Iberian Peninsula. Aiming to study the realized response of *Stauracanthus* species to environmental gradients, their potential distributions and realized bioclimatic niche overlap were used to assess the geographical and environmental commonalities and differences between these species, and relate them to the conditions throughout their recent process of diversification. Ecological Niche Factor Analysis (ENFA) and GLMs were used to obtain the potential distribution of the species. Environmental niche overlap was calculated using Schoener's index, which compares the occupancy of the environment between pairs of species. Finally, the spatial niche overlap among the species was explored by overlaying the habitat suitability maps obtained from ENFA. This chapter has been submitted for publication to *Evolutionary Ecology*.

**Chapter 5. A geographically consistent succession mediated by different environmental factors across regions.** The main objective of this chapter was to evaluate whether local communities follow a coherent ecological succession-like gradient throughout a large geographical extent or are driven by the individualistic responses of the species present in the pool of each locality. That is, whether they provide support for either local processes or regional constrains as the main drivers of community assembly. To do this, we evaluated the geographical coherence of the two successional gradients identified in Chapter 2. We conducted an extensive survey of 115 sites in adequate soils throughout SW Iberian Peninsula. These data were used to assess whether the abovementioned successions occur coherently beyond the original studied area and we characterized the environmental suitability for each species on each of these sites. This process involved both community analyses describing community structure and species distribution models doing so for the potential distribution of the indicator species of both communities. This chapter is in preparation for publication.

**Chapter 6. Conclusions**. In this chapter a synthesis of the major findings for the understanding of the xerophytic plant communities' dynamics system is presented. Additionally, and aiming to improve the conservation measures of these communities, we propose the implementation of dynamic conservation strategies to ensure the preservation of the natural functioning of xerophytic shrub communities guaranteeing the successional pathways between them.

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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).

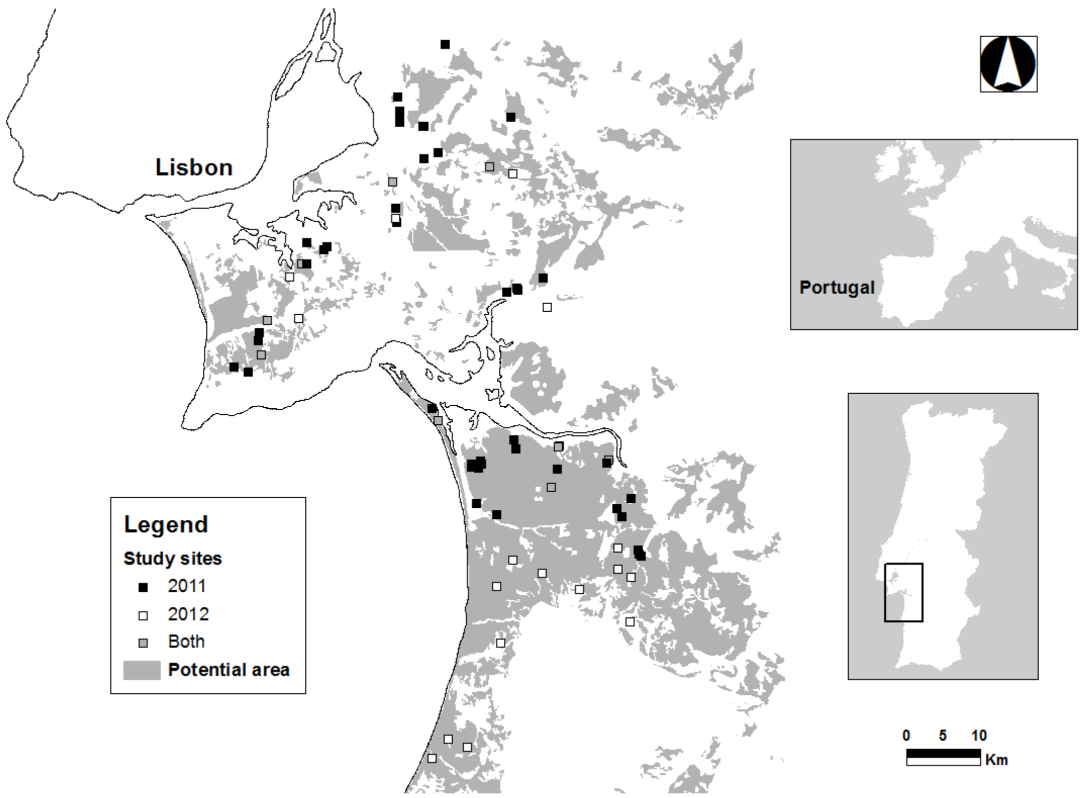



**Figure 2.1** Study sites and potential area of occurrence of inland sandy xerophytic shrub communities in Alentejo coast and Peninsula of Setúbal, SW Portugal.

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 multidimentional 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 |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 Legendre1998; Lichstein 2007). The MRM formula is $Y=X_1+X_2+\ldots+X_n$, where Y is the dependent distance matrix and $X_1,\ldots,X_n$ 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).

<u>Community gradients characterisation</u>

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 significantly 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* |
| *P pinaster* | 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.

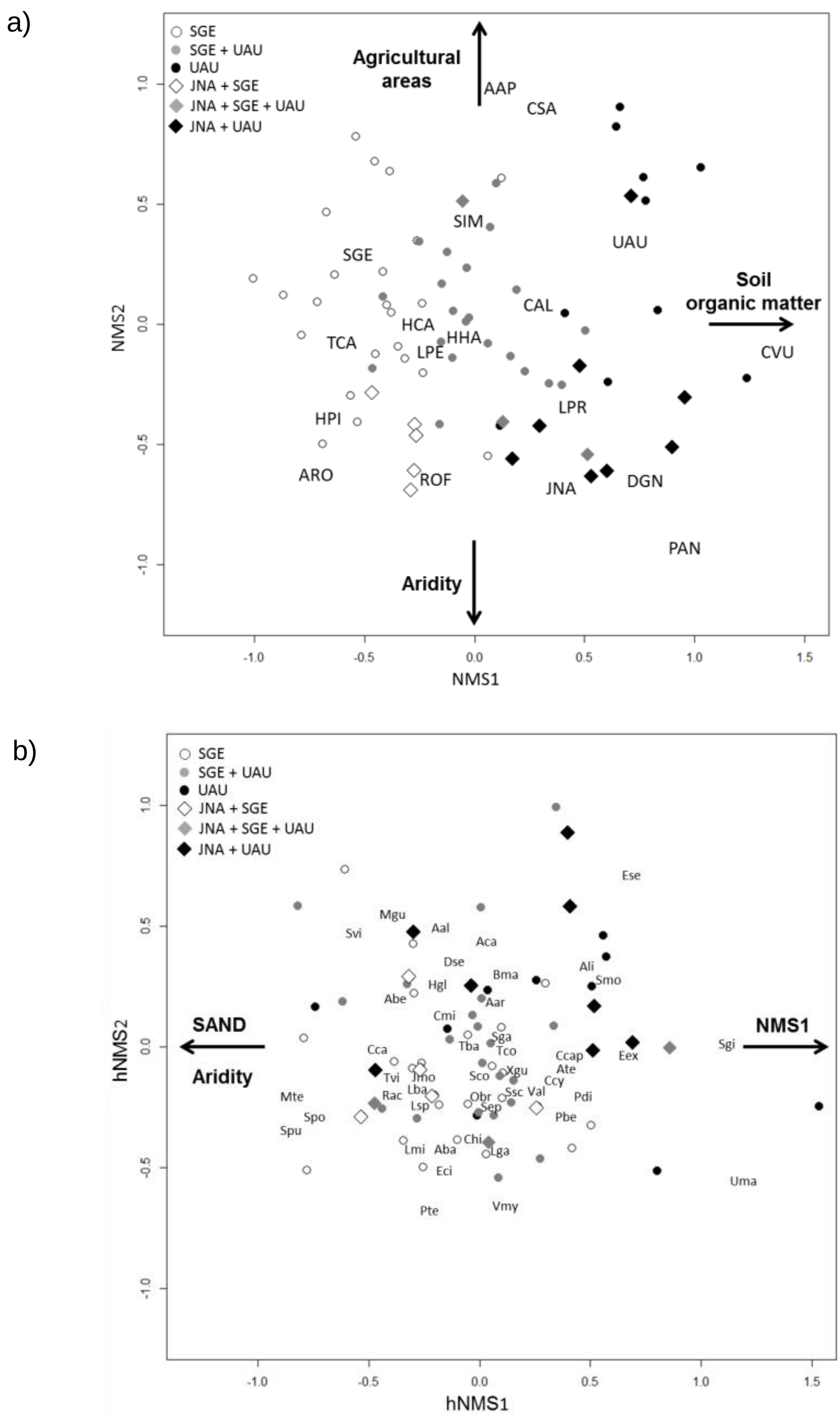



**Figure 2.2** Axes 1 and 2 of the 3-dimensional non-metric multidimensional scaling ordinations of study sites based on a) shrub cover (NMS1 and NMS2) and b) herbaceous presence and absence (hNMS1 and hNMS2). Final stress values for the 3-dimensional configuration were 0.15 and 0.18 for shrubs and herbs, 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.

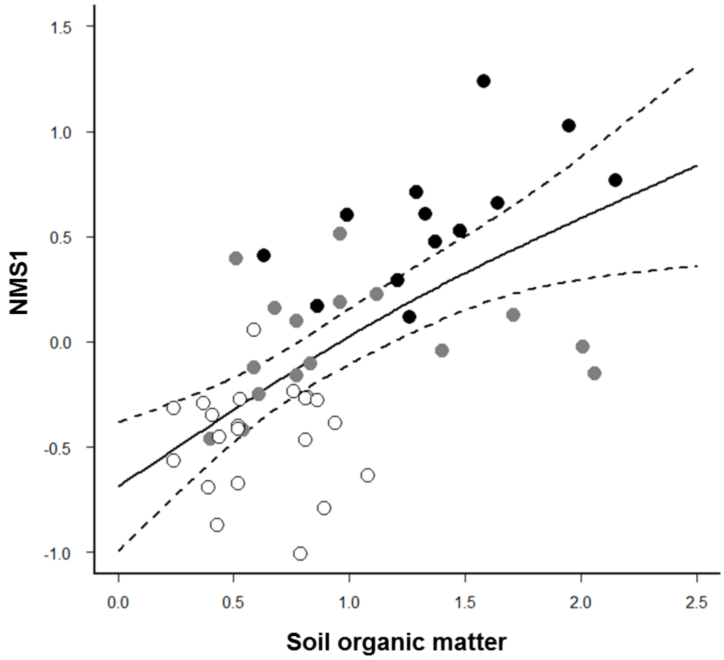



**Figure 2.3** Relationship between the first axes of the ordination based on scrub cover (NMS1) and percentage of soil organic matter (SOM). Solid and dashed lines represent the main trend and 95 % confidence intervals of a Generalized Additive Model (GAM); n=50, k=1.326, percentage variance explained= 39.3% and adj.r2 =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 Aditive 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** |
| ***P pinaster*** | **Con5000** | **Mixed forest** | **Mixed forest** |
| **Rabbits** | **Eucalyptus** | **Time-Mng** | **Montado** |
| **Relape-spp** | **Firebreaks** | N | **NMS1** |
| **Sand** | **Grasslands** | **NMS1** | **PC2** |
| **Shrub cover** | Invasive-spp | **PC1** | ***P pinaster*** |
| 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** | | |

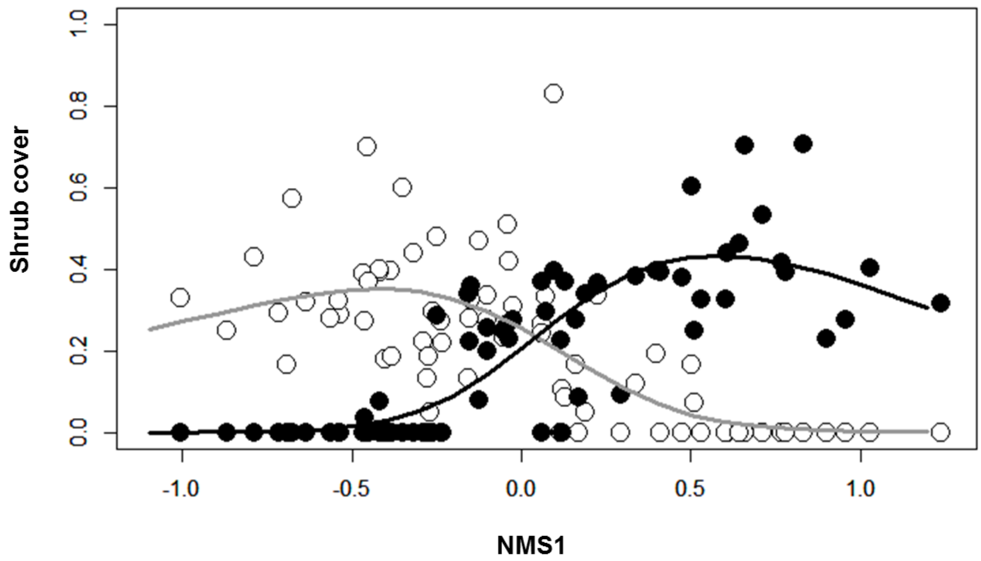
**Table 2.3** Regression coefficients and regression $R^2$ of the Multiple Regression on distance Matrices between each NMS axis and the predictors obtained by backward selection method. p-values were adjusted using Bonferroni correction.

| **Variables** | **NMS1** | **Variables** | **NMS2** | **Variables** | **hNMS1** | **Variables** | **hNMS2** |
|---|---|---|---|---|---|---|---|
| **SOM** | 0.32*** | **Agriculture** | 0.26*** | **NMS1** | 0.23*** | ***P pinaster*** | 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.



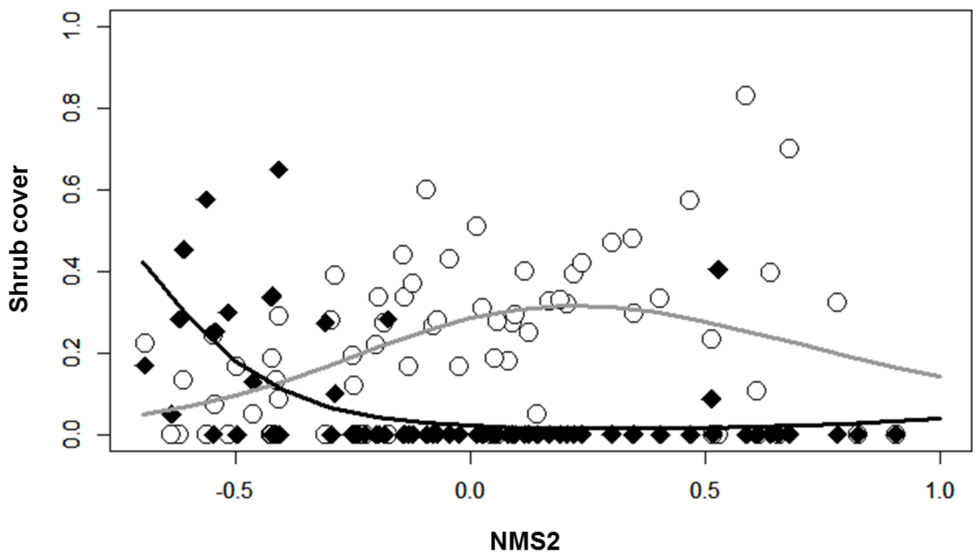




**Figure 2.4** Relationships identified by Generalized Additive Models of the binomial family between: a) *S.* genistoides (in grey) and *U. australis* (in black) cover and the first axis of the ordination based on scrub cover (NMS1), n=70. Effective degrees of freedom k= 1.99 and 2, percentages of variance explained= 51.8% and 65.9%, and adj.r2 =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 adj.r2 =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

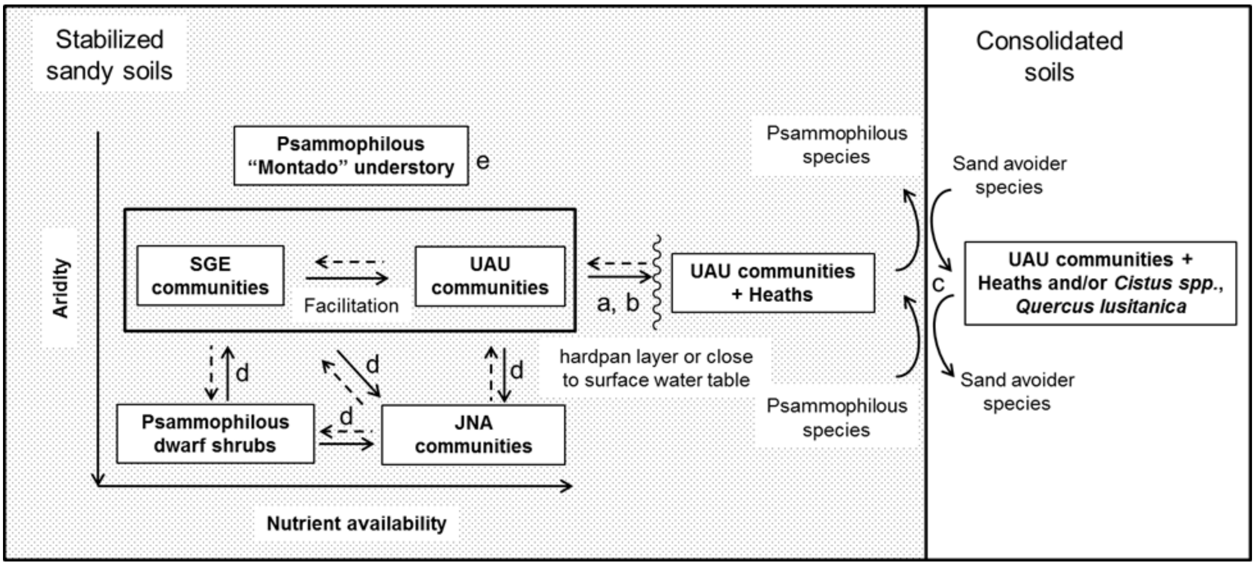



**Figure 2.5** Conceptual scheme of the xerophytic shrub community dynamics on stabilized dunes of the South-Western Iberian Peninsula. The relationships identified by our results, where scrub dynamics in Alentejo coast and Peninsula of Setúbal are mainly determined by soil organic matter and aridity, 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 (Olff *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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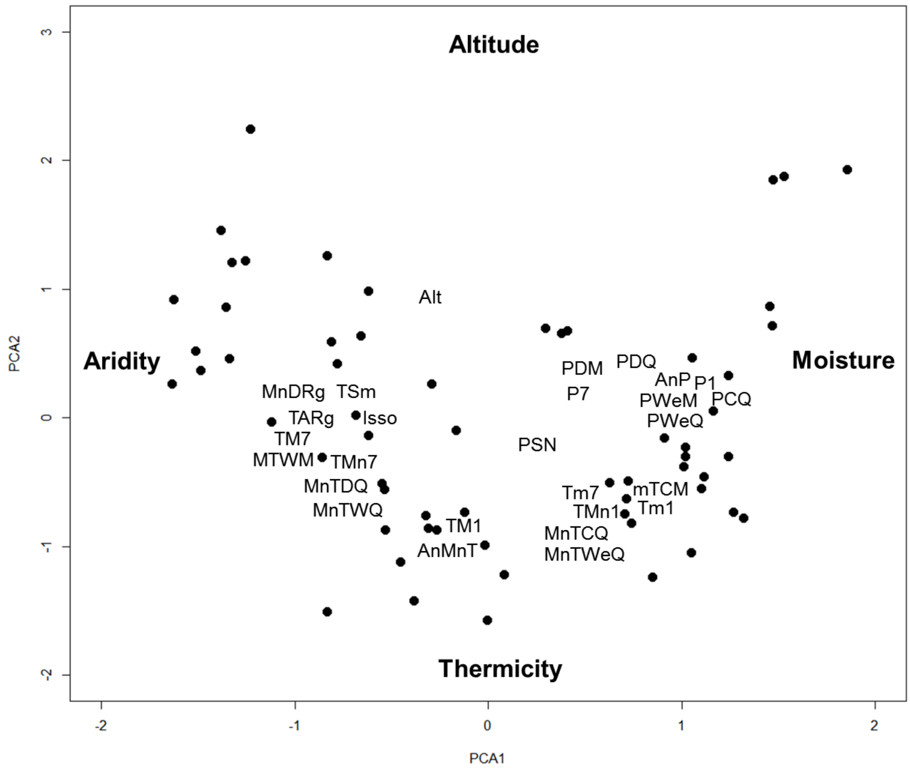
## Supporting Information




| 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. | TMn1-12 | 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.).

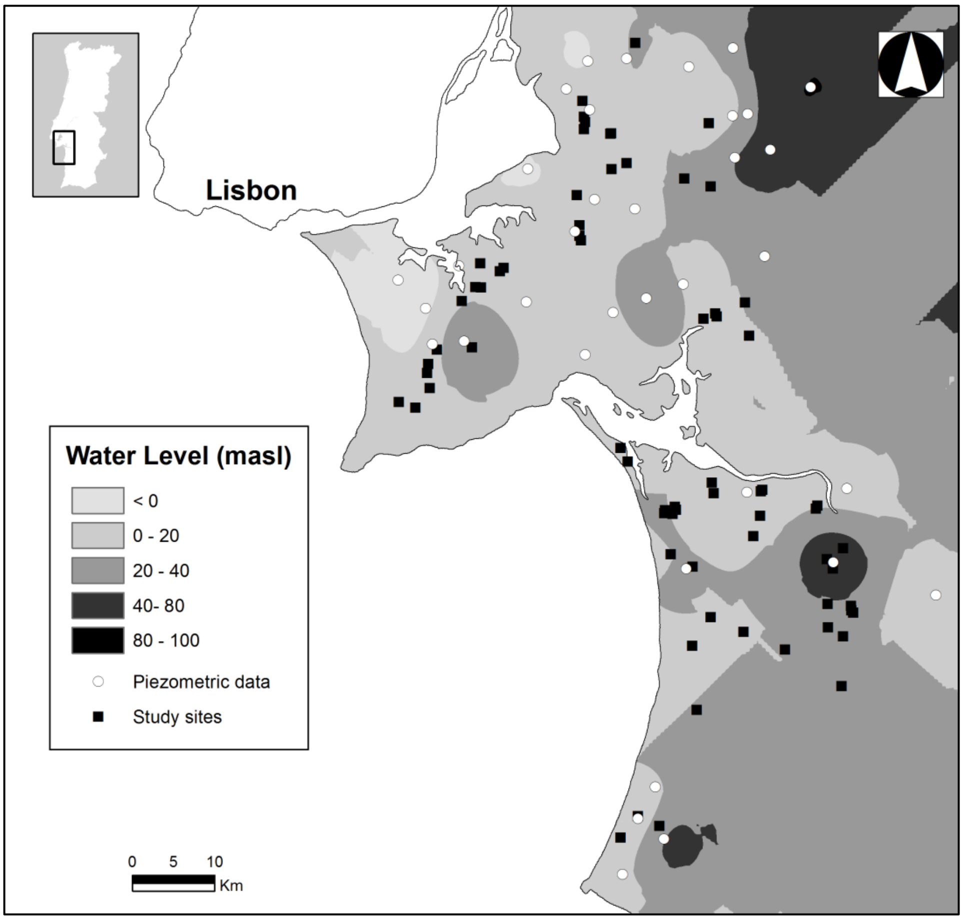



**Figure S2.2** Water table altitude, measured as meters above sea level. This GIS layer was constructed by kriging interpolation from the sites with piezometric data.

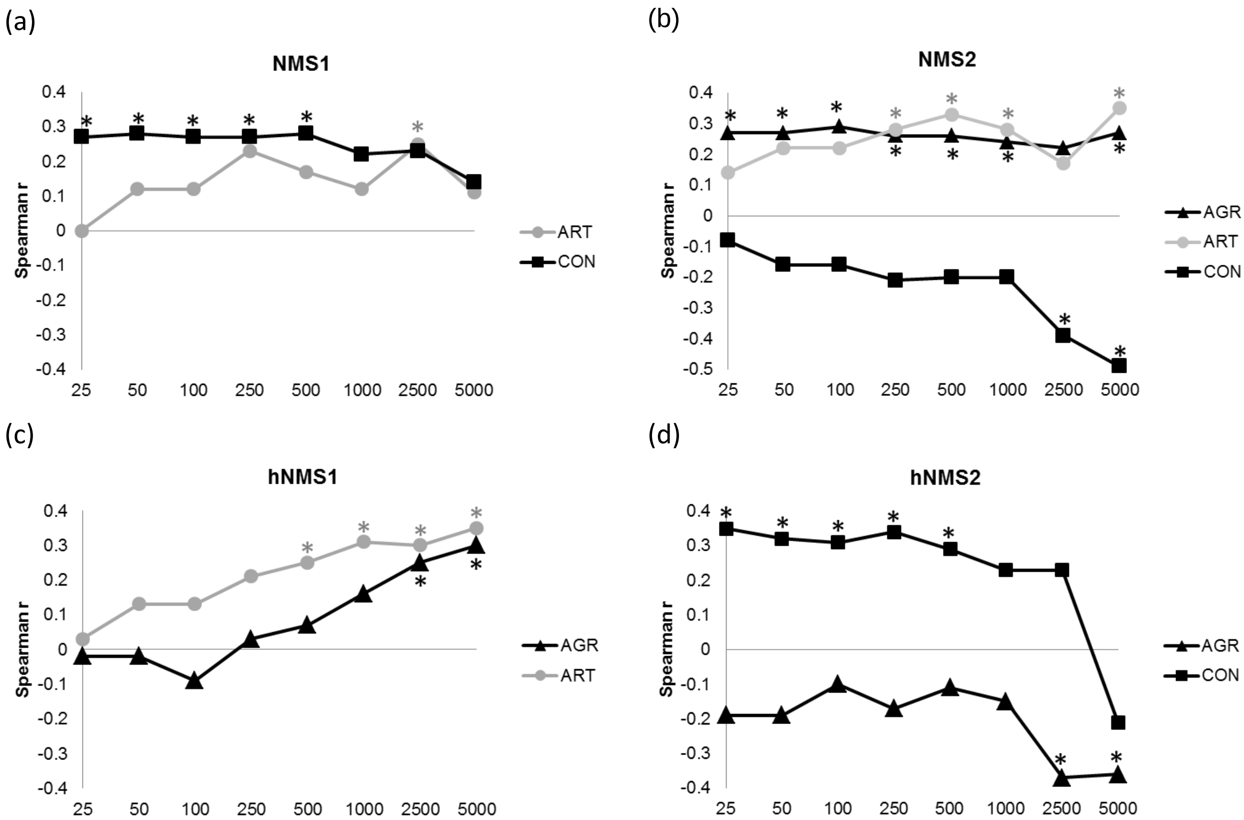



**Figure S2.3** Results of the Spearman R correlations between shrub and herbaceous NMS axes, (a) NMS1, (b) NMS2, (c) hNMS1 and (d) hNMS2), and land use cover along at different scales (calculated around each plot for concentric radii ranging from 25 to 5000m). Agricultural areas (AGR), Artificial areas (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 |
|---|---|
| *Ecological requirements* | |
| 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 |
| *Disturbance* | |
| 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 | *Eucalyptus* plantations | |
| Firebreaks | Firebreaks | |
| Grasslands | Grasslands | |
| Mixed forest | Mixed forest (coniferous and cork oaks) | |
| *Montado* | Cork oak *Montado*, open savannah-like landscape with cork oak (*Quercus suber*) | |
| 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 |

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

| **RELAPE Species** | |
|---|---|
| *Armeria pinifolia* (Brot.) Hoffmanns. & Link | *Euphorbia transtagana* Boiss. |
| *Armeria rouyana* Daveau | *Santolina impressa* Hoffmanns. & Link |
| *Cladina spp.* | *Thymus capitellatus* Hoffmanns. & Link |
| *Drosophyllum lusitanicum* (L.) Link | |
| **Invasive Species** | |
| *Acacia dealbata* Link | *Carpobrotus edulis* (L.) N.E.Br. |
| *Acacia longifolia* (Andrews) Willd. | *Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn. |
| *Acacia melanoxylon R.Br.* | *Hakea sericea* Schrad. |
| *Ailanthus altissima* (Mill.) Swingle | *Nicotiana glauca* Graham |
| *Arctotheca calendula* (L.) Levyns | *Opuntia ficus-indica* (L.) Miller |
| *Arundo donax* L. | *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** |
|---|---|
| **Silt** | -0.75*** |
| **Clay** | -0.84*** |

| | **SOM** |
|---|---|
| **Mg** | 0.76*** |
| **N** | 0.94*** |

| | **CON25** |
|---|---|
| **CON500** | -0.78*** |

| | **PC2** |
|---|---|
| **Elevation** | 0.83*** |
| **Water table level** | 0.73*** |

***p<0.001

# Chapter 3

## Dynamics of functional and trait structure during succession in xerophytic shrub communities on Mediterranean stabilized dunes

# 3 Dynamics of functional and trait structure during succession in xerophytic shrub communities on Mediterranean stabilized dunes

## 3.1 Abstract

Understanding the processes determining community assembly and dynamics is a central issue in ecology. The analysis of functional (trait) diversity measured as the variation of functional groups or traits can improve our understanding of these processes. We study functional diversity variations along successional dynamics of Mediterranean xerophytic scrubs occurring on stabilized dunes. More precisely, we assess the relationship between those variations and environmental factors, as well as the convergence or divergence in the trait structure of these communities. Our results confirm that successional community changes imply variations in species richness and both functional trait and functional group diversity, and involve a turnover in key functional traits. However, we found no significant converging or diverging factors explaining patterns in either species diversity or community assemblage. Our results support the existence of functional changes through two successions driven by nutrient availability and aridity, that were already described based on compositional changes, also allowing the identification of four main stages along these successions.

## 3.2 Introduction

Communities can be defined as groups of species that coexist in time and space. Understanding the processes leading to their assembly and composition is one of the central questions of ecology that has been subject to a long-term debate. Some early scholars understood communities as closed structures, where local interactions between species play a major role in determining community composition (Clements 1916). Others, in contrast, described communities as mere assemblages of co-occurring species where local habitat selection and regional scale processes act by filtering the existing species pool (Gleason 1917). 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 (Hortal *et al.* 2012). It follows that the maintenance of communities within a region depends not only on environmental conditions (Brooker *et al.* 2009), but also on the interactions between species and their capacity to disperse. These three types of processes restrict species coexistence and ultimately determine community composition (Götzenberger *et al.* 2012).

Functional diversity can be defined as the overall extent of functional differences among the species in an assemblage (Petchey and Gaston 2002; Lepš *et al.* 2006). Functional diversity approaches have proven useful to study community assembly processes (de Bello *et al.* 2012; Götzenberger *et al.* 2012; Mason *et al.* 2013). By studying the distribution of individuals and species within the functional space defined by the values of some of their (functional) traits, these approaches allow identifying eventual convergence or divergence in the structure of different communities. This can help determining the main drivers of the assembly of these communities; habitat filtering or competition result in functional convergence, whereas other biotic interactions and strong environmental gradients can lead to trait divergence (de Bello *et al.* 2012; Raevel *et al.* 2012).

Functional traits are thought to be good indicators of the processes governing both community assembly rules and ecosystem functioning (Violle *et al.* 2007; Suding *et al.* 2008; Freschet *et al.* 2011; Pérez-Harguindeguy *et al.* 2013). However, functional diversity can be also quantified through functional groups. Although several assumptions are needed to use them properly and some authors prevent from their use (see e.g. Petchey and Gaston 2006), functional groups have demonstrated their capacity to discriminate assembly processes (Zunzunegui *et al.* 2010; Gallego-Fernández and Martínez 2011; von Gillhaussen *et al.* 2014). Considering successions as the change of species over time (Walker and del Moral 2003), the analyses of the variations of either the main traits and functional groups along the successions can give insights about the species' environmental requirements and interactions that ultimately determine their capacity to establish and survive in any particular environment. Consequently, the concurrent analysis of variations in functional diversity and environmental variables along a given succession can provide an overview of the different drivers and processes acting throughout it.

The composition of xerophytic shrub communities inhabiting inland sand dunes in South-West Portugal mainly responds to local (i.e. nutrient availability, probably through facilitation and competition interactions) and regional (i.e. aridity) gradients, following both Clementsian and Gleasonian principles (Chozas *et al.* 2015). Therefore, they constitute an appropriate system for studying species interactions and environment–community co-variations based on functional traits. Here we evaluate the hypothesis that changes in the species composition of xerophytic shrub communities imply concurrent changes in functional structure, involving a turnover in functional traits and functional groups. We further analyse whether (and how) such trait turnover responds to environmental factors, as well as whether it follows a random pathway or not, thereby testing the hypothesis that functional trait diversity, particularly of those traits directly involved in the succession, is linked to the factors that drive successional dynamics (Mason *et al.* 2013).

## 3.3 Methods

### *Study system*

We study the shrub communities growing on the inland sandy soils of the Peninsula of Setúbal and the Alentejo shoreline, SW Portugal, located 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, and a varying altitude from sea level to 180 m a.s.l. (Figure 3.1). The climate is mild Mediterranean with ocean influence, characterized by a warm, dry summer period, and strong seasonal and inter-annual variability in precipitations. The vegetation of this region is mainly dominated by semi-natural Maritime Pine (*Pinus pinaster* Aiton) forests of variable density, ranging from open to dense formations with xerophytic shrub community understory (Neto *et al.* 2004).

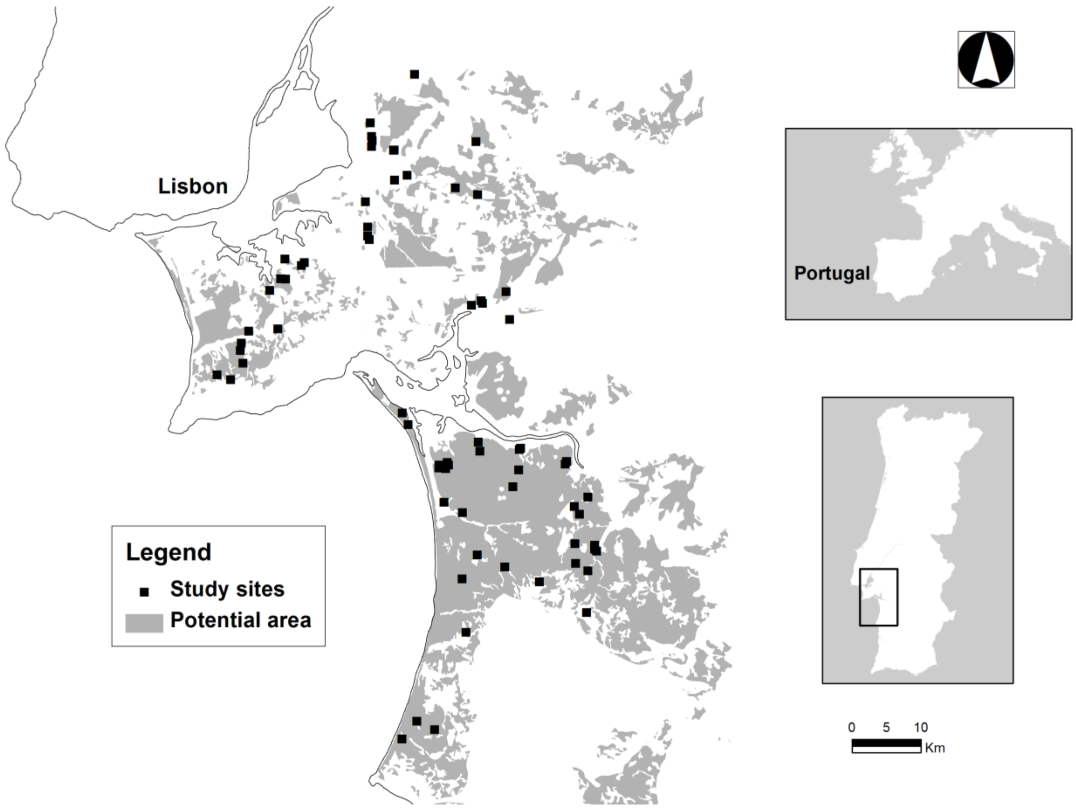



**Figure 3.1** Study sites and potential area of occurrence of inland sandy xerophytic shrub communities in Alentejo coast and Peninsula of Setúbal, SW Portugal.

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. These species are the main indicators of the compositional changes in these communities, and characterize three types of communities that were described in a previous work (Chozas *et al.* 2015). For simplicity herein we use the terms *J. navicularis*, *S. genistoides* or *U. australis* communities to refer to these three types of formations.

Seventy sites were randomly selected within the potential area of occurrence of sandy xerophytic shrub communities, defined by areas with forest and semi-natural land use cover on sandy soils (Figure 3.1). On each study site, one 10x10 m plot was placed at random and the cover of the eighteen more abundant shrub species (Table S3.1) in each plot was assessed. 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). Chozas *et al.* (2015) proposed that *J. navicularis*, *S. genistoides* and *U. australis* communities constitute the extremes of two plant successions identified by two axes of species composition, obtained in a non-metric multidimensional scaling ordination (NMS) – NMS1 and NMS2 (herein generically denominated “community NMS axes” for short). NMS1 defines a gradient between *S. genistoides* and *U. australis*-dominated communities, presenting a clear intermediate stage where both species co-dominate, and NMS2 between *S. genistoides* and *Juniperus navicularis*-dominated communities. In that study, we found that the gradient represented by NMS1 is driven by soil nutrient availability while aridity is the main driver acting on the gradient defined by NMS2 (Table 3.1; Chozas *et al.* 2015).

**Table 3.1** Xerophytic shrub communities' successions and main environmental gradients described for the first two axes of a three axis non-metric multidimensional scaling ordination of shrub cover (see Chozas *et al.* 2015 for details).

| Community axis | Succession | Gradients |
|---|---|---|
| NMS1 | *S. genistoides* to *U. australis* | Soil nutrient availability |
| NMS2 | *S. genistoides* to *J. navicularis* | Aridity |

### *Taxonomic and functional diversity*

We measured taxonomic diversity as species richness. We selected 26 traits to describe functional trait diversity (Tables S3.2 and S3.3). These traits are related to the adaptive responses of xerophytic shrubs to climate and disturbance and/or provide significant insights into competitive ability and defense against herbivory (Wright *et al.* 2006). Trait selection aimed to cover, as much as possible, the functional trade-offs enabling xerophytic shrub species to inhabit inland sand dunes. Trait nomenclature, collection and measurement protocols follow Cornelissen *et al.* (2003), Pérez-Harguindeguy *et al.* (2013) and Specht (1988) (Table S3.2).

Trait variations between communities were described by the community weighted mean of each trait (CWM), defined as the mean of values present in the community weighted by the relative abundance of the species bearing each value (Lavorel *et al.* 2007). We identified the traits showing succession-driven variations. First, multicollinearity among traits was handled by dropping collinear traits when their CWM values (Zuur *et al.* 2010) were correlated at |Spearman r|> 0.7 (Dormann *et al.* 2012). Then, we performed Spearman correlations between community NMS axes and CWM values of the remaining traits to assess which traits may be related with successional changes. Finally, we selected the subset of traits related with each succession through generalized additive models (GAMs), using a top-down approach for model selection (Marra *et al.* 2011) in the ''mgcv'' R software package (Wood 2006). The authors of this package suggest not to fit more than N/10 parameters (being N the number of sites) to avoid GAM overfitting. Therefore, we only included in the model the 6 covariates with higher |Spearman r| (Table S3.4). The main traits responding to the nutrient availability or aridity gradients were designated as nutrient or aridity-driven successional traits respectively (NDS and ADS traits for short).

Functional diversity was assessed using three functional indices described by Villéger *et al.* (2008), namely functional richness (Fric), functional evenness (Feve) and functional divergence (Fdiv), as well as Rao's quadratic entropy (Rao, Botta-Dukát 2005). These indices were selected with the aim of capturing the three dimensions of functional diversity described by Mason *et al.* (2005): Fric measures the volume of functional space occupied by the community, and Feve and Fdiv measure the regularity and divergence of the distribution of abundances in this volume, respectively. Rao combines functional richness and divergence, and was used due to its good performance in the analysis of community assembly patterns (Mouchet *et al.* 2010; Astor *et al.* 2014). Additionally, and aiming to assess how functional diversity of the succession-driven traits evolves along the successional process, the three functional indices were calculated using only those traits found to vary throughout the successions (i.e. NDS and ADS traits). Functional diversity indices and CWM were all estimated using the function "dbFD" of the "FD" R software package (Laliberté and Shipley 2013).

A NMS ordination of species based on the CWM of the 26 trait values was used to identify functional groups. The relationships between these functional groups and community gradients was analyzed through GAMs between functional groups and functional indices and community NMS axes, using the function "gam" of the ''mgcv'' R software package (Wood 2006).

### *Assessing functional responses throughout ecological gradients*

The response of functional groups and succession-driven traits to the community NMS axes was assessed through a graphic illustration of these relationships obtained by including vectors representing both environmental variables and functional groups and traits onto the community ordination using the “envfit” function of the “vegan” R software package. Squared correlation coefficient ($r^2$) was calculated to evaluate the strength of trait–NMS relationships.

### *Community assembly patterns*

The patterns in community structure, that would help identifying the community assembly processes that dominate succession dynamics, were assessed by comparing observed Rao values with those coming by null models (Gotelli and Graves 1996; Astor *et al.* 2014). To test for deviations from random assembly, we used a null model and we calculated the standard effect size (SES; Gotelli and McCabe 2002) as observed Rao minus mean of expected Rao divided by standard deviation of expected Rao. A significantly higher than expected observed Rao value indicates trait overdispersion, whereas a significantly lower Rao indicates trait underdispersion. Our null model assumed random assembly of species in each local community while keeping both local abundance and regional occurrence within the observed parameters. It was therefore obtained by randomizing communities (species x sites matrix) by reshuffling species identities among the sites while keeping the number of species per site and the total frequency of each species in the studied region. We compared the observed and expected values, evaluating the significance with one-sided permutation tests (with 1000 randomizations). Positive SES values indicate functional divergence (i.e. functional diversity is higher than expected by chance) and negative values indicate functional convergence (i.e. functional diversity is lower than expected by chance) (Kembel 2009). In one-tailed null model tests, |SES values|> 1.55 indicate significant ($\alpha = 0.05$) assembly pattern. These metrics were first calculated using all studied traits, and then using only NDS or ADS traits, in an attempt to detect the presence of convergence or divergence processes acting differently on the overall trait diversity or only on succession-driven trait diversity. All analyses were developed in R environment using the “Picante” (Kembel *et al.* 2010), “vegan” (Oksanen *et al.* 2013), “FD” (Laliberté and Shipley 2013), “ade4” (Dray and Dufour 2007) and “MatrixStats” (Bengtsson *et al.* 2015) software packages.

## 3.4 Results

### *Variations in taxonomic and functional diversity*

Both taxonomic richness and functional diversity (Figure 3.2) covariate along the successional gradients in xerophytic shrub community composition. All indices except functional evenness (Figure S3.1) showed significant relationships with, at least, one community NMS axes. Species richness increased along the replacement of *S. genistoides* communities by *U. australis* ones (NMS1), presenting maximum values in the transitional stage where species of both communities are present, and returning to lower values in *U. australis* communities (Figure 3.2a). On the contrary, species richness presented a constant and linear increase over *S. genistoides* to *J. navicularis* succession (NMS2; Figure 3.2b). When calculated with all the traits, functional richness (Fric) gradually increased along the replacement of *S. genistoides* by *U. australis* communities, tending to stabilize at the end of this succession (Figure 3.2c). However, when calculated only with the nutrient-driven successional (NDS) traits, Fric increased until the intermediate stage of the succession, decreasing significantly afterwards (Figure 3.2e). Additionally, functional divergence (Fdiv) slightly increased along *S. genistoides* to *U. australis* communities’ gradient when calculated with all studied traits (Figure 3.2g) but decreased when calculated only with NDS traits (Figure 3.2i).

This contrasts with the *S. genistoides* to *J. navicularis* gradient, where Fric decreased gradually to then rise considerably when calculated with all studied traits (Figure 3.2d). When calculated with ADS traits, Fric presented a moderate and linear increase (Figure 3.2f). Furthermore, Fdiv showed a significant decrease from *S. genistoides* to *J. navicularis* communities when calculated with all the studied traits (Figure 3.2h). Fdiv did not present significant differences between *S. genistoides* and *J. navicularis* communities when calculated with ADS traits (Figure 3.2j). Functional evenness did not show significant differences between communities either (Figure S3.1).

NMS ordination of species based on CWM trait values identified five main plant functional groups (Figure S3.2), analogous to those described by Valladares *et al.* (2004) for Mediterranean woody vegetation according to water-use strategies, namely: drought avoiders, shrubby conifers, evergreen sclerophyllous, heaths and legumes with photosynthetic stems. GAMs between functional groups and communities' NMS axes showed significant relationships between the cover of each functional group and successional gradients (Figure 3.3). The fit between heaths and *S. genistoides* to *U. australis* communities' gradient (NMS1) clearly separated both main stages of this succession, while the fit of drought avoiders delineated the intermediate stage between them. In *S. genistoides* to *J. navicularis* communities' gradient (NMS2), the fits of legumes with photosynthetic stems, evergreen sclerophyllous and shrubby conifers clearly defined the gradient between both types of communities.

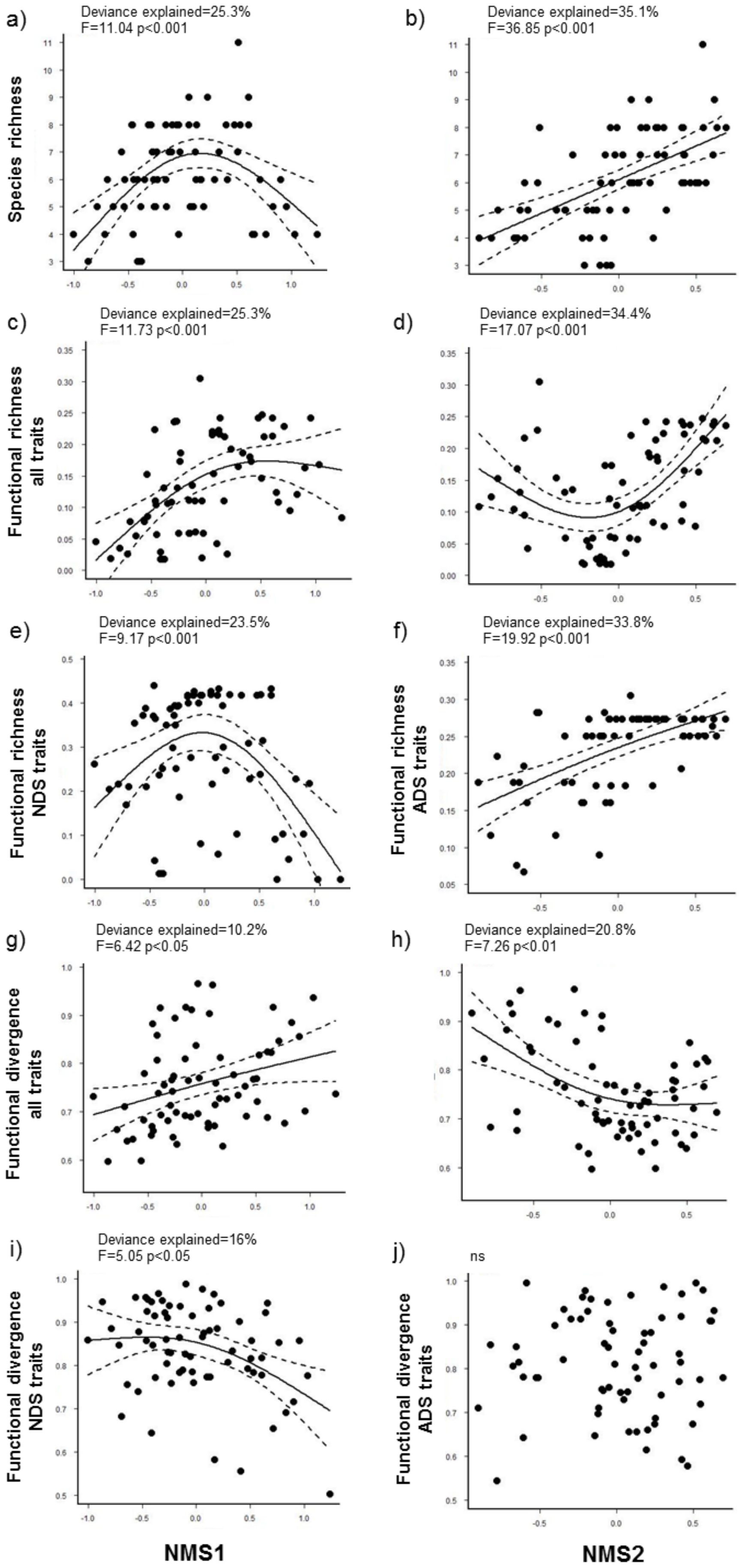


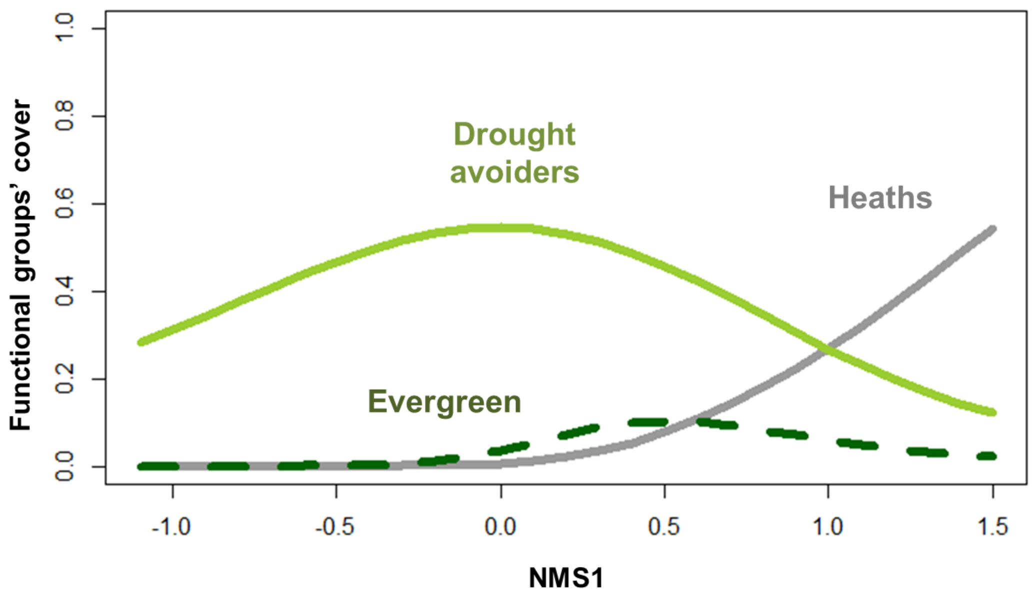

**Figure 3.2** Relationships between the *S. genistoides – U. australis* and the *S. genistoides – J. navicularis* successions, represented by the first and the second axes of the ordination based on scrub cover (NMS1 and NMS2 respectively), and species richness a) and b), and functional richness and functional divergence calculated with all studied traits c), d), g) and h), and with the traits resulting of GAM model selection e) and i) (NDS traits) and f and j) (ADS traits). Solid and dashed lines represent the main trend and 95 % confidence intervals of a Generalized Additive Model (GAM). See text for details.

GAM selection model results (Table S3.5) indicated the combination of height (Height), green photosynthetic organ colour (Green) and chamaephyte life form (Chamaephyte) as the most parsimonious and likely model explaining the trait variation along the sequence between *S. genistoides* and *U. australis*-dominated communities (NMS1), corresponding to the nutrient availability gradient. Similarly, the combination of spiniscence (Spiniscence), evergreen leaf life span (Evergreen), climber growth form (Climber) and presence of entire margin leaves (Entire) was the most parsimonious model explaining trait variation along the succession between *S. genistoides* and *J. navicularis* communities (NMS2), corresponding to the aridity gradient.

### *Assessing functional responses throughout ecological gradients*

Spearman correlations r (Table 3.2), vector fitting (Figure 3.4) and squared correlation coefficients $r^2$ (Table S3.6) between functional traits, functional groups, environmental variables and community NMS axes highlighted the existence of co-variations between climatic and edaphic variables and traits and functional groups along both successional gradients. Green photosynthetic organ colour (Green), height (Height), entire margin leaves (Entire) and soil organic matter are positively and significantly correlated with the nutrient availability gradient, while the chamaephyte life form and aridity are negatively correlated. Heaths, evergreen sclerophyllous species and shrubby conifers are equally positively and significantly correlated with this gradient. Likewise, aridity is positively and significantly correlated with the *S. genistoides* to *J. navicularis* gradient, characterised by a decrease in the cover of spiny legumes and climbing species and an increase of sclerophyllous and conifers functional groups. Additionally, an increase of entire margin leaf (Entire) and evergreen leaf life spam (Evergreen) traits and chamaephyte life form (Chamaephyte) is registered along the sequence (Table 3.2 and Figure 3.3). Finally, the number of sites departing significantly from the null expectations was residual (Figure S3.3), so no significant trend for either under or overdispersion of traits was detected.

a)




b)

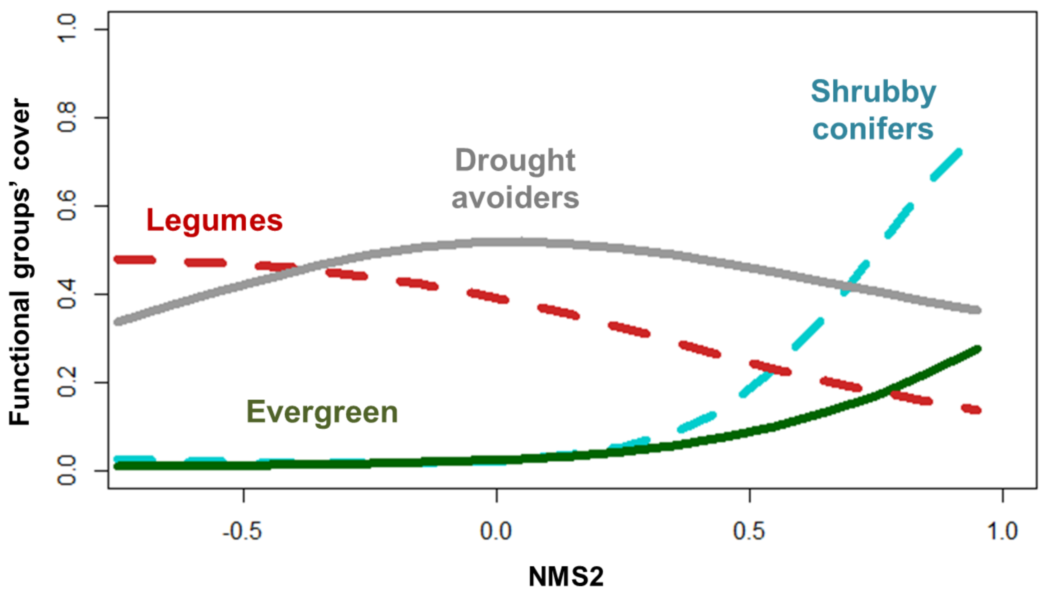



**Figure 3.3** Relationships between the *S. genistoides* to *U. australis* and *S. genistoides* to *J. navicularis*-dominated communities' successions, represented by the a) first and b) second axis of the ordination based on scrub cover (NMS1 and NMS2, respectively) and functional groups cover, as identified by Generalized Additive Models of the binomial family. Percentages of variance explained a) 53.4% (heaths), 33.4% (evergreen) and 18.2% (drought avoiders) and b) 35.8% (conifers), 26.5% (legumes) and 19.9% (evergreen) and 8.46% (drought avoiders). Cover values are square root transformed. All p values <0.001.

**Table 3.2** Spearman correlation (r) between variables (succession-driven traits, environmental variables and functional groups) vectors and NMS ordination axes.

| | **Nutrient availability gradient (NMS1)** | **Aridity gradient (NMS2)** |
|---|---|---|
| **Chamaephyte** | -0.38** | 0.31** |
| **Climber** | ns | -0.59*** |
| **Entire** | 0.28* | 0.36** |
| **Evergreen** | ns | 0.66*** |
| **Green** | 0.71*** | ns |
| **Height** | 0.75*** | ns |
| **Spiniscence** | ns | -0.75*** |
| **Aridity** | -0.33* | 0.59*** |
| **O. matter** | 0.65*** | ns |
| **Heaths** | 0.55*** | ns |
| **Evergreen** | 0.48*** | 0.46*** |
| **Legumes** | ns | -0.52*** |
| **Conifers** | 0.25* | 0.51*** |

## 3.5 Discussion

Our results confirm the existence of two successions driven by nutrient availability and aridity in the studied xerophytic shrub communities, previously reported by Chozas *et al.* (2015). But our analyses also show that these successional community changes involve variations in key functional traits, and result in variations in species richness and functional trait diversity. Differences in trait variation and functional trait diversity allowed identifying four main community stages along two different successions. The succession between *Stauracanthus genistoides* and *Ulex australis* communities is characterised by an increase of functional divergence (Fdiv) driven by nutrient availability. It involves a transition from species-poor *S. genistoides* communities, a transitional stage with richer communities where drought avoider species are preponderant, and a late successional stage dominated by *U. australis* with, again, lower richness values. Further, in areas with progressively higher aridity, *S. genistoides* communities are substituted by richer communities composed of species with increasing functional richness (Fric), dominated by *Juniperus navicularis*.

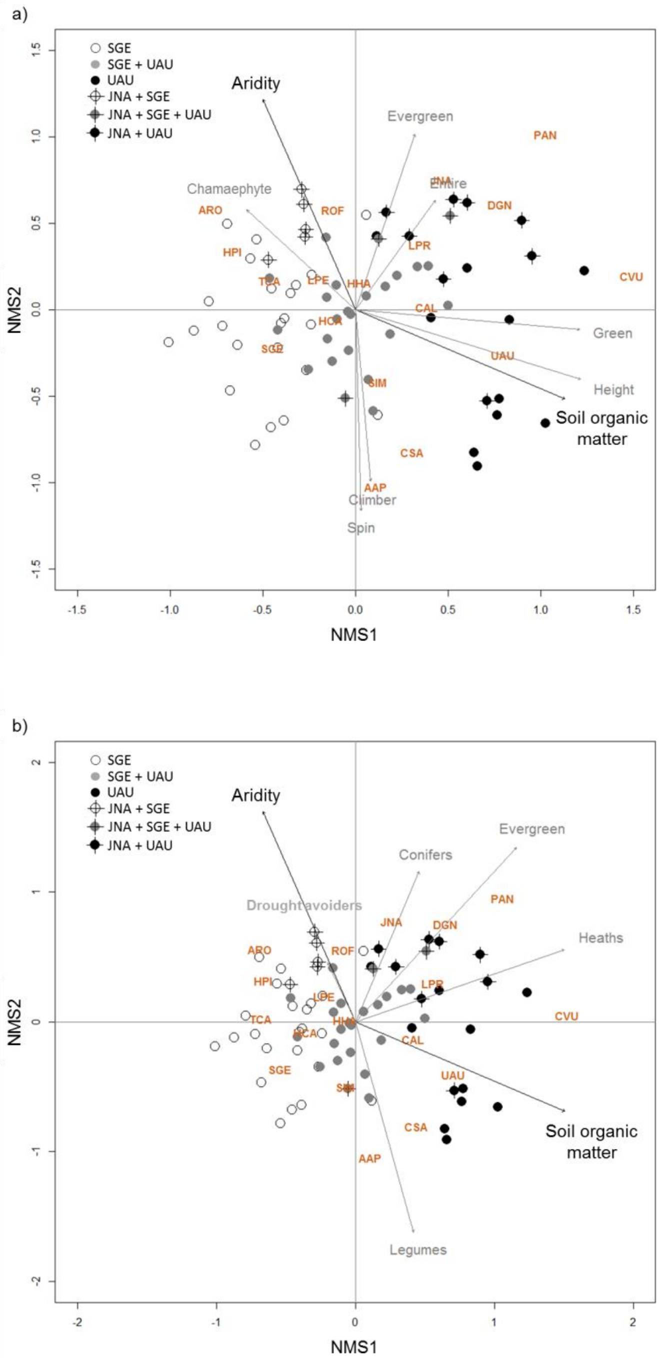



**Figure 3.4** Vector fitting of the main environmental variables driving xerophytic shrub communities (soil organic matter and aridity) and a) functional groups and b) traits resulting of GAM model selection (NDS and ADS traits) onto Axes 1 (NMS1) and 2 (NMS2) of the 3-dimensional nonmetric multidimensional scaling ordinations of study sites based on shrub cover. Codes of species (three capital letters) and traits according to tables S3.1 and S3.2. 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. Plus symbol represent study sites with *J. navicularis* (JNA).

Our data also shows that certain traits covariate with environmental variables along both successions. Such trait selection clearly responds to the abiotic changes occurring through the succession itself, namely the increase in nutrient availability and changes in aridity. The succession between *S. genistoides* and *U. australis* communities is characterized by increases in plant height and the occurrence of species with green photosynthetic organs, while the occurrence of chamaephytes decreases. In *U. australis* communities, the input of soil organic matter resulting from the facilitation processes performed by the species of the *S. genistoides* communities, together with increases in humidity, enable the occurrence of more ecologically-demanding and taller plants (micro and nanophanerophytes rather than chamaephytes), as is known for light-limited successional stages (e.g. Tilman 1985). These changes also reduce the need and advantage of possessing glaucous protection structures (trichomes) in leaves and stems, that increase reflectance (avoiding overheating) and water use efficiency, while simultaneously reducing photosynthetic performance (Johnson 1975). In fact, scrubs analogous to *S. genistoides* and *U. australis* communities covering stabilized dunes in Doñana National Park are traditionally named *monte blanco* (white scrub) and *monte negro* (black scrub) respectively (Muñoz-Reinoso 2009), due to the significant difference in reflectance between the dominant species that compose them. Similarly, the succession between *S. genistoides* and *J. navicularis* communities is characterised by the replacement of spiny shrubs by entire-margin-leaved evergreen species. Entire-margin-leaved evergreen shrubs are dominant in Mediterranean mature scrubs (Díaz-Barradas *et al.* 1999) substituting the less demanding and more disturbance tolerant spiny shrubs.

*S. genistoides* communities are characterised by the presence of pioneer species and the lack of the more ecologically demanding *taxa*, such as heaths, shrubby conifers and evergreen sclerophyllous (Figure 3.3). This ultimately determines their low values of both taxonomical and functional richness. Fdiv values of the overall traits point out to a community with species that are functionally similar, shaped by early-stage environmental conditions, mainly high radiation and low nutrient availability, and low rates of species interactions, following the resource-ratio hypothesis (Tilman 1985). Nevertheless, Fdiv of nutrient-driven successional (NDS) traits is higher in *S. genistoides* communities than on the following stages, pointing out to a higher variability in the combination of height, photosynthetic organ colour and life forms in the most abundant species of this initial stage.

The transitional stage between *S. genistoides* to *U. australis* is dominated by drought avoiders while maintaining species from both communities, resulting in the highest values of both taxonomic and functional richness of the succession. In contrast, *U. australis* communities show species richness values similar to those of *S. genistoides*. Although is commonly accepted that vegetation succession progress is usually accompanied by increases in species richness (Díaz and Cabido 2001; Grime 2001), decreasing species richness has been already described for communities dominated by strong competitors (Glenn-Lewin *et al.* 1992; Prach *et al.* 2014). This may explain the hump-shaped richness pattern found in the succession between *S. genistoides* and *U. australis* communities, for the dense shrub canopy of the later stage ultimately causes competitive exclusion of chamaephytes and, consequently, lower species richness (Lepš 2005). Interestingly, the increase in functional richness stabilises at this later stage when calculated with all the traits, but drops down when calculated only with NDS traits, evidencing a strong selection in these succession-related traits. On the one hand, the improvement of environmental conditions by facilitation, mainly through the incorporation of organic matter into the soil and nursing (Chozas *et al.* 2015), enlarges niche space allowing the incorporation of new and more demanding species into the community and, ultimately, increasing Fric. On the other hand, successional changes also allow the establishment, development and finally the dominance of the community by *U. australis*. This species ultimately reduced the functional richness of NDS traits by favouring the occurrence of species with specific values of those traits, namely high plants, life forms other than chamaephytes and reducing the advantage of possessing glaucous structures.

*J. navicularis* communities are characterised by the dominance of shrubby conifers and evergreen sclerophyllous species, and the significant decrease of legumes with photosynthetic stems. Species and functional richness clearly respond to the expectations that later successional stages are richer than early stages. The initial decrease of Fric of all traits in this successional path seem to reflect the seral phase when legumes are already decreasing but evergreen sclerophyllous and shrubby conifers are still missing. The high values of functional divergence, higher than in *S. genistoides* communities when calculated with all the traits (and showing no significant difference when using only ADS traits), may point to low levels of competition, probably due the effect of the higher aridity that results in habitat filtering processes through the selection of no spiny species, with evergreen leaf life span, no climbers and entire leaf margin.

Despite the clear structuration of functional diversity and trait variations along the successional gradients, our null-model analyses did not detect communities where either convergent or divergent processes result in significant differences in functional diversity. From a simplistic perspective, these results would suggest that plant species with different traits are randomly distributed. Nevertheless, we do find significant trait and functional group variations along the succession-driven compositional gradients described for these communities. Weiher and Keddy (1995) warned that the selection of traits included in the analyses can dilute a pattern due to mixing over- and under-dispersed traits. This could be the issue in the “all traits” analysis. However, it does not seem to be the case of the successional traits, precisely because the fact of being selected presupposes an analogous response to factors and processes conducting successional dynamics. Here it is important to take into account that *J. navicularis*, *S. genistoides* and *U. australis* communities are all the result of a strong filtering from the regional species pool, that selects species (with certain trait values) able to thrive on sandy soils, characterized by the porous nature of sands and little or no organic matter content. We propose that this strong effect that characterizes these xerophytic scrubs reduces trait variability to a point that masks the effect of the additional successional drivers, namely soil organic matter content and aridity. Consequently, the resulting homogenization of both species and traits ultimately conditions the capacity of identifying clear community assembly patterns. These patterns could perhaps be identified through the use of traits with a higher discriminating capacity, probably physiological traits, that are mainly connected to the nutrient uptake efficiency and drought surveillance (i.e. directly linked to the defined successional-driven factors), such as those used by Díaz-Barradas *et al.* (1999) to discriminate between xerophytic and hydrophytic communities in stabilized dunes of Doñana National Park (Spain). However, the small differences in soil humidity and organic matter in the studied communities, and their poor diversity, may impede finding significant patterns of trait selection even with these more specific traits.

Nonetheless, the combined study of trait variation, functional groups and functional trait diversity indices has allowed us to make an in-depth characterization of the ecological transitions involved in the successional and assembly processes of xerophytic shrub dune communities in South-West Portugal. These analyses allowed us to identify not only an intermediate stage located between early and late successional communities, but also to infer the existence of facilitation and competition processes linking the progressive increase of nutrient availability with, respectively, higher photosynthetic efficiency and taller plant height.

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## Supporting Information

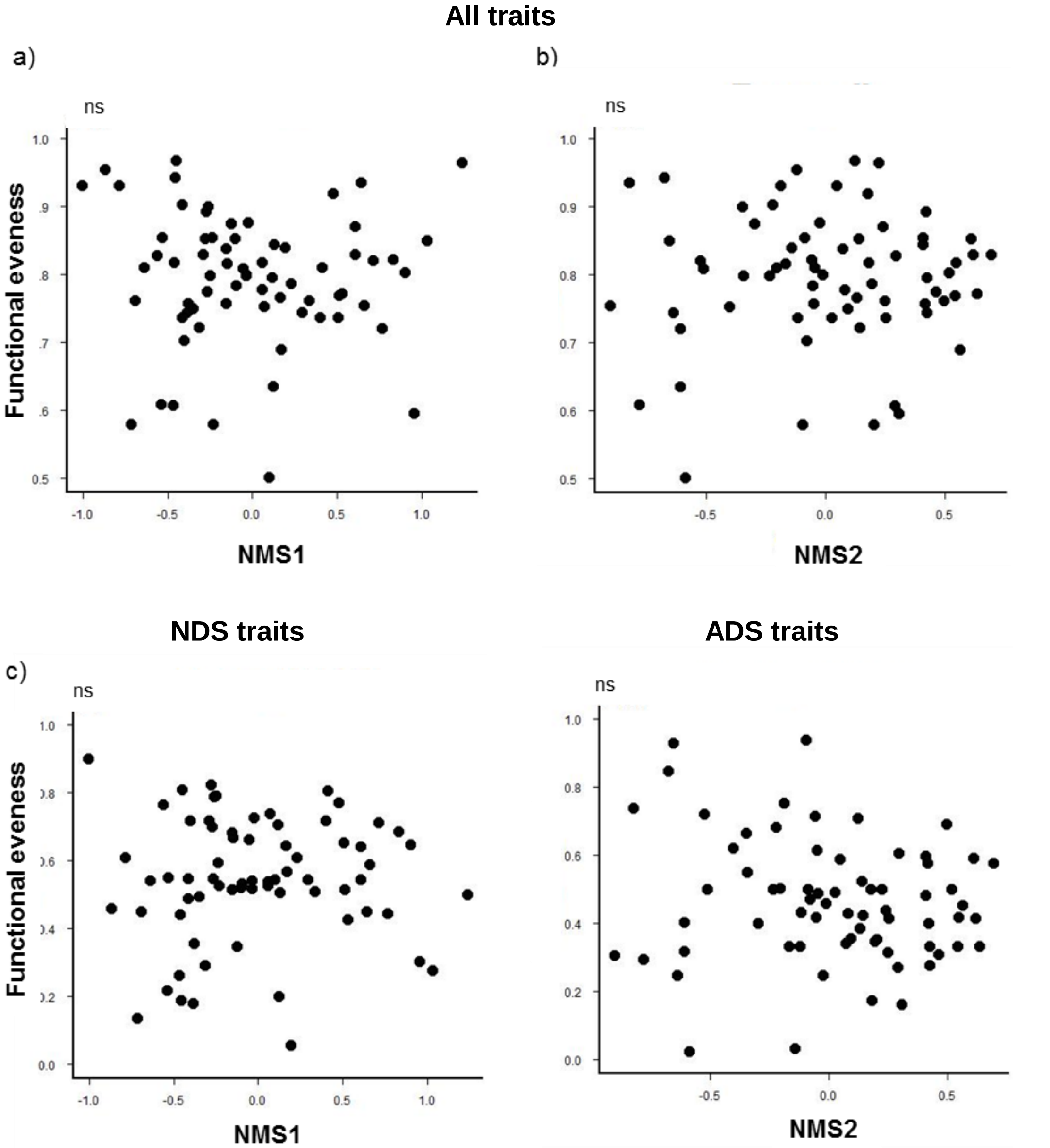



**Figure S3.1** Relationship between the first and second axes of the ordination based on scrub cover (NMS1 and NMS2) and functional eveness calculated with a) and b) all studied traits, c) the nutrient-driven successional (NDS) traits, and d) aridity-driven succession (ADS) traits.

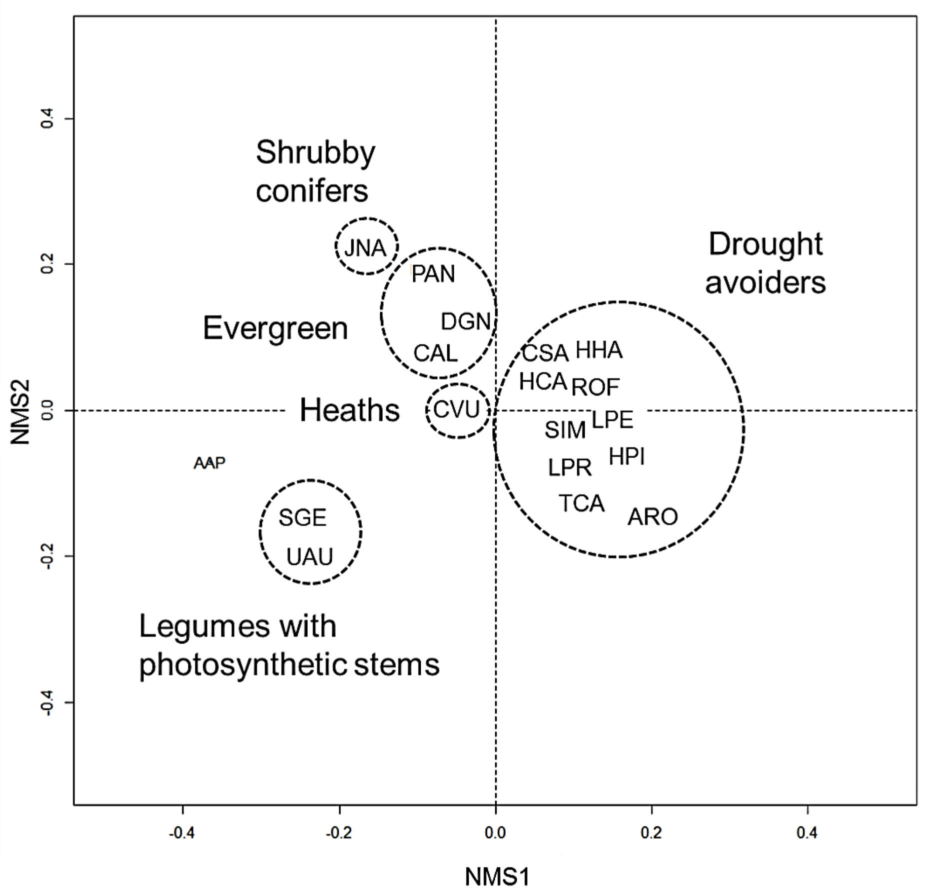



**Figure S3.2** Functional groups identified by a NMS ordination based on the CWM trait values of the 18 more abundant species identified. Codes of species (three capital letters) according to Table S.3.1.

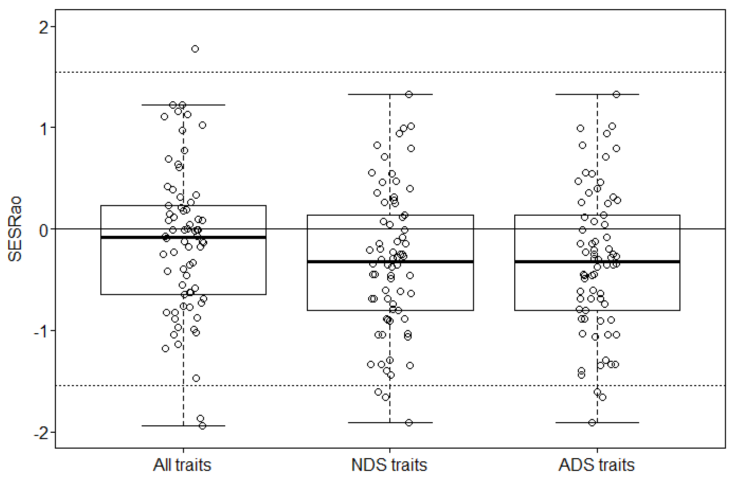



**Figure S3.3** Standard effect sizes of Rao for all, NDS and ADS (nutrient or aridity-driven successional) traits from the assembly test. SES values < 1.55 indicate significant underdispersion assembly pattern and >1.55 significant overdispersion.

**Table S3.1** Species names of the surveyed shrubs. Codes used in figures 3.6 and S3.2 and in Table S3.3

| Shrub species | Code | Shrub species | Code |
|---|---|---|---|
| *Armeria rouyana* Daveau | ARO | *Juniperus navicularis* Gand. | JNA |
| *Asparagus aphyllus* L. | AAP | *Lavandula pedunculata* (Mill.) Cav. subsp. *pedunculata* | LPE |
| *Calluna vulgaris* (L.) Hull | CVU | *Lithodora prostrata* (Loisel.) Griseb. subsp. *lusitanica* (Samp.) Valdés | LPR |
| *Cistus salviifolius* L. | CSA | *Phillyrea angustifolia* L. | PAN |
| *Corema album (L.)* D.Don | CAL | *Rosmarinus officinalis* L. | ROF |
| *Daphne gnidium* L. | DGN | *Santolina impressa* Hoffmanns. & Link | SIM |
| *Halimium calycinum* (L.) K.Koch | HCA | *Stauracanthus genistoides* (Brot.) Samp. | SGE |
| *Halimium halimifolium* (L.) Willk. | HHA | *Thymus capitellatus* Hoffmanns. & Link | TCA |
| *Helichrysum italicum* (Roth) G. Don subsp. *picardi* (Boiss. & Reut.) Franco | HPI | *Ulex australis* Clemente subsp. *welwitschianus (*Planch.) Esp.Santo, Cubas, Lousã, C.Pardo & J.C.C | UAU |

**Table S3.2** Set of traits selected to characterize functional trait diversity in xerophytic shrub communities. In bold succession-driven traits selected by model selection (see main text for details). Trait association refers to established associations of traits with environmental gradients, climate and disturbance, competitive ability and defense (for more details see Wright *et al.* 2006).

| Trait | Code | Description | Association of trait with | Classes | Font |
|---|---|---|---|---|---|
| Assimilating organ | Assi | | Climate and Competitive ability | Stems; Leaves | Field observation |
| Clonality | Clon | | Climate, Disturbance and Competitive ability | Y/N | Bibliography (1, 2, 3) and field observation |
| Crown area | Crow | Average plant crown area | Disturbance and Competitive ability | Continuous values | Field work |
| Fruit dehiscence | Fdeh | | Disturbance | Dry indehiscent; Dry dehiscent; Fleshy indehiscent | Bibliography (1, 2, 3) and field observation |
| Growth form | Grow | | Climate, Disturbance, Competitive ability and Defense | **Climber**; **Tussock**; Erect leafy stem | Bibliography (1, 2, 3) and field observation |
| Height | **Height** | Average plant height | Climate, Disturbance, Competitive ability and Defense | Continuous values | Field work |
| Leaf consistency | Lcon | | Climate, Disturbance, Competitive ability and Defense | Aphyllous; **Sclerophyllous**; **Semi-sclerophyllous** | Bibliography (1, 2, 3) and field observation |
| Leaf life span | Span | | Climate, Disturbance, Competitive ability and Defense | Aphyllous; **Evergreen**; Semidecidous | Bibliography (1, 2, 3) and field observation |
| Leaf margin | Lmar | | Climate, Disturbance, Competitive ability and Defense | Aphyllous; Revolute; **Entire** | Bibliography (1, 2, 3) and field observation |
| Leaf size cm | Lsiz | Average leaf size | Climate, Competitive ability and Defense | Continuous values | Bibliography (1, 2, 3) and field work |
| Leaf tomentosity | Ltom | | Climate and Defense | Non hairy; Upper; Both; Low | Bibliography (1, 2, 3) and field observation |
| Life form (Renewal buds ) | Rbud | | Climate, Disturbance, Competitive ability and Defense | Microphanerophyte; Nanophanerophyte; **Chamaephyte** | Bibliography (1, 2, 3) |
| Photosynthetic organ colour | Pcol | | Climate and Competitive ability | **Green**/Glaucous | Field observation |
| Pollination mode | Poli | | Climate, Disturbance and Competitive ability | Entomophyllous; Anemophyllous | Bibliography (5) and field observation |

| | | | | | |
|---|---|---|---|---|---|
| Regeneration: | | Regeneration after major disturbance | | | Bibliography (4, 6, 7, 8) and field observation |
| Post-fire seedling | Fsee | Fire | Disturbance | Y/N | |
| Resprouter | Resprouter | Others | Disturbance | Y/N | |
| Seeder | Seeder | Others | Disturbance | Y/N | |
| Spinescence | **Spiniscence** | | Climate, Competitive ability and Defense | Y/N | Field observation |
| Seed weigh (g 1000 seeds) | Swei | | Disturbance, Competitive ability and Defense | | Seed Bank A.L. Belo Correia |
| Trophic type | Ttyp | | Competitive ability | Autotrophic; Nitrogen fixer | Bibliography (1, 2, 3) and field observation |
| %C | C | Average leaf carbon concentration | Climate, Disturbance, Competitive ability and Defense | Continuous values | Following Cornelissen *et al.* 2003, 10 leaves/top 2 cm young twigs of 5 individuals of the shrubs (Table S3.3) present in selected plots (n=31) were collected. Isotopes and C and N content in leaves were determined at the SIIAF(9) |
| %N | N | Average leaf nitrogen concentration | Climate, Disturbance, Competitive ability and Defense | Continuous values | |
| C/N | **C/N** | Average leaf Carbon/Nitrogen ratio | Climate, Disturbance, Competitive ability and Defense | Continuous values | |
| d13C | d13C | Average leaf carbon isotope ratio | Climate, Disturbance, Competitive ability and Defense | Continuous values | |
| d15N | d15N | Average leaf nitrogen isotope ratio | Climate, Disturbance, Competitive ability and Defense | Continuous values | |
| SLA (mm2/mg) | SLA | Average specific leaf area | Climate, Competitive ability and Defense | Continuous values | |

1 Castroviejo S (1986-2012)
2 Flora-On: Flora de Portugal Interactiva. (2014
3 Franco JA (1971-1984)
4 Guerrero-Campo *et al.* 2006
5 Herrera 1987
6 Luna *et al.* 2007
7 Ojeda *et al.* 2010
8 Santos *et al.* 2010
9 SIIAF: Stable Isotopes and Instrumental Analysis, CE3C, Faculty of Science of University of Lisbon

**Table S3.3** Mean trait values of studied species.

| | Assi | Clon | Crow | Fdeh | Grow | Heig | Lcon | Lmar | Span | Lsiz | Ltom | Pcol | Rbud |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **AAP** | Stems | Y | 0.05 | Fleshy | Climber | 71.88 | Aphyllous | Aphyllous | Aphyllous | 0.00 | Nonhairy | Green | Nano |
| **ARO** | Leaves | N | 0.02 | Dryund | Tussock | 15.51 | Scler | Revolute | Evergreen | 1.00 | Nonhairy | Glaucous | Cham |
| **CAL** | Leaves | N | 0.59 | Fleshy | Erectleafy | 53.06 | Scler | Revolute | Evergreen | 0.11 | Nonhairy | Green | Nano |
| **CSA** | Leaves | N | 0.52 | Drydeh | Erectleafy | 56.10 | Semscler | Entire | Semidec | 1.76 | Upper | Green | Nano |
| **CVU** | Leaves | N | 0.57 | Dryund | Erectleafy | 82.51 | Scler | Entire | Evergreen | 0.06 | Nonhairy | Green | Nano |
| **DGN** | Leaves | N | 0.46 | Fleshy | Erectleafy | 102.78 | Semscler | Entire | Evergreen | 1.25 | Nonhairy | Green | Nano |
| **HCA** | Leaves | N | 0.23 | Drydeh | Erectleafy | 39.47 | Semscler | Revolute | Semidec | 0.84 | Low | Green | Nano |
| **HHA** | Leaves | N | 1.26 | Drydeh | Erectleafy | 90.52 | Semscler | Entire | Semidec | 3.08 | Upper | Glaucous | Nano |
| **HPI** | Leaves | N | 0.18 | Dryund | Erectleafy | 39.13 | Semscler | Revolute | Evergreen | 0.49 | Upper | Glaucous | Cham |
| **JNA** | Leaves | Y | 0.38 | Fleshy | Erectleafy | 73.55 | Scler | Entire | Evergreen | 0.10 | Nonhairy | Green | Micro |
| **LPE** | Leaves | N | 0.20 | Dryund | Erectleafy | 50.39 | Semscler | Revolute | Semidec | 1.07 | Upper | Glaucous | Cham |
| **LPR** | Leaves | N | 0.06 | Dryund | Erectleafy | 38.03 | Semscler | Revolute | Evergreen | 2.10 | Both | Green | Cham |
| **PAN** | Leaves | N | 0.40 | Fleshy | Erectleafy | 85.18 | Scler | Entire | Evergreen | 4.05 | Nonhairy | Green | Nano |
| **ROF** | Leaves | N | 1.21 | Dryund | Erectleafy | 85.75 | Semscler | Revolute | Semidec | 0.51 | Low | Both | Nano |
| **SGE** | Stems | N | 0.53 | Drydeh | Erectleafy | 76.76 | Aphyllous | Aphyllous | Aphyllous | 0.00 | Nonhairy | Glaucous | Nano |
| **SIM** | Leaves | N | 1.21 | Dryund | Erectleafy | 71.83 | Semscler | Revolute | Evergreen | 0.30 | Both | Glaucous | Cham |
| **TCA** | Leaves | N | 0.15 | Dryund | Erectleafy | 37.23 | Semscler | Entire | Evergreen | 0.07 | Low | Green | Cham |
| **UAU** | Stems | N | 1.12 | Drydeh | Erectleafy | 99.72 | Aphyllous | Aphyllous | Aphyllous | 0.00 | Both | Green | Nano |

| | Poli | Fsee | Seeder | Resprouter | Spin | Swei | Ttyp | d15N | d13C | N | C/N | C | SLA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **AAP** | Entomophyllous | Nofire | N | Y | Y | 19.27 | Autotr | NA | NA | NA | NA | NA | NA |
| **ARO** | Entomophyllous | Nofire | Y | N | N | 0.86 | Autotr | 1.62 | -28.64 | 1.17 | 41.25 | 48.20 | 4.44 |
| **CAL** | Anemophyllous | Nofire | N | Y | N | 8.98 | Autotr | NA | NA | NA | NA | NA | NA |
| **CSA** | Entomophyllous | Fireseed | Y | N | N | 1.10 | Autotr | -3.55 | -28.51 | 1.45 | 31.74 | 45.94 | 6.84 |
| **CVU** | Entomophyllous | Fireseed | N | Y | N | 0.03 | Autotr | -2.76 | -29.48 | 1.10 | 47.24 | 51.84 | 4.20 |
| **DGN** | Entomophyllous | Nofire | N | Y | N | 4.17 | Autotr | NA | NA | NA | NA | NA | NA |
| **HCA** | Entomophyllous | Nofire | Y | N | N | 3.80 | Autotr | -3.40 | -28.45 | 1.18 | 40.52 | 47.76 | 4.06 |
| **HHA** | Entomophyllous | Nofire | Y | N | N | 0.52 | Autotr | -2.33 | -28.20 | 1.41 | 34.83 | 49.13 | 6.35 |
| **HPI** | Entomophyllous | Fireseed | Y | N | N | 0.05 | Autotr | 0.07 | -28.78 | 1.21 | 42.76 | 51.69 | 6.06 |
| **JNA** | Anemophyllous | Nofire | N | Y | N | 45.63 | Autotr | -1.37 | -26.41 | 0.92 | 57.70 | 53.18 | 3.89 |
| **LPE** | Entomophyllous | Fireseed | Y | N | N | 0.69 | Autotr | -0.29 | -28.84 | 1.38 | 35.26 | 48.75 | 6.84 |
| **LPR** | Entomophyllous | Fireseed | N | Y | N | 8.66 | Autotr | NA | NA | NA | NA | NA | NA |
| **PAN** | Anemophyllous | Nofire | N | Y | N | 14.61 | Autotr | -3.60 | -26.86 | 1.32 | 38.69 | 51.26 | 4.99 |
| **ROF** | Entomophyllous | Fireseed | Y | N | N | 0.83 | Autotr | NA | NA | NA | NA | NA | NA |
| **SGE** | Entomophyllous | Fireseed | Y | Y | Y | 4.00 | Nfix | -1.58 | -27.19 | 1.33 | 37.66 | 50.13 | 1.82 |
| **SIM** | Entomophyllous | Nofire | Y | N | N | 0.24 | Autotr | NA | NA | NA | | NA | NA |
| **TCA** | Entomophyllous | Fireseed | Y | N | N | 0.15 | Autotr | NA | NA | NA | | NA | NA |
| **UAU** | Entomophyllous | Fireseed | Y | Y | Y | 6.32 | Nfix | -0.67 | -27.39 | 1.29 | | 49.87 | 1.71 |

**Table S3.4** Spearman R correlations between the selected traits included in the model selection and the NMS ordination axes (NMS1 and NMS2).

| Nutrient availability gradient (NMS1) | | Aridity gradient (NMS2) | |
|---|---|---|---|
| **Selected traits** | **Spearman r** | **Selected traits** | **Spearman r** |
| **Height** | 0.63 | **Spiniscence** | -0.75 |
| **Green** | 0.62 | **Evergreen** | 0.66 |
| **Sclerophyllous** | 0.4 | **Climber** | -0.59 |
| **Tussock** | -0.39 | **Sclerophyllous** | 0.58 |
| **Semi-sclerophyllous** | -0.34 | **C/N** | 0.38 |
| **Chamaephyte** | -0.32 | **Entire** | 0.36 |

**Table S3.5** Selected models using GAM model selection for trait variation along communities' succession.

| Model | edf | F | p | Deviance explained (%) |
|---|---|---|---|---|
| **NMS1~Height+Green+Chamaephyte** | | | | 85.9 |
| Height | 1.481 | 69.91 | <0.001 | |
| Green | 1 | 121.312 | <0.001 | |
| Chamaephyte | 1 | 9.882 | <0.01 | |
| **NMS2~Spiniscence+Evergreen+Climber+Entire** | | | | 82.80 |
| Spiniscence | 2.124 | 4.453 | <0.01 | |
| Evergreen | 1.922 | 22.451 | <0.001 | |
| Climber | 1 | 24.868 | <0.001 | |
| Entire | 2.123 | 21.329 | <0.001 | |

**Table S3.6** Squared correlation coefficient ($r^2$) of variables (traits, environmental variables and functional groups) vectors onto NMS ordination

| | $r^2$ | | $r^2$ |
|---|---|---|---|
| **Height** | 0.64*** | **Aridity** | 0.48*** |
| **Spin** | 0.58*** | **O. matter** | 0.43*** |
| **Green** | 0.56*** | **Evergreen** | 0.29*** |
| **Evergreen** | 0.46*** | **Legumes** | 0.25*** |
| **Chamaephyte** | 0.37*** | **Heaths** | 0.23*** |
| **Entire** | 0.32*** | **Conifers** | 0.14** |
| **Climber** | 0.30*** | | |

# 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).

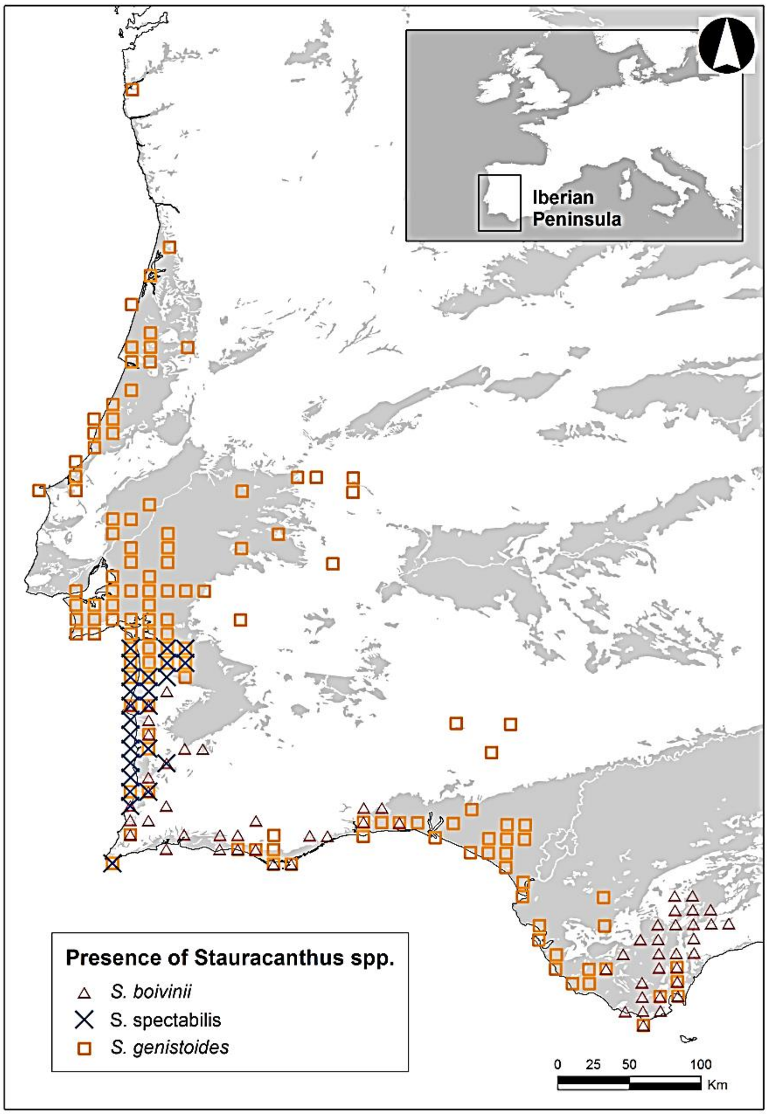



**Figure 4.1** Distribution of *Stauracanthus* species in the Iberian Peninsula. Each symbol represents a 10x10 km UTM cell. Shaded area represents the suitable soils for the genus, namely sandy soils.

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

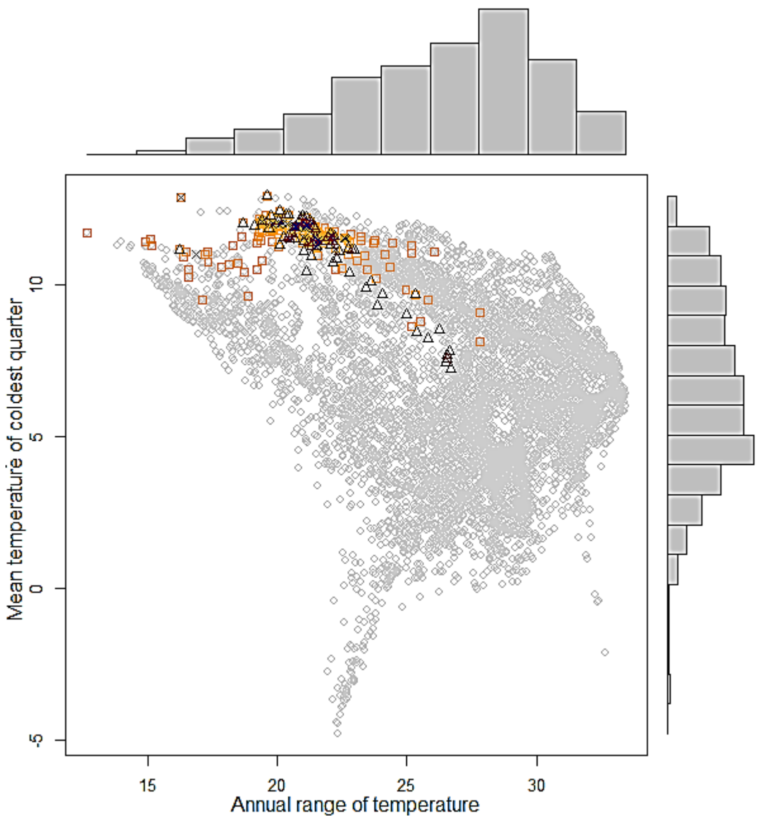
**Table 4.1** Results of the ENFA analysis using all the variables, showing the contributions of each variable to the marginality // specificity factors of each species (SBO: *S. boivinii*; SGE: *S. genistoides*; SSP: *S. spectabilis*). Contributions for the marginality factor higher than 0.2 are in 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 |
| 1$^{st}$ 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 |

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 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.



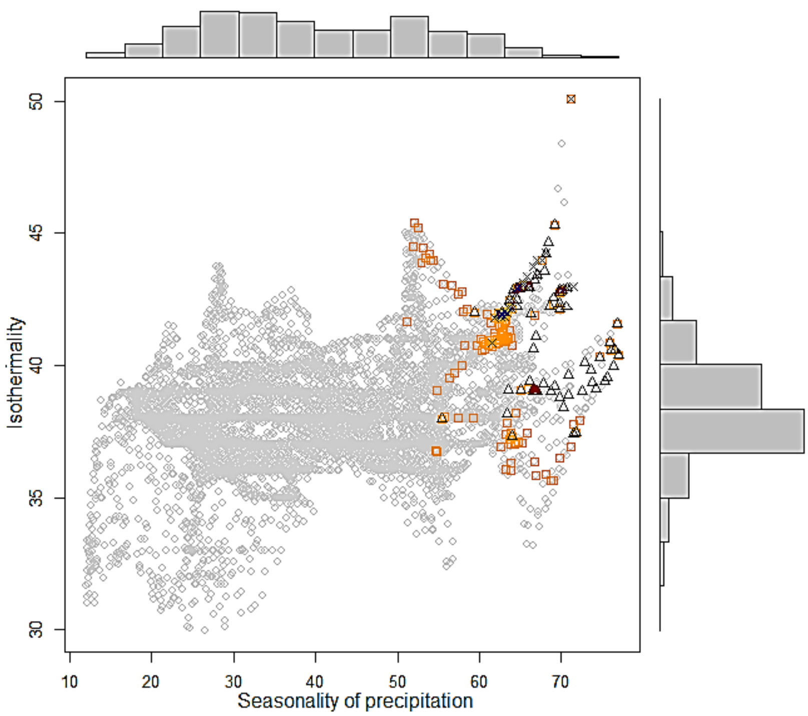




**Figure 4.2** Responses to the most significant bioclimatic variables determining the three *Stauracanthus* species according to the Ecological Niche Factor Analysis (ENFA) and Generalized Linear Models (GLM). Circles = cells without presences, triangles = *S. boivinii*, squares = *S. genistoides*,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

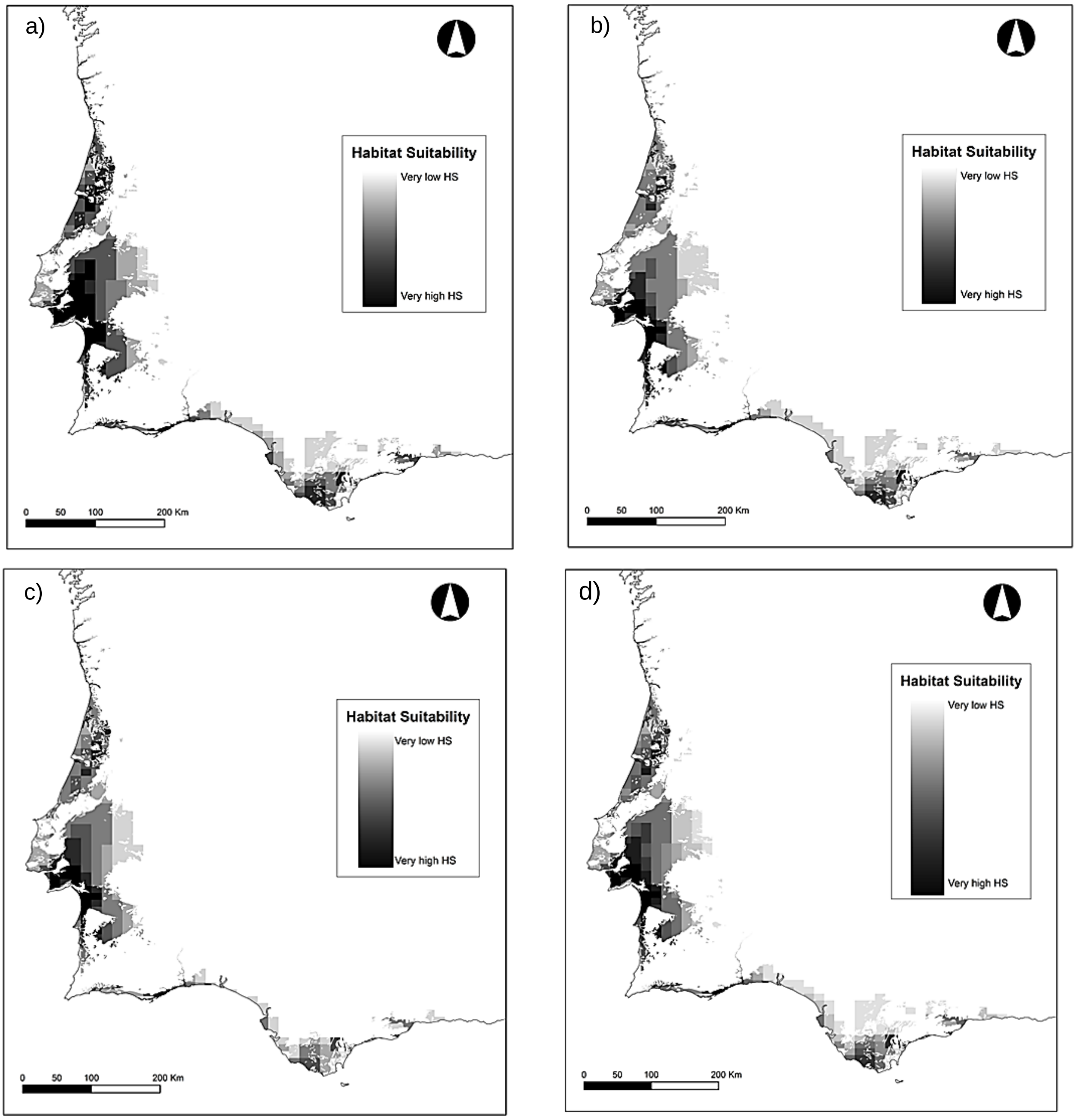



**Figure 4.3** Overlap of the habitat suitability (HS) maps obtained with Ecological Niche Factor Analysis (ENFA) using the set of four variables which coincided in relevance both in ENFAs and Generalized Linear Models (GLM) for the three species. Overlap of HS maps between *S. boivinii* and *S. genistoides* (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.

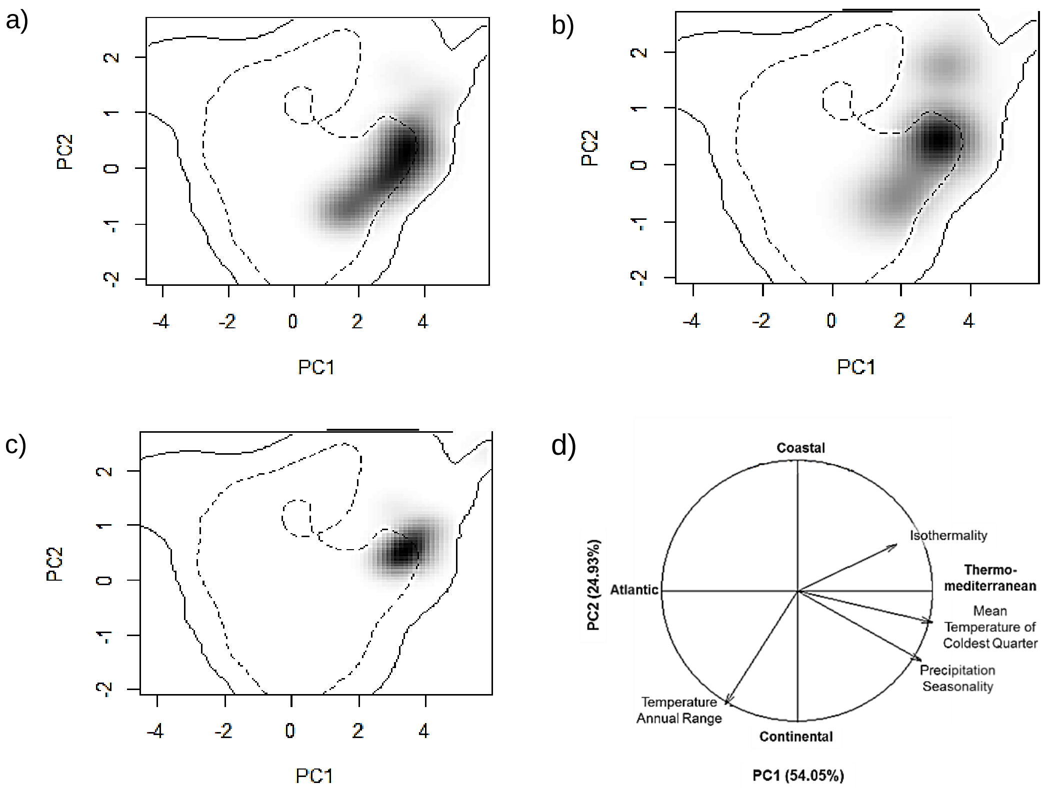



**Figure 4.4** Realized niches of the *Stauracanthus* species in the climatic space available in the Iberian Peninsula: (a) represents the niche of *S. boivinii*, (b) the niche of *S. genistoides* and (c) the niche of *S. spectabilis* along the two first axes of the PCA in the Iberian Peninsula. Grey 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).

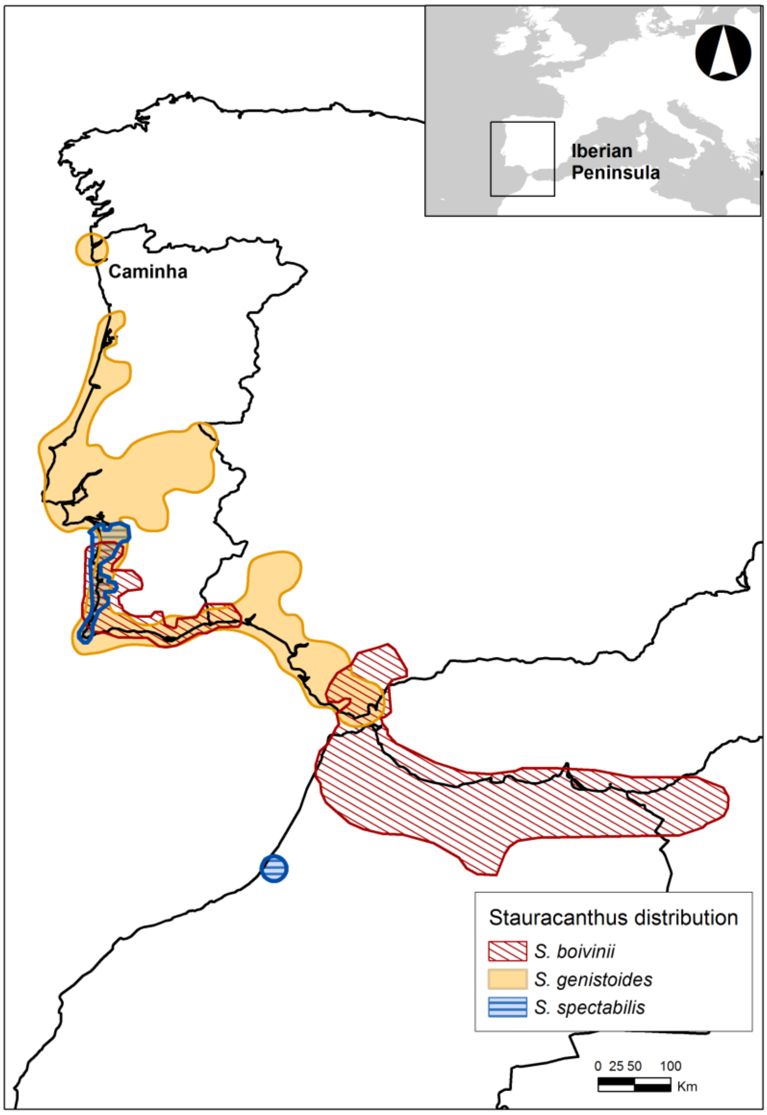



**Figure 4.5** Current known distribution of *Stauracanthus* species.

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*

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## 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) | - | - | - |

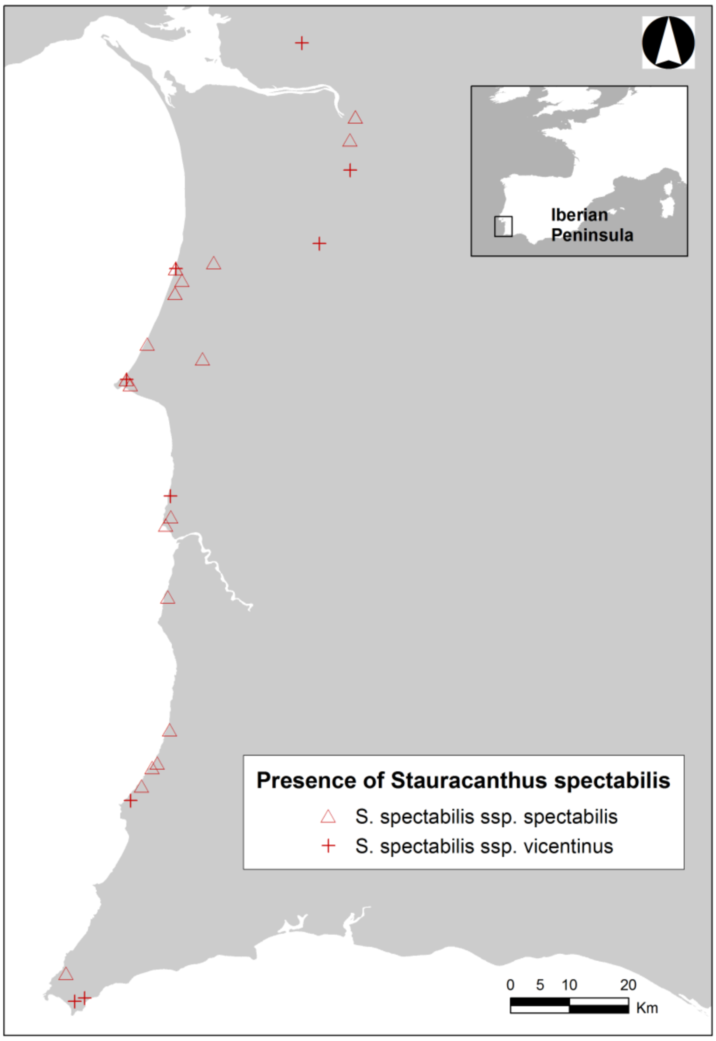


**Figure S4.1** Map showing the location of S. spectabilis ssp. spectabilis and S. spectabilis ssp. vicentinus. Note that each symbol corresponds to a single 1x1 km UTM grid square, corresponding to, at least, one presence record of S. spectabilis subspecies.

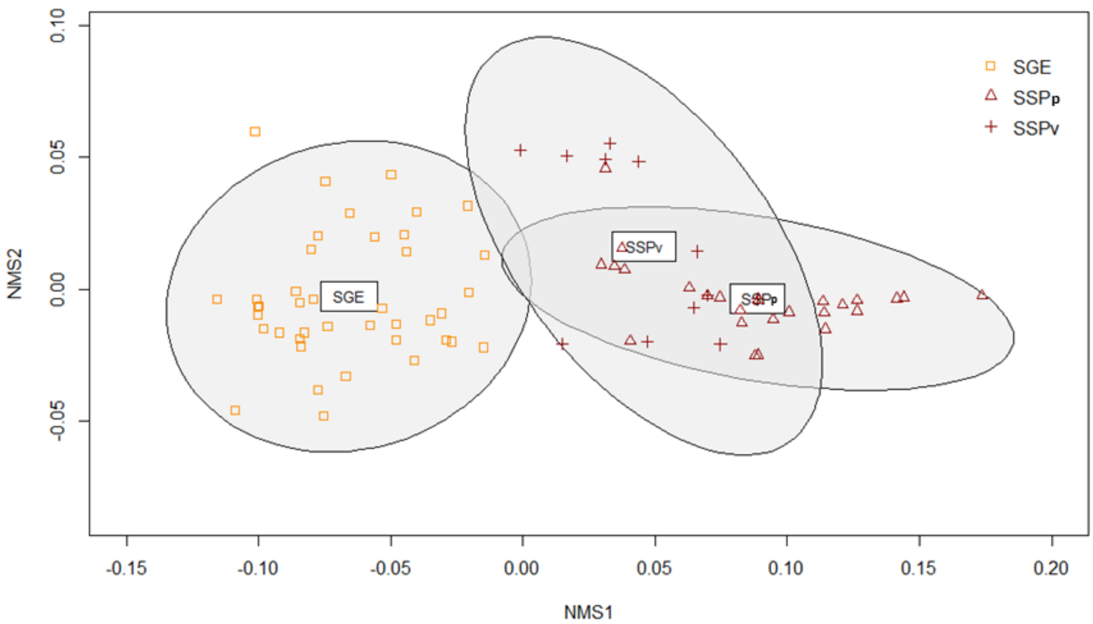


**Figure S4.2** Axes 1 and 2 of the 2-dimensional nonmetric multidimensional scaling ordinations of specimens based on bracteole sizes and the four climate variables most relevant to characterise *Stauracanthus* species distribution: seasonality of precipitation, isothermality, annual range of temperature, 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).

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**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 |

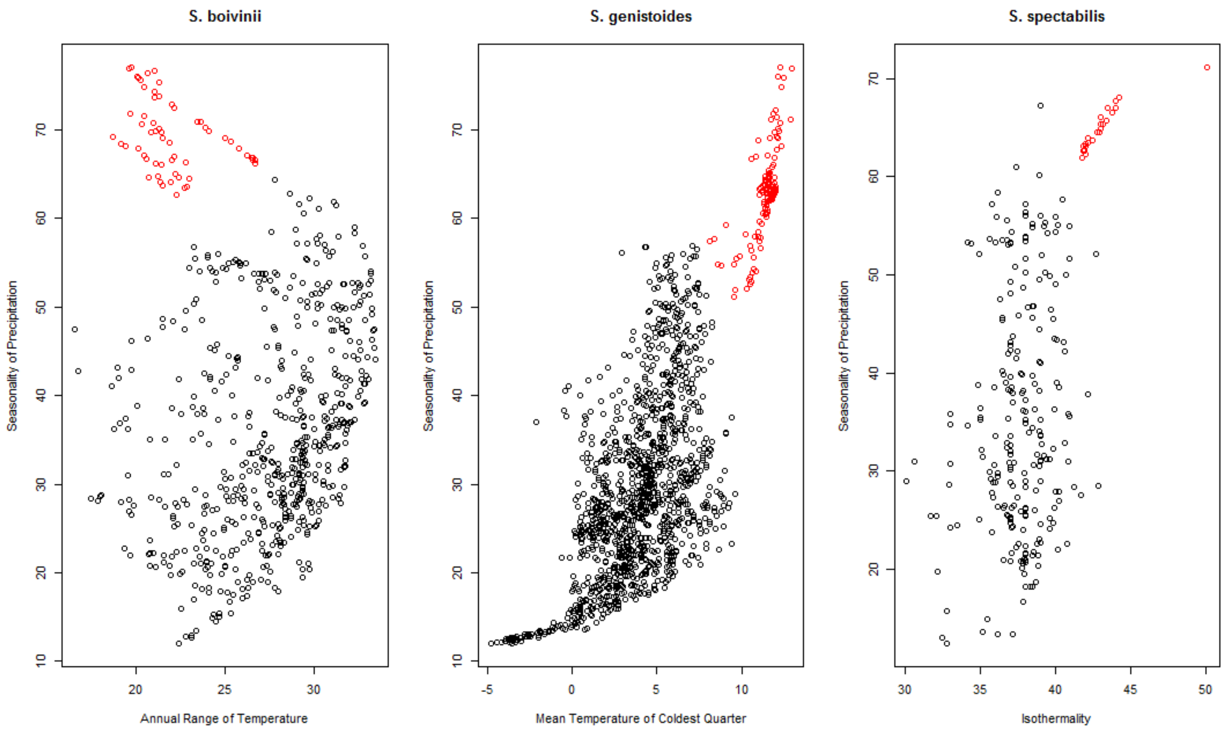


**Figure S4.3** Environmental response of *Stauracanthus* species in relation to GLM significant variables. Contrasting conditions of presence locations (in red), with respect to the less suitable locations (pseudo-absences; black), show the power of these variables as predictors.

**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 |

# Chapter 5

## A geographically consistent succession mediated by different environmental factors across regions

# 5 A geographically consistent succession mediated by different environmental factors across regions

## 5.1 Abstract

The environmental requirements of species and a series of large-scale spatial and evolutionary processes are known to determine the structure and composition of local communities. But species interactions and the functional characteristics of the species integrating the community are also pointed out as significant drivers of community assembly at landscape and local scales. We assessed the role of both individualistic species responses to the environment and local processes on the assembly of ecological communities through two ecological successions of xerophytic shrub communities growing on inland dune habitats in SW Iberian Peninsula. More precisely, we evaluated the geographical coherence of *Stauracanthus genistoides to Ulex australis* and *S. genistoides* to *Juniperus navicularis* successions that were previously identified in a delimited area, throughout most of the area of co-occurrence of the three species. Our results show a significant consistence in the succession throughout the whole geographical area, but also that these communities respond differently to the environmental gradients present in each region. We propose that the main factors causing successional changes do vary according to historical processes and how suitable are scenopoetic conditions for the keystone species in these communities, but also that these successional changes are determined by intrinsic community mechanisms that result in a high degree of similarity in the successional stages in different regions.

## 5.2 Introduction

The origin and nature of ecological communities is a central question of ecology. A large amount of evidence points to a major importance of large-scale evolutionary and biogeographical processes for the composition and structure of local communities, through both the individualistic responses of species to environmental gradients and historical effects (Ricklefs 2007; Hawkins 2008). This has led to the recent claim for the 'disintegration' of ecological communities, as a mere aggregate of their parts, i.e. the species that coincide in a particular time and space, but whose ecological relationships are determined by coevolutionary processes acting at the regional level (Ricklefs 2008). However, species do interact among them, forming ecological networks that in turn bring about ecosystem functioning. These interactions determine the status of their populations locally (Polis *et al.* 2004), and have therefore an spatially-explicit component (Soberón 2007). As a result, species distributions are determined not only by their environmental requirements and species-specific spatial and evolutionary processes, but also by the interactions with other species (Naeem et al 2002), in a scale-structured fashion towards more deterministic importance at landscape and local scales (Hortal et al 2010). Also, the functional characteristics of the species locally present determine the ecological structure of these communities and hence their functioning (Díaz and Cabido 2001; Violle *et al.* 2014).

This local–regional dichotomy poses a dilemma about ecological communities being either dynamic or static entities, driven by either extrinsic or intrinsic processes, respectively. Gleason (1926) described communities as groups of species that coincide in time and space due to the effects of local habitat selection and regional scale filter the existing species pool. Clements (1936), in contrast, thought of communities as relatively closed structures defined by the ecological functions of the species that compose them and where local interactions play the main role in determining community composition. Despite this debate dating back to the early XXth Century, to date no clear agreement exists on it, perhaps in part due to the strong positions taken during the acrimonious debate on the assembly rules carried out during the 1970s and 1980s (see Gotelli and Graves 1996). Here, the current state-of-the-art in both biogeography and community ecology may allow pursuing a synthesis on the degree of interaction between biogeographical and synecological processes and their relative importance for the structuration of local communities. 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.* 2012a); community composition is 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).

The main aim of this work is to evaluate whether local communities follow a coherent ecological succession throughout large geographical extents, or their composition is rather driven by the individualistic responses of the species present in the pool of each locality. Evidence on either one of these patters would provide support for local processes or regional constrains as the main drivers of community assembly. More precisely, we assess the geographical coherence of two ecological community gradients previously identified at a delimited area in a larger geographical extent. Local plant communities growing at inland dune habitats of the Setúbal Peninsula-Alentejo coastal region (Portugal) follow two clear gradients between *Stauracanthus genistoides* and *Ulex australis*-dominated shrublands and between *S. genistoides* and *J. navicularis*-dominated shrublands. These three shrub communities are the extremes of two plant successions related with soil organic matter content and aridity respectively, that determine species composition and functional structure (Chozas *et al.* 2015, Chapter 2). Here we analyse the results of an extensive survey conducted to evaluate whether these successions occur coherently beyond the original studied area in adequate soils throughout SW Iberian Peninsula, or community assembly is mainly driven by local environmental suitability for each species. To do this, we use community analyses describing community structure and species distribution models doing so for the potential distribution of the indicator species of both communities. Our results therefore constitute a formal test of the importance of local and regional drivers in ecological succession at different scales.

## 5.3 Methods

*Study system*

The study area was located at South-West Portugal, on sandy soils between the left margin of Tagus River (38°53′N, 8°49′W) and the Guadiana River Estuary (37°10N, 7°24′W) in an area of about 2900 km² (Figure 5.1). Altitude varies from 0 to 180 m a.s.l. The climate is Mediterranean, with ocean influences but considerable intra and inter-annual variations in mean monthly precipitation and mean monthly temperatures (SNIRH 2009). The dominant soil type is podzol, with some regosols and cambisols (with moderate and very weak soil development, respectively) (APA 1992). 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). The xerophytic shrub communities are characterized by the dominance or presence of *Stauracanthus genistoides* and/or *Ulex australis*, two thorny shrubs of the legume family (Fabaceae) endemic to the Iberian Peninsula, and *Juniperus navicularis,* a shrubby juniper endemic to the Iberian Peninsula. For simplicity herein we use *J. navicularis*, *S. genistoides* or *U. australis* communities to refer to these three types of formations.

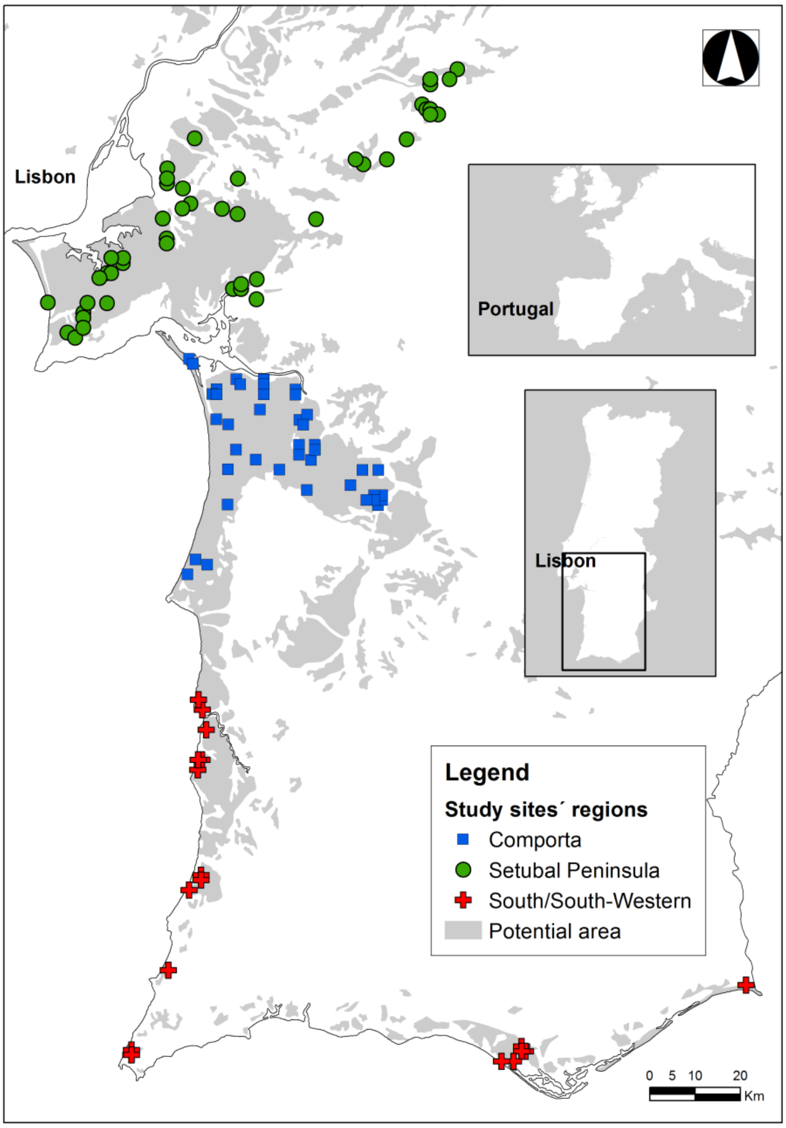


**Figure 5.1** Study sites and potential area of occurrence of inland sandy xerophytic shrub communities in South Portugal. Sites were divided in three regions: Comporta region, squares, Setúbal Peninsula region, circles, and South/South-Western region (SSW), crosses.

## *Community surveys*

Plant communities were sampled at 115 sites randomly selected with Hawth's Analysis Tools for ArcGIS (Beyer 2004) within the potential area of occurrence of sandy xerophytic shrub communities (Figure 5.1). This 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). Sites were divided in three regions (Figure 5.1): Setúbal Peninsula (49 sites), Comporta (45 sites) and South/South-Western region (SSW, 20 sites), following geographical, sand morphogenesis, dominant land use at regional level and connectivity criteria. Setúbal sites are located in the Setúbal Peninsula, an industrialized and densely populated area but with shrublands, conifer forests and cork oak *Montados* – open savannah-like landscape with cork oak (*Quercus suber*) – of high ecological value. These sites are distributed on a heterogeneous matrix constituted by dunes and eolic sands, with some rounded pebbles and poorly consolidated sandstone areas. Comporta sites are situated on a non-costal, massive and continuous sand formation, dominated by semi-natural conifer forests and, finally, South/South-Western (SSW) sites are distributed along the Portuguese Southern coast on localized littoral sand formations with heterogeneous morphogenesis and highly diverse natural and artificial contexts.

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 two meter intervals. Five sample soils, one in each the 2x2 m quadrats placed at the corners 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 (see Chozas *et al.* 2015, Chapter 2). Soil samples were collected only in 95 out of the 115 sites.

Plant nomenclature follows the Checklist da Flora de Portugal (ALFA 2010), and species identities 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 (see also Chapter 4).

Additionally, the two subspecies of *Ulex australis, U. australis* ssp*. australis and Ulex australis ssp. welwitschianus,* were considered as the single specific taxa *U. australis*.

### *Explanatory variables*

In order to assess the importance of the different factors affecting the composition of inland dune xerophytic shrub communities, we evaluate the role of (a) local microenvironmental conditions, that have been previously identified as predictors of succession in these communities (Chozas *et al.* 2015b); (b) the direct effect of mesoscale environmental gradients, that could determine changes in community structure (i.e. macroecological constraints *sensu* Guisan and Rahbek 2011); and (c) the individualistic responses of keystone species to these mesoscale gradients (i.e. habitat suitability *sensu* Guisan and Rahbek (2011).

Chozas *et al.* (2015) identified soil organic matter and aridity as the main factors acting on the local distribution of the successional stages of xerophytic shrub communities. Soil organic matter content was measured directly from the soil samples at the LAS/INIAV (Laboratório de Analises de Solos do Instituto Nacional de Investigação Agrária e Veterinaria, Lisbon). We represent aridity as the first 1 of a PCA performed with climate data from the WORLDCLIM interpolated map database with a 30 arc-seconds (~1 km) resolution (Hijmans *et al.* 2005; http://www.worldclim.org/).

Mesoscale environmental gradients were measured through a range of GIS variables at 10 $km^2$ resolution. Topographic and climatic variables were extracted from WorldClim database of interpolated maps (Hijmans *et al.* 2005; http://www.worldclim.org/) and EDIT GeoPlatform (Sastre *et al.* 2009; http://edit.csic.es/GISdownloads.html). Lithological variables were extracted from the lithological map of Portugal (APA 1992). Additionally, distance to coast was calculated using ArcGIS 10.

We identified the keystone species in these communities by calculating the indicator value (IndVal; Legendre and Legendre 1998) of all shrub species for each type of community, namely those dominated by *S. genistoides*, *U. australis* and *J. navicularis*. This index quantifies the fidelity and specificity of each species to a given type of community. It has a maximum value (of 1) when the individuals of a single species are observed at all sites belonging to a single community. IndVal values were calculated using the ‘‘labdsv” R Package (Roberts 2015),

For the species with statistically significant indicator values, we then modelled their realized environmental niche considering their entire distribution in the Iberian Peninsula. To do this, we obtained occurrence records for each species from the main herbaria holding Iberian Mediterranean collections (COI, LISI, LISU, MA, MACB, MAF and SEV), Flora-on database (http://www.flora-on.pt/), Anthos database (http://www.anthos.es/) and field work. We selected a resolution of 10km×10km UTM grid square (6171 cells) for these analyses since most occurrences could be safely referred to this resolution. All environmental variables (Table S5.1) were analyzed using a Pearson correlation test to eliminate highly correlated predictors ($r \geq |0.70|$, $p < 0.001$) before their inclusion in the models. We used ENFA (Ecological Niche Factor Analysis, Hirzel *et al.* 2002a) a presence-only species distribution modelling technique, to model the realized scenopoetic niche of the selected species. That is, the quantitative set of abiotic conditions used by the species in the studied region (see Hutchinson 1978; Soberón 2007; Hortal *et al.* 2012b). ENFA is an ordination technique that identifies the set of orthogonal factors that best characterize the response of the species to the environmental conditions present in the region. More precisely, it identifies a Marginality Factor, that accounts for the direction of maximum difference between the conditions occupied by the species and all available conditions in the study area, as well as one or several Specialisation Factors, that quantify the ecological variance of the species in relation to other progressively less important environmental gradients. The responses to these Factors can then be used to project the realized response of the species back into the geographical space. Further, ENFA allows calculating the overall Marginality and Specialisation of the species, that characterize how far is its response from the predominant conditions in the region, and how much is it affected by minor environmental and habitat gradients (Hirzel *et al.* 2002b).

ENFA allows quantifying the contribution of each variable to the marginality and the specialisation factors, thereby providing a description of the realized response of the species to each predictor. Therefore, we first performed a preliminary ENFA to select the set of uncorrelated variables (in terms of marginality and specialisation) that best explain the distribution of the species, in order to avoid problems of multicollinearity. Subsequently, we used those selected variables to perform a definitive ENFA to model the realized environmental niche of each species and estimate the importance of each predictor and the global marginality coefficients of the different species. Finally, the potential distributions of the species were calculated based on the variables selected in the first step by means of Mahalanobis distance (MD; Farber and Kadmon 2003). This presence-only species distribution modelling algorithm generates an elliptic climate envelope of the response of the species in the multidimensional space defined by the predictor variables, around the optimum conditions. MD allows projecting an habitat suitability map by means of obtaining the distance to such optimum in the environmental space (Clark *et al.* 1993). ENFA and MD were fit using the “adehabitat” R Package (Calenge 2006).

### *Community analyses*

Shrub cover values were square-rooted to reduce the influence of large values. To avoid an excessive influence of rare species, shrubs occurring in less than 5% of the plots (i.e. with less than five occurrences) were excluded from the ordination analyses, which resulted in maintaining 25 (out of 50) shrubs (Table S5.2). The main gradients of vegetation composition were described with a NMS ordination of shrub cover data, with the function metaMDS of R Package “vegan” (Oksanen *et al.* 2013b). Square root transformed data were subject to a Wisconsin double standardization (i.e. species are first standardized by maxima and then sites by site totals). The similarity between plots was measured with the Bray-Curtis distance, and the goodness-of-fit of the ordination was assessed through the percentage of variance represented by each consecutive axis (see McCune and Grace 2002 for details). NMS axes resulting from these analyses represent the changes in shrub composition along successions, and are herein denominated “community NMS axes” for short.

To identify the drivers affecting successional changes in composition we examined the relationships between the NMS axes and the explanatory variables through Spearman correlation tests and Generalized Additive Models (GAMs). These variables include microenvironmental conditions, the variables selected from the ENFA analyses (as a measure of mesoscale environmental gradients), and the habitat suitability of keystone species (as a measure of their individualistic responses). Multicollinearity among explanatory variables was handled by dropping collinear covariates (Graham 2003; Zuur *et al.* 2010) when correlated at |Spearman r|> 0.7 (Dormann *et al.* 2012). This selection resulted in a set of potential predictors for each community NMS axis. Then, General Additive Models were used to select the most relevant explanatory variables following a top-down approach model selection (Marra and Wood 2011) using the ‘‘mgcv’’ tool of “mgR software package (Wood 2006). To assess the effect of the extent of analysis in the variables affecting shrub communities (Whittaker *et al.* 2001; Anderson and Raza 2010), model selection was performed using all sites and then each one of the three surveyed regions (Setúbal, Comporta and SSW) thereby obtaining four final models. To evaluate the predicting power of the four performed models, the coefficient of determination ($R^2$) between observed and fitted NMS values was calculated for the four datasets – all sites, Setúbal, Comporta and SSW– in each model. Additionally, paired Wilcoxon tests between residuals and pseudo-residuals for each group, with Bonferroni corrections for multiple testing, were implemented to analyse the different performance of each model in the four different datasets.

Variance partitioning was performed using “varpart” tool of “vegan” R software package to calculate the explanatory power of the selected explanatory variables. This function partitions the variation in the explanatory capacity of the response variables (measured as the adjusted R-square) in a redundancy analysis ordination (RDA). Then, “envfit” tool of “vegan” was used to fit graphically the selected variables into the ordination space. We also performed GAMs to characterise and compare the relationships of the gradients identified from NMS analyses with the cover of the keystone shrub species selected by IndVal using the ‘‘mgcv’’ R software package (Wood 2006) along the four datasets.

To evaluate whether there is any structure in the co-occurrence of indicator species in the studied communities, we calculated the checkerboard score (C-score) (Stone and Roberts 1990) using the “C.score” tool of “bipartite” software package (Dormann *et al.* 2008). Low c-score values indicate high randomness in species distribution whilst high values point out to the distribution of each species being affected by the others. Data normalization implies that this index ranges between 0 (no checkerboards, i.e. presence of one species do not interfere with the presence of another) and 1 (only checkerboards, i.e. the two species do not coexist). All analyses were performed on R statistical software V.3.2.0 (R Development Core Team 2011) using the R Studio V 0.98.1103 interface.

## 5.4 Results

The main gradient in species composition was described by the first axis (herein NMS1) of a three axis non-metric multidimensional scaling ordination of shrub cover (Figure 5.2), with final stress values of 0.20. NMS1 accounted for most variance (22.45% out of 40%) and identified the gradient between sites dominated by *Stauracanthus genistoides* (negative values) and sites dominated by *Ulex australis*.

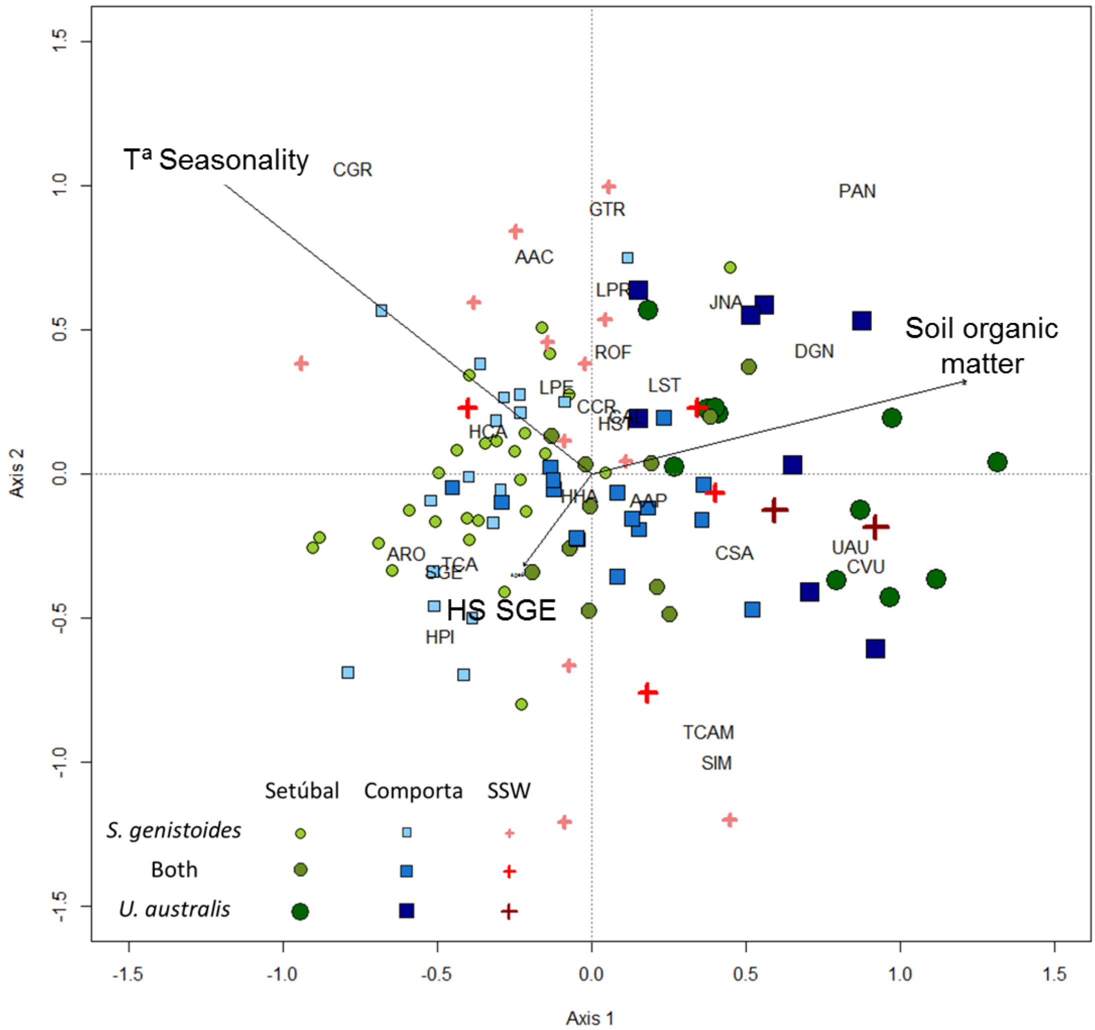


**Figure 5.2** Axes 1 and 2 of the 3-dimensional non-metric multidimensional scaling ordinations of COMDUNES study sites based on shrub cover (NMS1 and NMS2). Small and pale coloured symbols represent study sites without *U. australis* (UAU), high and dark coloured dots are study sites without *S. genistoides* (SGE), and medium sized and coloured dots represent study sites with both species. Arrows reflect the main gradients identified by Spearman correlations: soil organic matter, Tª seasonality and habitat suitability of *S. genistoides*. Species codes according to Table S2.

The gradient between *S. genistoides* and *J. navicularis* was not reflected in the ordination, probably because of the local distribution of the endemic species *J. navicularis* (which occurred in only 16 out of the 115 sites). Therefore, subsequent analyses were performed focusing only on the gradient between *S. genistoides* and *U. australis*. The indicator value (IndVal) for both types of communities identified *S. genistoides* and *U. australis* as the only indicators of their respective communities (IndVal = 0.63, $p<0.001$ and IndVal = 0.74, $p<0.001$, respectively).

A total of eleven uncorrelated variables were evaluated for their significance to explain the distribution of the two species using a preliminary ENFA. This analysis identified six predictors with significant contributions to marginality and specialisation factors (Table S5.3), which were used to model the realized scenopoetic niches of *S. genistoides* and *U. australis*. From these predictors, annual mean temperature, isothermality and temperature seasonality were able to explain most of the marginality of the two species with respect to the study area. Both species occur in localities where the annual mean temperature and the isothermality are higher than the average conditions in the study area, whilst the seasonality of temperature is lower. Further, mean monthly radiation and the mean temperature of the wettest quarter were the most influential for the specialisation factor of *S. genistoides* and *U. australis*, respectively. This indicates a more restricted range of ecological variance of the species in relation to these predictors with respect to the study area. Habitat suitability maps of *S. genistoides* and *U. australis* (HS SGE and HS UAU respectively) were then calculated with the six significant predictors (Figure 5.3).

After dropping collinear covariates, three potential drivers explain the successional gradient measured by NMS1 according to Spearman correlations: soil organic matter, temperature seasonality and habitat suitability of *S. genistoides* (HS SGE); and four according to GAMs: the latter three plus habitat suitability of *U. australis* (HS UAU) (Figures 5.2 and 5.4 respectively). These four predictors were included in a GAM selection. The results of this procedure (Table S5.4) indicated that soil organic matter content is the most parsimonious model explaining the gradient between *S. genistoides* and *U. australis* in Setúbal and Comporta regions. This contrasts with the South/South-

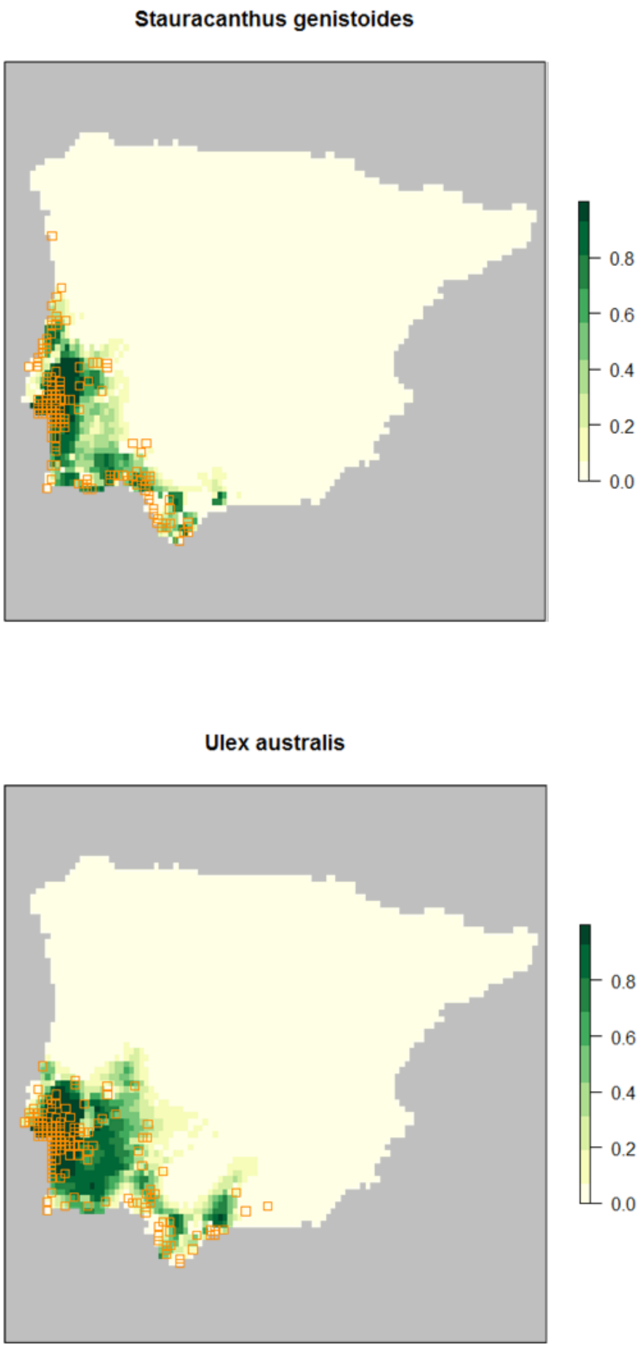


**Figure 5.3** Habitat suitability maps of *S. genistoides* and *U. australis*.

Western (SSW) region, where this successional gradient is explained by the combination of temperature seasonality and habitat suitability of *S. genistoides*. The combination of soil organic matter with the latter two variables were identified as the model that best explains this gradient along the whole study area (Table S.5.4). Adjusted coefficients of determination (Adj. $R^2$) from the variance partitioning analyses confirmed and quantified the role of each explanatory variable in each area (Figure S5.1). Soil organic matter was the variable explaining the highest percentage of deviance in all the regions but SSW, whilst temperature seasonality and HS SGE had a main role in SSW but secondary in the other regions.

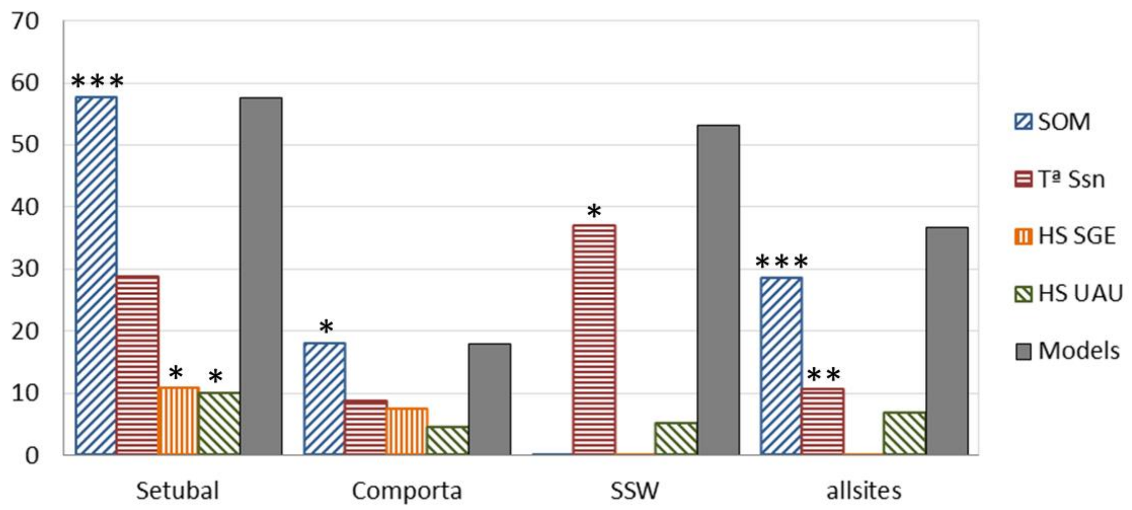


**Figure 5.4** Deviance explained by GAMs performed between each selected explanatory variable (semi-filled bars) and by the best model selected by GAM selection in each region (solid bars) and the first axis of the ordination based on scrub cover (NMS1).

The success of the models for predicting successional changes in other regions is variable (Figure S5.2). Setúbal and Comporta models successfully explain succession in Setúbal Peninsula ($R^2$=0.58/0.51) and have a fair performance in Comporta ($R^2$=0.29/0.25); such performance slightly decays for the complete study area ($R^2$=0.22/0.18) and that fails completely for predicting successional variations in SSW region ($R^2$=0/0). On the other hand, SSW model only presents a good performance explaining succession in SSW region ($R^2$= 0.53), showing a reduced performance in the other two ($R^2$= 0.09/0.07). The results of Paired Wilcoxon tests between residuals and pseudo-residuals confirm the different performance of SSW model from the other three models (Setúbal, Comporta and all sites) and also point out to differences between Comporta and Setúbal models (Figure S5.3).

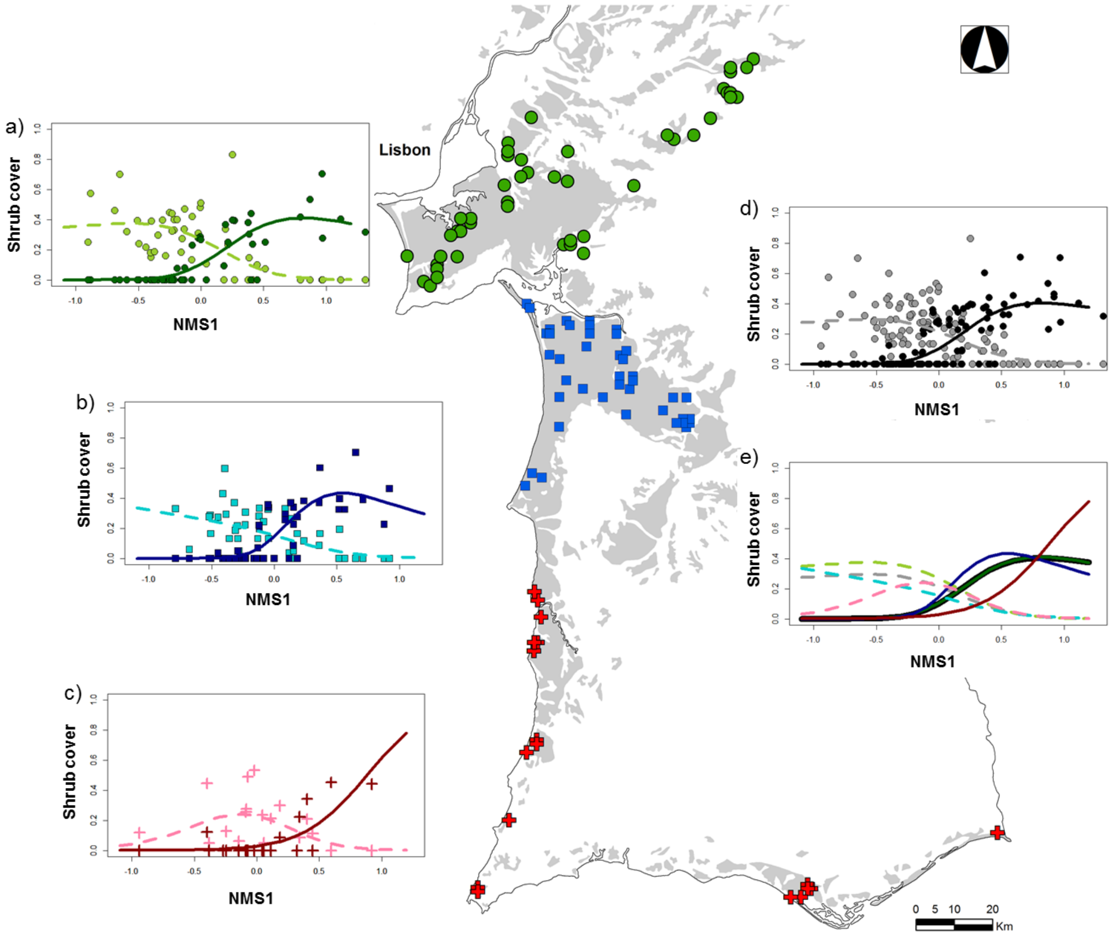


**Figure 5.5** Relationships identified by Generalized Additive Models of the binomial family between: *S. genistoides* (in pale coloured and dashed lines) and *U. australis* (in dark coloured and continuous lines) cover and the first axis of the ordination based on scrub cover (NMS1) in a) Setúbal Peninsula region, circles, b) Comporta region, squares, c) South/South-Western region (SSW), crosses and d) all sites. In e) all the fits of the models are included for visual comparison.

Interestingly, the GAMs comparing NMS1 and the cover of the indicator species for each region (Figure 5.5 and Table S5.5) clearly identified the substitution of *S. genistoides* by *U. australis* along the gradient, underlining the distinctiveness of SSW comparatively to the other three regions. Further, C-scores calculated both between first *S. genistoides* and *U. australis* species and between the whole set of species occurring in both communities clearly identified a lower randomness (i.e. higher spatial segregation of both species) in Comporta (0.88 and 0.63 respectively) than in Setúbal (0.47 and 0.31) and SSW (0.43 and 0.30). Values for the overall region point out to the overall existence of some segregation between the species pertaining to both types of communities (0.63/0.58).

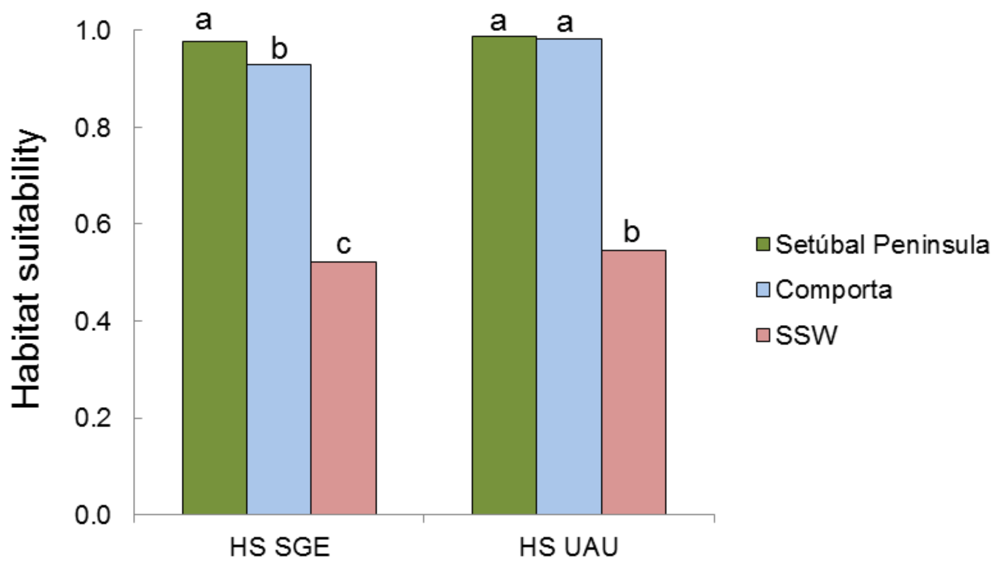


**Figure 5.6** Bar plots and paired Wilcoxon test results between habitat suitability of each group with Bonferroni corrections for multiple testing.

## 5.5 Discussion

Ours results show a remarkable consistence in the succession between *Stauracanthus genistoides* and *Ulex australis* throughout most of the area of co-occurrence of both species. Despite such homogeneity in the pattern of compositional variation, the factors mediating this gradient change from one region to another. A local factor, soil organic matter content, seems to be the main driver of the succession in Setúbal and Comporta regions. Although the preponderance of this factor stands out also for the whole study area, in the South/South-Western region most of the variability of the successional gradient is explained by two factors acting at regional level, temperature seasonality and the habitat suitability of *S. genistoides*. The role of these two latter factors in the study area as a whole was of minor importance, though significant.

Several processes determine the transition between community stages along successions (Gleason 1926). These processes can affect succession at different extents and be highly variable (Connell and Slatyer 1977; Pickett *et al.*. 1987). The evidence about the congruence of the successions in different places is therefore heterogeneous. While in some cases successional mechanisms that are consistent in different regions or throughout geographical gradients (see Prach and Řehounková 2006 for a detailed review), in others successions do not consistently result in the same climax community composition (Drury and Nisbet 1973). Our results add a new perspective to this heterogeneity, showing that different factors can lead to the very same successional process in different regions. In fact, the substitution between *S. genistoides* by *U. australis* is consistently found in all regions throughout the geographical area shared by both species, although its shape and the variables that act as main drivers follow a clear N–S gradient.

Addressing how different processes acting on a similar species pool in different regions converge into the same successional paths it is not a simple issue. We propose that additional underlying mechanisms can be somehow regulating the relevance of the main factors acting in the transition between different successional stages. The succession between *S. genistoides* and *U. australis* communities responds significantly but with different intensities to the amount of organic matter in the soil in Setúbal Peninsula and Comporta regions – and its significance stands out as well for the whole extent of the studied area. While in Setúbal Peninsula soil organic matter highly explains successional gradient, in Comporta other processes seem to be also determining this succession. 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 this latter region. This would have facilitated the preservation of a relict and more humidity-demanding community in Comporta, characterised by the co-dominance of *U. australis* and heaths (mainly *Erica umbellata and E. scoparia*). Although recent historical agricultural practices and forestry destroyed most of that cemented sandy layer and therefore more demanding species of those communities have already disappeared (mainly the heaths), the distribution of *U. australis* communities in these disturbed soils follows a different relationship with soil nutrient content than it does in the Setúbal Peninsula under higher human pressure (historical and present) and different sand morphogenesis. This explanation is reinforced by the higher c-score values of both indicator species and communities in Comporta region. These values denote a checkerboard distribution, where succession between both communities is less frequent – or less evident since current patterns are biased by historical processes. This points to a probable scenario of shrub encroachment of *S. genistoides* communities in poorer and more disturbed soils and *U. australis* communities in more well conserved soils where the original hardpan layer was not completely destroyed. These processes underline the significance of historical processes in succession, linking previous configuration of the landscape to the present one and highlighting that historical differences can result in different successional patterns (Drake 1990).

Climatic gradients are more important in determining successional changes in the SSW region. Here, the keystone species of both communities present the lowest levels of habitat suitability of the studied area (averages of 0.52 for *S. genistoides* and 0.55 for *U. australis*, compared to averages of 0.98 and 0.99, and 0.93 and 0.98 in the Setúbal Peninsula and Comporta, respectively; Figure 5.6). Since these communities are far from their climatic optimum, their distribution is more dependent on the environmental conditions. Consequently, *S. genistoides* prevails in areas with drier conditions and larger variations in temperature throughout the year, hence the high predictive power of the habitat suitability for this species and temperature seasonality in explaining the successional gradient in this region.

Despite the difficulty of attributing a precise functional explanation to the differences in the main drivers mediating the composition of the studied xerophytic shrub communities, it is clear that several species interactions consistently shape up their succession. Working in Comporta and Setúbal, Chozas *et al.* (2015) attributed the initial stages of the succession between *S. genistoides* and *U. australis* communities to a process of facilitation through the accumulation of organic matter in the soil, which would explain the predictive power of this variable in these regions. However, soil organic matter has no effects on the replacement of *S. genistoides* by *U. australis* in the Southern region, where both species are far from their realized climatic optimum. Here, it is likely that the competition for occupying the small pockets of sand of heterogeneous origin determines the replacement between the two types of communities. In fact, competition is also part of the successional process described by Chozas *et al.* (2015); after establishing, the species from the community dominated by *U. australis* outcompete those present in the early stages dominated by *S. genistoides*. We believe that it is the prevalence of competitive displacement processes which is responsible for the geographical consistency of the succession throughout largely different environmental conditions. In areas that are optimal for both species, *S. genistoides* is pioneer in colonizing sands with no or poor soil development, which allows the more edaphically exigent species of the *U. australis* communities to establish later on. In the areas with harsher climatic conditions, the species form these latter communities will prevail in all available patches of sand, except in those where the climatic conditions are so severe that they cannot thrive, thereby allowing then species from *S. genistoides* communities to dominate.

To summarize, we show a remarkably consistent –in terms of compositional changes– process of succession throughout the heterogeneous soil and climate conditions of the inland sand dune habitats of the South of Portugal. Rather than a consistency in the determinants of such succession, our results evidence that communities respond to different environmental gradients in different regions. This helps reconciling both Clementsian and Gleasonian perspectives through the Hutchinsonian definition of the niche (Hutchinson 1978). The variations in scenopoetic conditions (i.e. the environmental setup; in this case soil and climate) throughout the geographical space affect the outcome of a succession process driven by biotic interactions (facilitation first and then competition) between the species of two different types of communities. Only a proper conceptualization of the niche concept –as was already done by Hutchinson (1957; 1978), and how is it related with the geographical space (see Soberón 2007 and Colwell and Rangel 2009) may help solving the debate between the Clementsian and Gleasonian views on community ecology.

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## Supporting Information

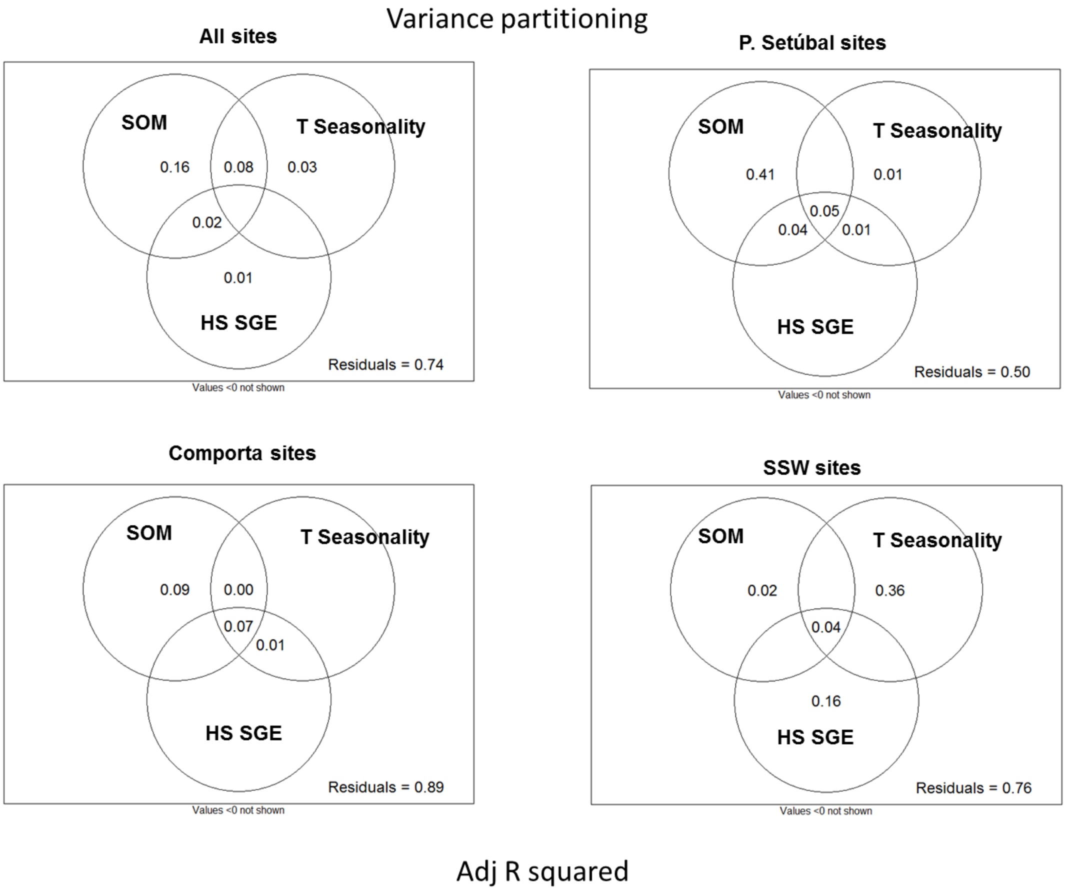


**Figure S5.1** Venn diagram scheme displaying the results of variance partitioning analyses of the first community axis (NMS1) values in a) all sites, b) Setúbal Peninsula sites, c) Comporta sites and d) SSW sites between organic matter (SOM), Tª seasonality, and Habitat suitability of *S. genistoides* (HS SGE), using redundancy analysis ordination (RDA). Values correspond to the adjusted coefficients of determination (Adj. R2).

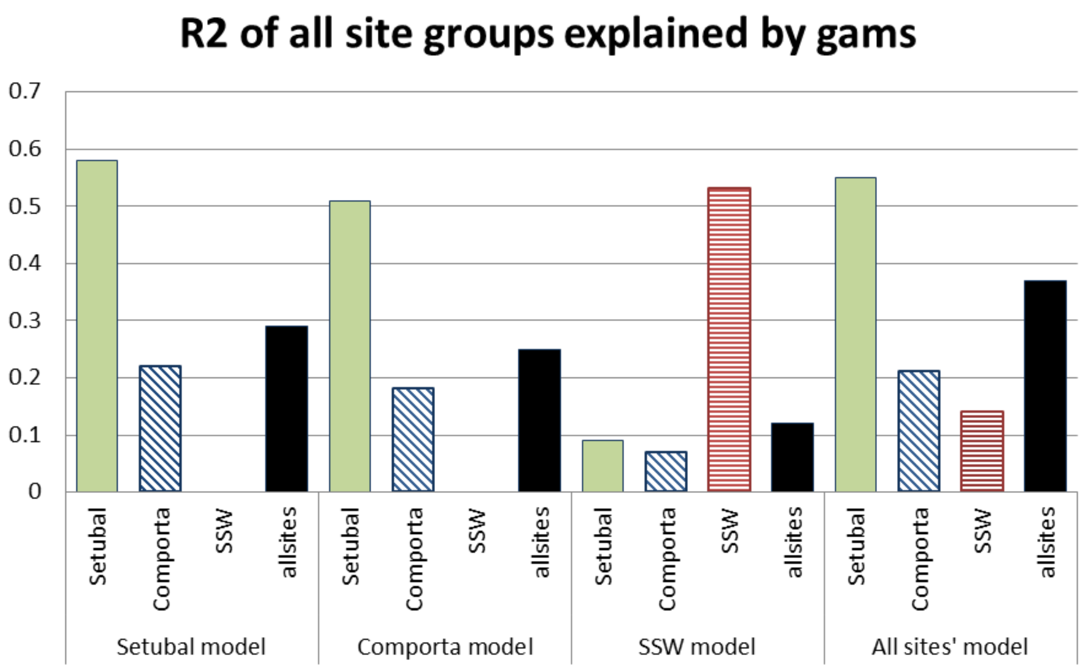


**Figure S5.2** Coefficient of determination ($R^2$) between observed and fitted NMS1 values of the four data sets in each model.

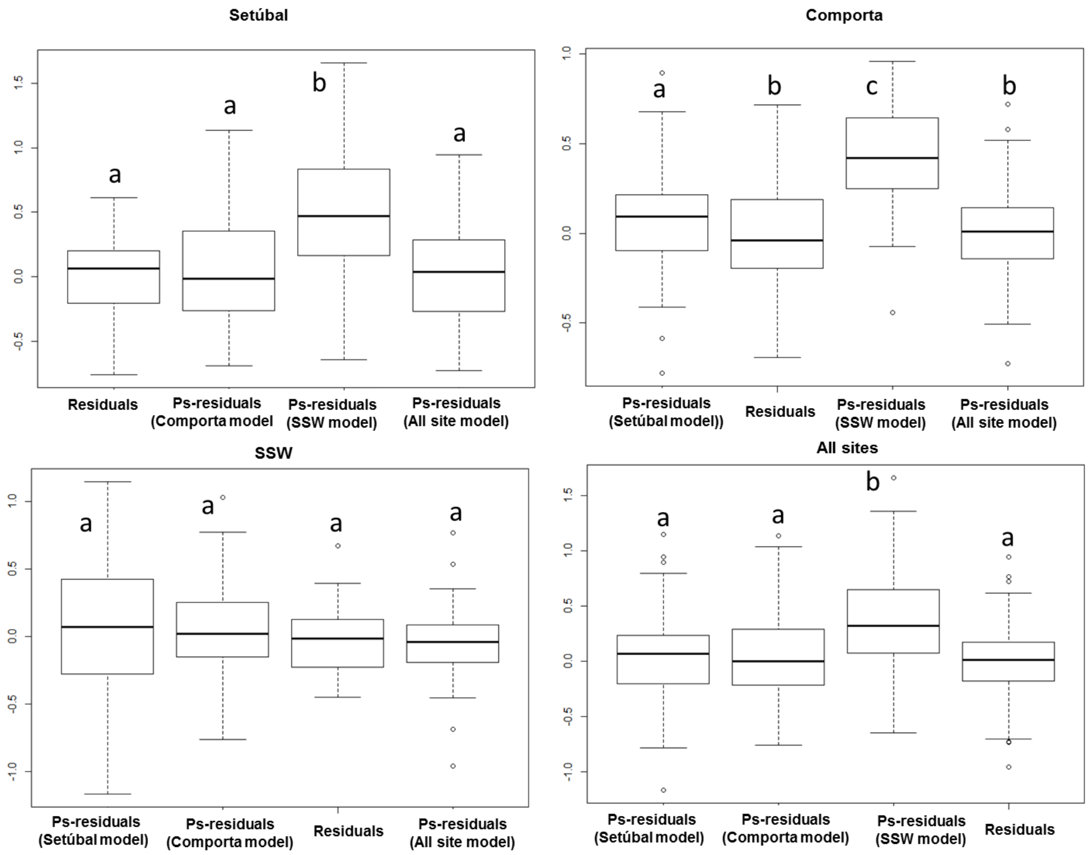


**Figure S5.3** Box plots and paired Wilcoxon test results between residuals and pseudo-residuals for each group with Bonferroni corrections for multiple testing.

**Table S5.1** 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 | Pliocene and Miocene sedimentary rocks |
| Metamorphic and sedimentary rocks (excluding prior classes ) | Plutonic rocks |
| Volcanic rocks | |

**Table S5.2** Surveyed shrubs.

| Shrub species | Code | Shrub species | Code |
|---|---|---|---|
| *Armeria rouyana* Daveau | ARO | *Helichrysum stoechas* (L.) Moench subsp. *stoechas* | HST |
| *Asparagus acutifolius* L. | AAC | *Juniperus navicularis* Gand. | JNA |
| *Asparagus aphyllus* L. | AAP | *Lavandula stoechas* L. subsp. *stoechas* | LST |
| *Calluna vulgaris* (L.) Hull | CVU | *Lavandula pedunculata* (Mill.) Cav. subsp. *pedunculata* | LPE |
| *Cistus crispus* L. | CCR | *Lithodora prostrata* (Loisel.) Griseb. subsp. *lusitanica* (Samp.) Valdés | LPR |
| *Cistus salviifolius* L. | CSA | *Phillyrea angustifolia* L. | PAN |
| *Corema album (L.)* D.Don | CAL | *Rosmarinus officinalis* L. | ROF |
| *Cytisus grandiflorus* (Brot.) DC. *subsp. cabezudoi* Talavera | CGR | *Santolina impressa* Hoffmanns. & Link | SIM |
| *Daphne gnidium* L. | DGN | *Stauracanthus genistoides* (Brot.) Samp. | SGE |
| *Genista triacanthos* Brot. | GTR | *Thymus camphoratus* Hoffmanns. & Link | TCAM |
| *Halimium calycinum* (L.) K.Koch | HCA | *Thymus capitellatus* Hoffmanns. & Link | TCA |
| *Halimium halimifolium* (L.) Willk. | HHA | *Ulex australis* Clemente | UAU |
| *Helichrysum italicum* (Roth) G. Don subsp. *picardi* (Boiss. & Reut.) Franco | HPI | | |

**Table S5.3** ENFA results of community indicator species with the 6 more informative variables (after variable selection).

| | scores_sge6 | | scores_uau6 | |
|---|---|---|---|---|
| | **Mar** | **Spe1** | **Mar** | **Spe1** |
| **ann_mn_t** | 0.51 | 0.10 | 0.56 | 0.06 |
| **ann_prec** | 0.02 | -0.12 | -0.03 | -0.23 |
| **isother** | 0.49 | 0.00 | 0.52 | -0.10 |
| **mn_mon_rad** | 0.07 | -0.98 | 0.05 | 0.25 |
| **mn_t_wet_qrt** | 0.24 | -0.08 | 0.21 | -0.88 |
| **t_ssn** | -0.66 | -0.06 | -0.61 | -0.31 |
| **marginality:** | 5.29 | | 4.09 | |

**Table S5.4** Selected models using GAM model selection for explanatory variables along community succession.

| Region | Model | df | Deviance explained (%) |
|---|---|---|---|
| **Setúbal** | **NMS1~SOM** | - | 57.5 |
| **Comporta** | **NMS1~SOM** | - | 18 |
| **SSW** | ***NMS1~ Tª Ssn + HS SGE*** | 4.88 | 53.2 |
| **All sites** | **NMS1~SOM + Tª Ssn + HS SGE** | 7.51 | 36.7 |

**Table S5.5** Deviance explained, p, k and n of GAM models between SGE and UAU cover and the first community axis (NMS1) values in each region.

| | | Deviance explained(%) | p | k | n |
|---|---|---|---|---|---|
| **All sites** | **SGE** | 31.3 | <0.001 | 1.991 | 115 |
| | **UAU** | 58.2 | <0.001 | 1.995 | 115 |
| **Setúbal** | **SGE** | 47 | <0.001 | 1.988 | 49 |
| | **UAU** | 63.6 | <0.001 | 1.993 | 49 |
| **Comporta** | **SGE** | 25.5 | <0.001 | 1.993 | 46 |
| | **UAU** | 66.6 | <0.001 | 1.996 | 46 |
| **SSW** | **SGE** | 23 | <0.001 | 1.98 | 20 |
| | **UAU** | 56.8 | <0.001 | 1 | 20 |

# Chapter 6

## General Discussion

# 6 General Discussion

The principal objective of this thesis was to study the spatial and successional dynamics of xerophytic shrub communities from inland stabilized sand dunes at different scales. The analysis of the role of environmental requirements and biotic interactions on the organization and distribution of these communities aimed to conciliate the individualistic and holistic paradigms dominating community ecology since the first half of the 20$^{th}$ Century, by highlighting the importance of those factors at local, landscape and regional scales. Along the previous chapters, several specific questions linked with this subject were addressed and major conclusions discussed. This section presents a synthesis of the implications of the major findings of this thesis in the understanding of the dynamics of xerophytic plant communities systems. Additionally, and aiming to improve the success of the conservation efforts devoted to these communities, we propose the implementation of dynamic conservation strategies. These strategies are designed to identify changes across spatial and temporal scales withing these systems, and to take adaptative actions to guarantee the successional dynamics of xerophytic shrub communities and thus ensure their preservation.

## 6.1 A conceptual model of xerophytic shrub communities on stabilized dune dynamics

This thesis demonstrates that both local and regional factors drive the distribution of xerophytic shrub communities on the stabilized dunes of SW Portugal (Chapter 1). Some clear relationships between these communities and edaphic and climatic gradients in this region were identified. Species composition and abundance vary mainly according to changes in soil organic matter and aridity. Additionally, a negative correlation between the occurrence of *Juniperus navicularis* communities and the presence of agricultural areas was detected. 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. Moreover, variations in aridity discriminate between sites with or without *J. navicularis*. These drivers shape up a spatial mosaic of communities mainly determined by differences in nutrient availability and aridity (Figure 6.1). The role of the presence of agricultural areas in *J. navicularis* communities is less clear. Although management practices associated to agriculture are not compatible with the presence of this community, and less arid areas are more suitable for agriculture, the localised

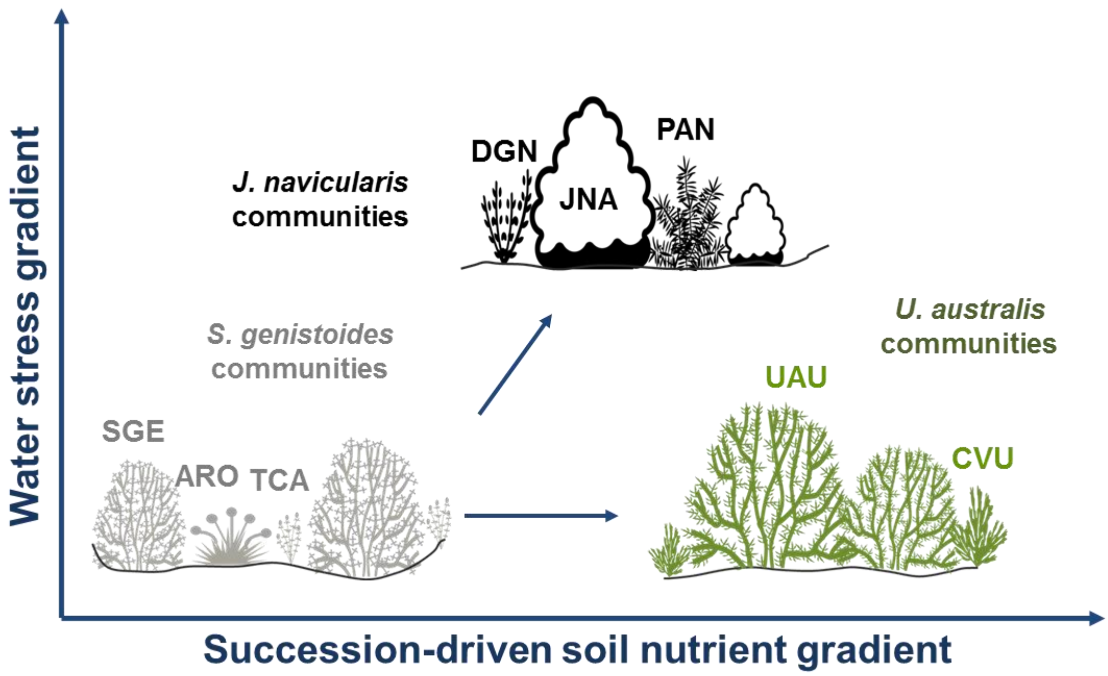


**Figure 6.1** Conceptual model of the xerophytic shrub community successional dynamics on stabilized dunes of the South-Western Iberian Peninsula. We propose that scrub dynamics in Alentejo coast and Peninsula of Setúbal are mainly determined by the soil nutrient matter content, driven by successional processes, and water stress, following an aridity gradient. Arrows identify successional pathways. ARO: *Armeria rouyana*; CVU: *Calluna vulgaris*; DGN: *Daphne gnidium*; JNA: *Juniperus navicularis*; PAN: *Phillyrea angustifolia*; SGE: *Stauracanthus genistoides*; TCA: *Thymus capitellatus*; UAU: *Ulex australis*.

distribution of *J. navicularis* communities within the study area and the small number of sites occupied by them did not allow to separate the eventual effects of micro-environmental gradients from the possibility of a mere spatial bias.

The central role of soil organic matter content (as proxies of nutrient availability) in the composition and distribution of xerophytic shrub communities points to the existence of successional dynamics between these communities and emphasizes the role of plants in altering the environmental conditions and triggering autogenic environmental changes. Considering that facilitation and competition mechanisms play an essential role in plant successions (see Chapter 1), we hypothesize that initial *S. genistoides* communities improve soil conditions by introducing organic matter and nitrogen symbiotically fixed into the system. In agreement, Ulm *et al.* (2014) quantified the impact of *S. spectabilis (=S. genistoides ssp. spectabilis*) presence on the foliage of adjacent non-legume species due to nitrogen transference from the legume to the non-legume neighbours as shown by an increase in foliar total nitrogen and smaller depletion in $^{15}N$ isotopes (evidence of symbiotic nitrogen fixation). Other facilitation processes, such as the 'nurse plant syndrome' (Armas and Pugnaire 2005) are probably simultaneously acting increasing the recruitment of the species of *U. australis* and *J. navicularis* communities (see Chapter 2). At a later stage, species of *U. australis* and *J. navicularis* communities likely reduce the availability of light to smaller-size species of *S. genistoides* communities (see Figures 6.2 and 6.3). Thus, in our opinion, succession in xerophytic shrub communities will most likely be modelled by facilitation processes followed by successive changes in the competitive ability of plant species framed in an autogenically-shifting fluctuating environment.

Based on the above, we propose a conceptual model (Figure 6.1) where *S. genistoides* communities increase soil organic matter enabling colonisation by the more nutrient-demanding species conforming *U. australis* and *J. navicularis* communities, which in turn will also produce a positive feedback of nutrient incorporation into the soil, thereby enhancing light and nutrient competition eliminating colonizer species. Arguably, *S. genistoides* and *U. australis* communities would arise as a result of soil disturbances that impede the maintenance of the climax *J. navicularis* formations (García-Novo 1977; Neto 2002; Neto et al. 2004). Although the role of disturbance in the successional dynamics between *J. navicularis* and both *S. genistoides* and *U. australis* communities is clearly referred by these authors, as included in the conceptual scheme presented in Figure 2.5, the analyses developed during this thesis were not able to confirm them directly.

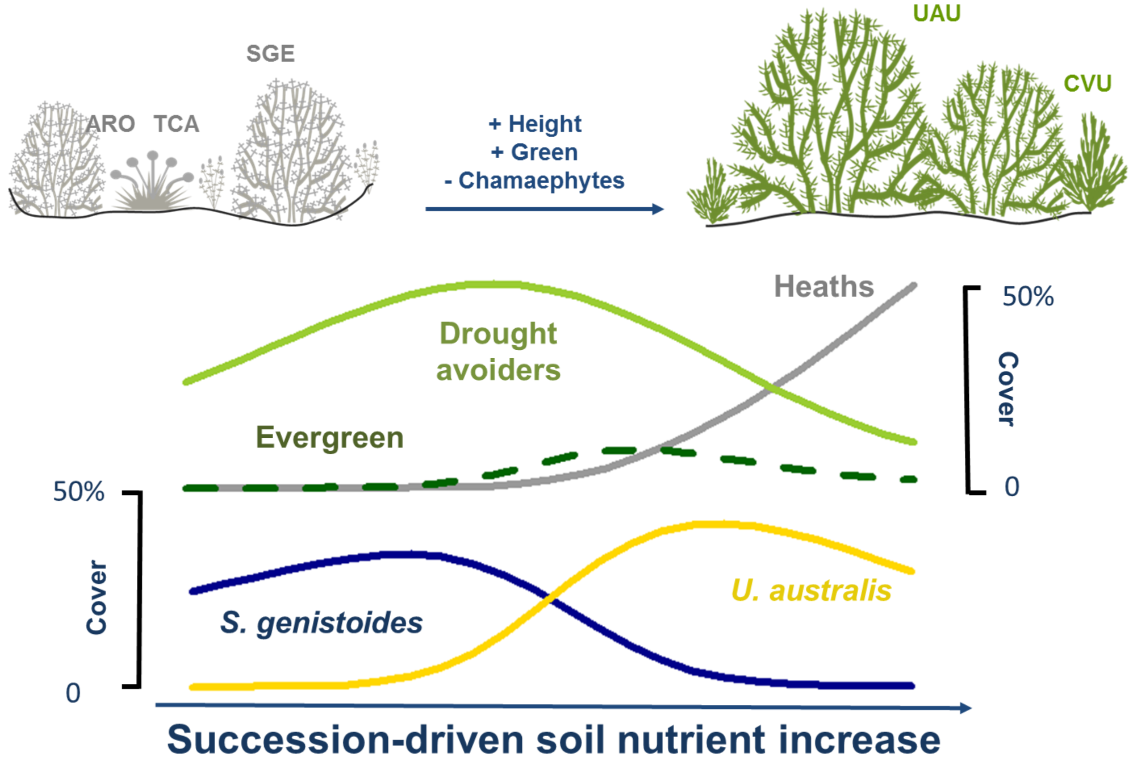


**Figure 6.2** Scheme with the main ecological dynamics found in our work along the succession between *S. genistoides* and *U. australis* communities, defined by the first axes of the ordination based on scrub cover (NMS1), namely variations in traits (top), functional groups (centre) and cover of the species with higher indicator value of both communities (bottom). Relationships were identified by Generalized Additive Models (see Chapters 2 and 3 for details). Percentages of variance explained: 51.8% (*S. genistoides*), 65.9% (*U. australis*), 53.4% (heaths), 33.4% (evergreen) and 18.2% (drought avoiders). Cover values are square root transformed. All p values < 0.001. ARO: *Armeria rouyana*; CVU: *Calluna vulgaris*; SGE: *Stauracanthus genistoides*; TCA: *Thymus capitellatus*; UAU: *Ulex australis*.

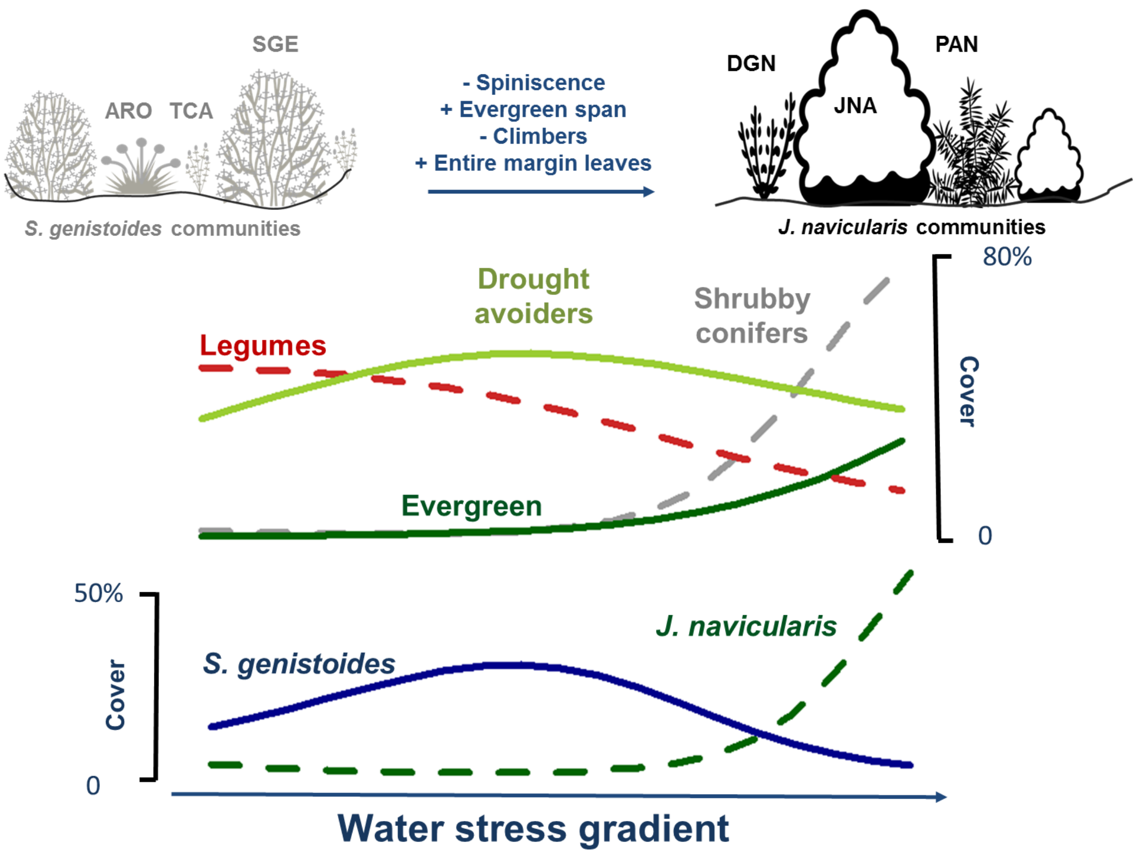


**Figure 6.3** Scheme with the main ecological dynamics found in our work along the succession between *S. genistoides* and *J. navicularis* communities, defined by the second axes of the ordination based on scrub cover (NMS2), namely variations in traits (top), functional groups (centre) and cover of the species with higher indicator value of both communities (bottom). Relationships were identified by Generalized Additive Models (see Chapters 2 and 3 for details). Percentages of variance explained: 16.9% (*S. genistoides*), 35.8% (*J. navicularis*), 35.8% (conifers), 26.5% (legumes), 19.9% (evergreen) and 8.46% (drought avoiders). Cover values are square root transformed. All p values < 0.001. ARO: *Armeria rouyana,* DGN: *Daphne gnidium*; JNA: *Juniperus navicularis*; PAN: *Phillyrea angustifolia*; SGE: *Stauracanthus genistoides*; TCA: *Thymus capitellatus*.

Successional community changes in the studied system involve a turnover in key functional traits (Figures 6.2 and 6.3) and imply variations in species richness and (trait) functional diversity (Figure 6.4), highlighting the importance of the selection of traits involved in the analyses of functional indices, since they strongly influence their results and interpretation.

*S. genistoides* communities presented low values of both taxonomical and functional richness (Figure 6.4), mainly determined by the presence and dominance of a reduced number of pioneer species, such as *Thymus capitellatus*, *Armeria rouyana* and *Helichrysum picardii*, shaped by early stage environmental conditions, such as high radiation and low nutrient availability (see Tilman's resource-ratio model, Chapter 1.1). The values of Rao's quadratic entropy (Rao) calculated with the set of all traits (see Chapter 3) pointed to a community dominated by species that are, in general, functionally similar (Figure 6.4). By contrast, Rao values of height , colour of the green photosynthetic organ and presence of chamaephyte life form (nutrient-driven successional (NDS) traits) are quite similar to Rao values in the transitional stage found between *S. genistoides* and *U. australis* communities and higher than in the latter, even with low functional and taxonomical richness values. This suggests a higher heterogeneity in the combination of these three traits in this initial stage and denotes a higher filtering effect of NDS traits in later successional stages than in earlier stages. In fact, it is likely that additional factors related to colonization (e.g. arrival time) are acting during these early stages (Walker and Chapin 1987), consequently diluting the relevance of NDS traits.

The transitional stage between *S. genistoides* and *U. australis* is dominated by drought avoiders, mainly *Halimium halimifolium*, *H. calycinum* and *Lavandula pedunculata*, together with species from both communities (Figure.6.2), resulting in higher species and functional richness and functional divergence (Rao - Figure 6.4).

*U. australis* communities showed species richness values similar to those of *S. genistoides*. In fact, an inverted-U-shaped curve pattern was found for both taxonomic richness and functional richness when calculated with NDS traits (Figure 6.4). These patterns seem to respond to biotic interactions, namely facilitation in the early successional stages, that is later followed by competition, in accordance with the facilitation model proposed by Connell and Slatyer (1977). The improvement of environmental conditions by facilitation, through the incorporation of organic matter into the soil and nursing effects enlarges the niche space allowing the incorporation of new and more demanding species into the community and, consequently, increasing taxonomic and functional richness. Ultimately, these successional changes also allow the establishment, development and finally the dominance of the communities characterized by *U. australis*. The dominance of this species ultimately reduces both indices by turning the environment less suitable to early- and intermediate-stage species and favouring the occurrence of species with specific values of NDS traits, namely tall stems and greener coloration, due to the lack of glaucous structures. This contrasts with *J. navicularis* communities, which present higher taxonomical and functional richness values than early stage communities as expected for later successional stages (Figure 6.4). Here, the initial decrease showed in functional richness and Rao values, calculated with all the traits, seems to reflect the seral phase when legumes are already decreasing but evergreen sclerophyllous and shrubby conifers are still missing.

## 6.2 Geographic distribution of species and communities

Determination of the realized abiotic (i.e. Grinnellian) niche and the geographic distribution of the environmental suitability for *Stauracanthus genistoides* and *Ulex australis* (chapters 4 and 5) show than both species grow on coastal sandy soils, with relatively mild winters and moderately low daily and yearly variations in temperature, which characterize the Thermo-Mediterranean bioclimate with Atlantic influence (Barbero and Quezel 1982). These analysis also point to a high range of variance in the response of *S. genistoides* to monthly variations in radiation, and also of *U. australis* to the mean temperature of the wettest quarter.

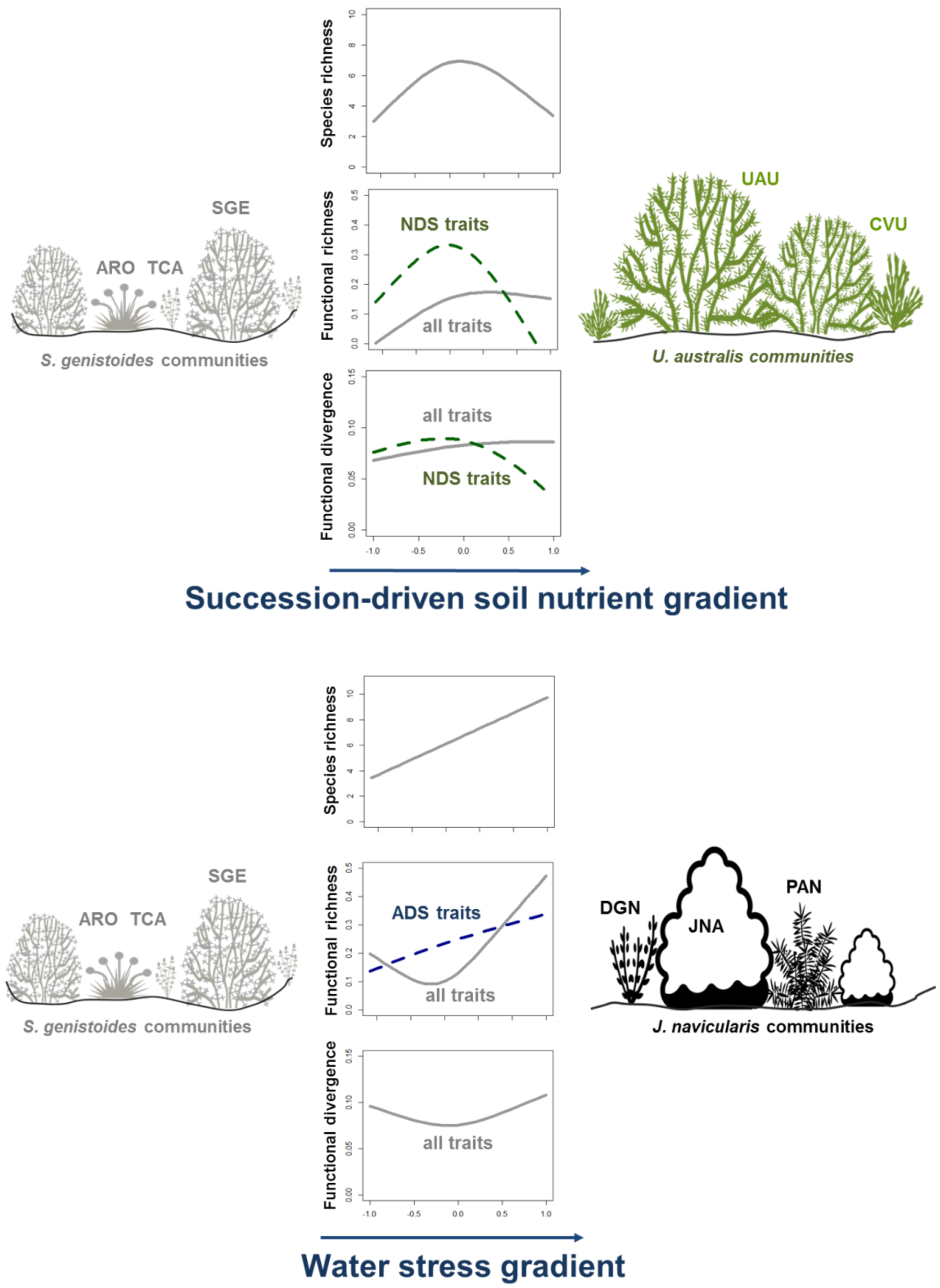


**Figure 6.4** Scheme with the relationships between species richness, functional richness and Rao's quadratic entropy (Rao) and: (top) the *S. genistoides* to *U. australis*-dominated communities' succession, represented by the first axis of the ordination based on scrub cover (NMS1) and defining a soil nutrient gradient; (bottom) the *S. genistoides* to *Juniperus*-dominated communities' succession, represented by the second axis of the ordination based on scrub cover (NMS2) and defining a water stress gradient. Relationships were identified by Generalized Additive Models (see Chapter 3 for details). Percentages of variance explained: Top: 25.3% (Richness), 25.3% all traits and 23.5 NDS traits (F. richness), and 12.2%** all traits and 22.3% NDS traits (Rao); bottom: 35.1% (Richness), 34.4% all traits and 33.8% ADS traits (F. richness) and 22.4% all traits (Rao). ARO: *Armeria rouyana,* DGN: *Daphne gnidium*; JNA: *Juniperus navicularis*; PAN: *Phillyrea angustifolia*; SGE: *Stauracanthus genistoides*; TCA: *Thymus capitellatus*. NDS and ADS traits: nutrient and aridity-driven successional traits respectively. All p values < 0.001 except where indicated with a ** (p <0.01).

*S. genistoides and U. australis* share several environmental responses: are spiny legumes and drought avoiders with no photoinhibition (Zunzunegui *et al.* 2010), and possess resprouting and seeder strategies. These adaptations ultimately determine their environmental tolerances and, consequently, their geographic distribution. Therefore, it can be argued that the key functional traits shared by both species may to some extent determine the high similarity in their environmental responses and geographic distributions. Such similarity is evident in the relatively low variation in functional richness and, in particular, functional divergence (as measured by Rao) throughout the succession between both species (see Chapter 3 and Figure 6.4).

Combined analyses on the abiotic niche and published analyses on genetic differentiation within the clade formed by the genera *Stauracanthus* and *Ulex* (Cubas 1987; Ainouche *et al.* 2003; Pardo *et al.* 2004; Cubas *et al.* 2005; Pardo *et al.* 2008) provides important insights on the role of species diversification in shaping current patterns of distribution of xerophytic shrub communities in the Iberian Peninsula. The lineage that originated these genera may have appeared before the end of the Paleogene (Pardo *et al.* 2008), so they could have been distributed along the Betic-Rif mountain belt formed during the African-Iberian collision (Early Miocene). Firstly, the formation of the Alboran Sea by the Middle Miocene, and then the dryer climate conditions of the Messinian Salinity Crisis reduced and fragmented the geographic ranges of *Stauracanthus* and *Ulex* species. However, while the former event reduced gene flow, the latter also allowed the recolonization of new areas of suitable environment. Apart from increasing fragmentation through the creation of salinity gradients and islands of low salinity within its basin, the cycle of partial, or even nearly complete, desiccation of the Mediterranean Sea during the Messinian Salinity Crisis also resulted in the disappearance of the Mediterranean as barrier to dispersal. This allowed existing and differentiated species of both taxa to colonize new habitats associated with the novel climate and geologic conditions. Later, the expansion of psammophilous taxa of both genera along the Atlantic coast of the Iberian Peninsula 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).

There was a remarkable consistence in the succession between *S. genistoides* and *U. australis* (and consequently between the communities of which they are indicators) throughout most of the area of co-occurrence of both species, despite the factors driving this successional gradient changing regionally (Figure 6.5). While in Setubal and Comporta regions (as well as in the whole study area) a local factor, soil organic matter content, was the main driver, in South/South-Western region, two regional drivers explain most of the gradient, namely temperature seasonality and the habitat suitability of *S. genistoides*. Both regional factors had a minor, but significant role in explaining the successional gradient when the whole geographic context of Southern Portugal sandy soils is taken into account.

Ascertaining how different processes acting on a relatively similar species pool in different regions converge in the same succession it is not a simple issue. Here it is proposed that additional mechanisms acting at both species and community levels can be regulating the relevance of the main factors determining the transition between different successional stages. Both *Stauracanthus* and *Ulex* communities present a clear patchy distribution in Comporta region (Chapter 5), showing that the presence of one community highly affects the presence of the other. Climatic and historical reasons are suggested to explain this patchiness. The Comporta region presents significantly lower annual precipitation and higher aridity than Setúbal Peninsula (average total annual precipitation 500-600mm vs. 600-700 mm; Aridity index 0.5-0.6 vs. 0.6-0.7,

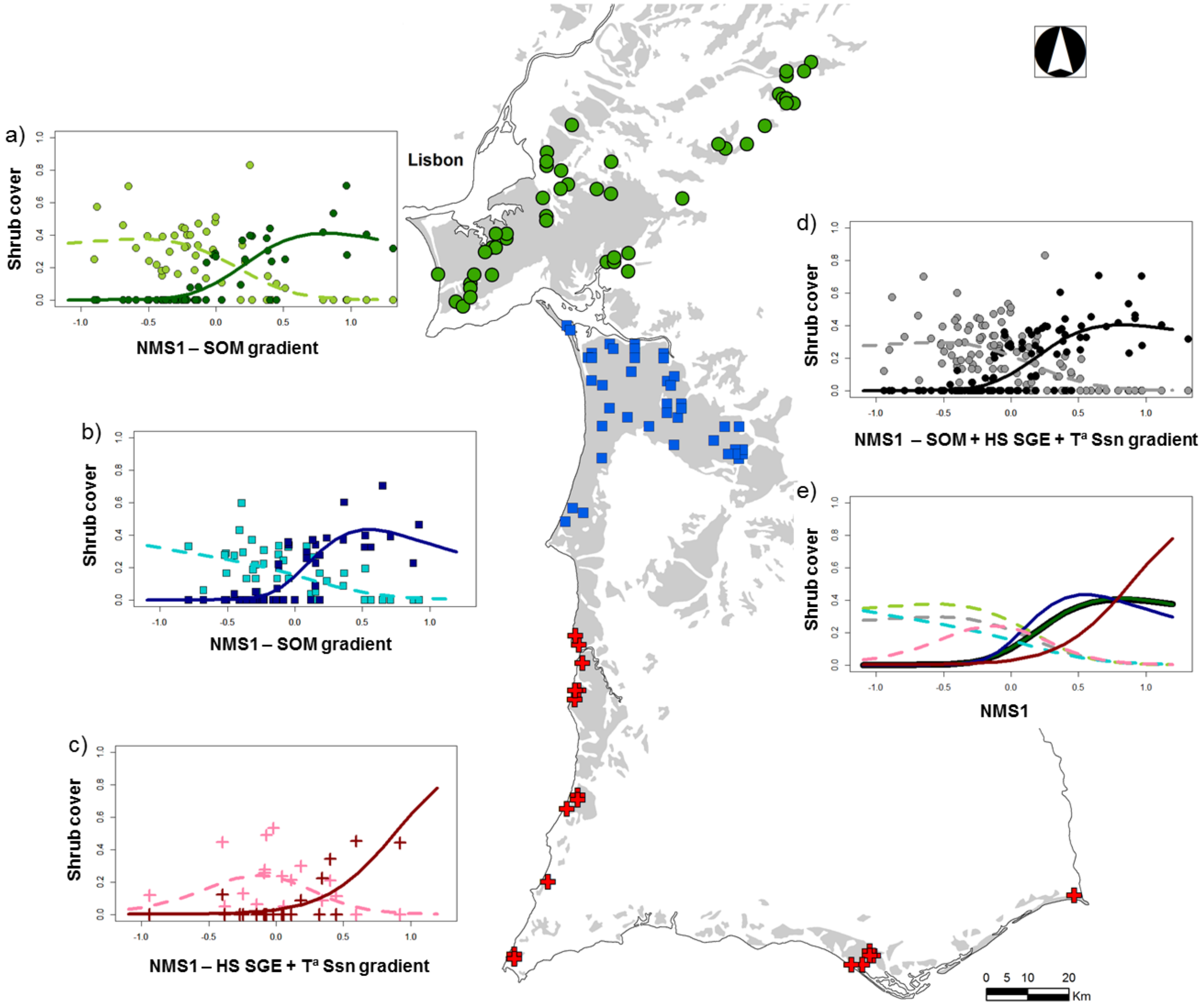


**Figure 6.5** Relationships identified by Generalized Additive Models of the binomial family between *S. genistoides* (in pale coloured and dashed lines) and *U. australis* (in dark coloured and continuous lines) cover and the first axis of the ordination based on scrub cover (NMS1) in a) Setúbal Peninsula region, circles, b) Comporta region, squares, c) South/South-Western region (SSW), crosses and d) all sites. In e) all the fits of the models are included for visual comparison. SOM: Soil organic matter; HS SGE: Habitat suitability of *S. genistoides*; and Tª Ssn: Temperature seasonality.

respectively; Trabucco and Zomer 2009; AEMET-IM 2011). It is likely that, under these drier conditions, *S. genistoides* communities result from shrub encroachment in poorer and more disturbed soils. In contrast, *U. australis* communities would persist in better-preserved soils as “residuals” of the original community (i.e. plant propagules and chemical and physical properties of once-inhabited sites, in the sense described by

MacMahon 1980; see Chapter 1), occupying sites with a developed hardpan layer (see chapters 2 and 5). These processes would underline the importante role of historical processes in successional dynamics, linking previous to present landscapes and highlighting that different successional patterns can be produced by historical differences (Drake 1990).

The factors determining successional dynamics change between Setúbal and Comporta regions and the South/South-Western region. The latter presents the lowest levels of habitat suitability for both *S. genistoides* and *U. australis.* Populations of the communities dominated by both species in the SSW region occur in locations with highly significant differences in habitat suitability (average ≈ 0.5) compared to both Setúbal Peninsula and Comporta regions (> 0.9) (see Figure 5.5). Communities occurring far from their climatic optimum are thought to be more dependent on environmental conditions than on biotic interactions (see *facilitation waning models* in Soliveres *et al.* 2011). This would justify the high predictive power of *S. genistoides'* habitat suitability and temperature seasonality for explaining the successional gradient in SSW region. As a consequence of the importance of environmental constraints for the occurrence of these species under conditions near the limit of their abiotic niches, *S. genistoides* communities prevail in areas with drier conditions and larger variations in temperature throughout the year, while *U. australis* communities are unable to overcome these environmental constraints, being successful only in wetter and more isothermal locations. This result evidences that succession patterns may occur in space associated with environmental gradients due to the inhibition of their inherent successional dynamics under conditions that are particularly harsh for several of the species involved in the succession.

## 6.3 Refining the taxonomy of *Stauracanthus* Link.

*Stauracanthus* taxonomy is not yet completely consensual (see Chapter 4). But analysis of the relationship between floral bracteole sizes, that are commonly used in taxonomic studies to differentiate *Stauracanthus* specimens, and the four climate variables most relevant to characterize their distribution (seasonality of precipitation, isothermality, annual range of temperature, and mean temperature of the coldest quarter) clearly separated *S. genistoides* and *S. spectabilis sensu lato* (see confidence ellipses in Figure S4.2). However, the analysis of the bracteoles failed to discriminate between *S. spectabilis* subspecies. Since the taxonomy of a species is typically recognized by gaps in the patterns of variation in individual morphological characters (Zapata and Jiménez 2012), the existence of a continuous gradient in bracteole width in the studied specimens indicates the existence of a single taxon presenting phenotypic plasticity in bracteole morphology. These findings support Paiva and Coutinho (1999) taxonomy, that differentiates three species: *Stauracanthus boivinii* (Webb) Samp., distributed throughout Western Iberia and North Western Africa; *S. genistoides* (Brot) Samp., and *S. spectabilis* Webb, both growing on coastal sandy soils in South-Western Iberia. Futhermore, our results reject the recognition of the taxa *S. spectabilis* ssp. *vicentinus* based on the existence of individuals with intermediate floral character states, namely bracteole width, between the type forms of both *S. spectabilis* ssp *spectabilis* and *S. spectabilis* ssp. *vicentinus*.

## 6.4 Preserving inland dune xerophytic shrub communities in Portugal

Xerophytic shrub communities on stabilized dunes in SW Portugal are home for an important number of rare, endangered and endemic plant species such as *Armeria rouyana, Euphorbia transtagana, Jonopsidium acaule, Thymus capitellatus or*

*Santolina impressa* (see Chapter 1). The relevance of their flora led the Portuguese government to the establishment of the Site of Community importance (SCI) Comporta-Galé under the Habitats Directive, with approximately 310 $Km^2$ where these habitats dominate the landscape. Additionally, these habitats have a significant presence in other SCIs, namely in Fernão Ferro-Lagoa da Albufeira, Costa Sudoeste and Estuário do Sado. The conservation strategies applied in these sites are focused on the endangered species and/or in the habitats listed in the Annexes of the Habitats Directive. Consequently, processes occurring above these organizational levels are not addressed, and important ecological functions or species depending on heterogeneous landscape may be missed (Noss 1987). Nevertheless, ecologists have recognized that successional patterns are critical to the sustainability and maintenance of biodiversity (e.g. Noss 1990; Levin 2000) and, therefore, to successful conservation. Further, many ecologists have long underlined the importance of including the diversifying effects of disturbance to maintain the natural landscape mosaic (e.g. Pickett and Thompson 1978). More recently, several works stressed the role of disturbance (Fuhlendorf *et al.* 2006) in maintaining biological diversity while others highlighted the need of protected areas integrating different successional stages to guarantee the conservation of both species requiring heterogeneous landscapes and species linked to certain successional stage (Martín and Lopez 2002; King and Schlossberg 2014).

Accordingly and since *Juniperus navicularis*, *Stauracanthus genistoides* and *Ulex australis*-dominated communities could in fact be continuous successional stages of a single entity (see Figure 6.1), a change of strategy in the preservation of these communities is needed, aiming to ensure the successional dynamics between *S. genistoides* communities towards the other two communities. Additionally, monitoring both conservation practices and habitat quality is necessary, especially for these habitats directly impacted by human activities, namely forestry, agriculture and tourism. In fact, although the importance of disturbance in the successional dynamics between *J. navicularis* and *S. genistoides* and *U. australis* communities was not directly demonstrated in this work, other authors stressed the role of disturbance in the dynamics between them (see Chapter 2), underlining the necessity of linking monitoring and management to successfully achieve the aim of preserving the natural functioning of these communities and, potentially, introduce active management to guarantee their successional dynamics.

Nonetheless, the tough character and attractiveness of several plants of these communities make them ideal species for landscape design, roadside revegetation and gardening within their area of distribution. The capacity of these species of enduring over the long term without watering, their low nutrient requirements and relative low growth would significantly reduce the need of maintenance practices.

## 6.5 Concluding Remarks

To summarize, during this PhD work I found that the patchy distribution of xerophytic plant communities on inland sandy habitats in SW Portugal mainly responds to local (i.e. soil organic matter), and regional (i.e. climate) factors. A conceptual model including the successional dynamics between the three communities studied, and where facilitation and competition mechanisms play a key role was proposed. This model was supported by further analyses of the variation of both drivers and functional diversity along the successional community changes.

Additionally, this work highlights the need of a paradigm shift in the management of inland dune xerophytic shrub habitats for conservation, precisely due to their successional character. Only dynamic conservation strategies capable of identifying spatial and temporal changes and perform different actions to adapt to them will be able to ensure the preservation of the natural functioning of this landscape.

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