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SYNOPSIS

Community dynamics of stabilized dune xerophytic shrubs

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Abstract. To conciliate the individualistic and holistic paradigms dominating community ecology, I analysed the main factors driving the distribution of xerophytic shrub communities at different scales. I found that the patchy distribution of xerophytic shrubs in southwestern Portugal mainly responds to both local (i.e., soil organic matter) and regional (i.e., climate) factors, confirming the importance of processes acting at different scales. I propose a conceptual model including the ecological dynamics of these communities supported by the analyses of both kinds of drivers and changes in functional diversity. The ecological dynamics between the communities dominated by *Stauracanthus genistoides* and *Ulex australis* throughout their co-occurrence area were significantly consistent, despite the factors driving this successional gradient changing regionally. An integrative approach for linking species diversification and distribution assessed the role of edaphic and climatic requirements in the current parapatric distribution of the three species of the genus *Stauracanthus*.

Keywords. biogeography, community ecology, ecological niche, functional diversity, succession .

Introduction

Describing ecological communities as either dynamic or static entities is a dilemma that has accompanied ecology since the beginning of the last century. Clements (1916) described communities as closed structures, where local interactions between species, mainly competition and facilitation, play a major role in determining community composition. On the other hand, Gleason (1917) defined communities as assemblages of species where local habitat selection and regional scale processes act by filtering the existing species pool. The challenge of combining both concepts is currently done mainly by 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 limitations to local coexistence (Guisan and Rahbek 2011). Then, local species composition and community dynamics will respond to ecological processes, named assembly rules, selecting for or against species from the regional species pool (Götzenberger et al. 2012)

Stabilized sand dunes occur at the inland limit of coastal sand dunes. Under a Mediterranean climate they frequently present patchily distributed shrub communities (Zunzunegui et al. 2005). Several studies emphasize the role of water availability in explaining such patchiness (Díaz Barradas et al. 1999, Muñoz-Reinoso and García Novo 2005). These communities are affected by severe environmental stresses and several biotic interactions are described for dune habitats providing an appropriate system for studying the duality between assemblages and communities and factors determining communities' composition and distribution.

In this context, I studied the spatial and ecological dynamics (defined as variations in community composition; Cottenie 2005) of the xerophytic shrub communities growing on stabilized sand dunes in southwestern Portugal at different scales. These communities are typically characterized by their dominant species, namely *Juniperus navicularis*, *Stauracanthus genistoides* and *Ulex australis*. More precisely I aimed:

1) to provide a broader understanding of the community dynamics of xerophytic shrubs occurring on stabilized sand dunes by analysing the main drivers acting on these communities and identifying the key functional traits associated to their dynamics,
2) to evaluate whether local communities of xerophytic shrubs follow a consistent 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 constraints as the main drivers of community assembly.

Additionally, and because I found that main factors driving community dynamics in *S. genistoides* and *U. australis* communities do vary according to the suitability of scenopoetic conditions for their dominant species (Chozas 2016), I analysed the effects of environmental factors on the distribution on these two key species. Further, aiming to understand whether current distributions of both species also depended on drivers other than environmental ones (such as phylogenetic and biogeographic factors) and potentially affect community dynamics, I enlarged the analyses to the three species of the genus *Stauracanthus* (Chozas et al. 2017a). Complex taxonomical disagreements prevented me from performing similar analyses for the genus *Ulex*.

Sampling and Data

A conceptual model of xerophytic shrub communities on stabilized dune dynamics

Shrub cover, soil characteristics, land use cover, climatic and topographical variables and human disturbance were assessed in 70 sites selected randomly throughout an area of about 1700 km^2 of inland sandy soils on the Peninsula of Setúbal and Alentejo coast (Portugal), with the aim of determining the main drivers acting on xerophytic shrub communities at different scales (Chozas 2016). To validate the geographical consistency of the community dynamics of these communities, 45 additional sites were sampled throughout all inland sandy soils of the southwestern (SW) Iberian Peninsula between the left margin of the Tagus River (38°53’N, 8°49’W) and the Guadiana River Estuary (37°10N, 7°24’W), totalling 115 sites and about 2900 km^2. Then, these sites were divided in three regions: Setúbal Peninsula, Comporta and south/south-western (SSW) regions, following geographical, sand morphogenesis, dominant land use and connectivity criteria.

PCA performed with climate data and altitude and Non-metric Multidimensional Scaling (NMDS, McCune and Grace 2002) of the cover of the eighteen most abundant shrubs were used to describe environmental and changes in species composition respectively. To identify the drivers affecting changes in composition, I examined the relationships between the NMDS axes and the explanatory variables through Spearman correlation tests. The effects of main drivers on communities were assessed through Mantel Tests (Legendre and Legendre 1998), taking spatial structure into account.

Twenty-six traits associated with climate, competitive ability, disturbance and defense were selected to fully characterise the adaptive responses of the previously identified xerophytic shrubs to environmental variables and/or provide significant insights into competitive ability and defence against herbivory (Wright et al. 2006). Trait values for species were determined by field work and literature. Trait variations were described by the community weighted mean of the studied traits. Functional diversity was assessed using three functional indices described by Villéger et al. (2008), namely functional richness, functional evenness and functional divergence, as well as Rao’s quadratic entropy (Botta-Dukát 2005). The functional responses through successional gradients were analysed by performing Spearman correlations between functional groups and traits and NMS axes and overlaying the significant variables onto the community ordination (Matos et al. 2015). Generalized Additive Models (GAMs; Wood 2006) were used to model both the community dynamics and the variations of functional indices across environmental gradients.

Factors affecting shrub communities across Setúbal Peninsula, Comporta and SSW regions were evaluated via the role of a set of explanatory variables namely: [i] local microenvironmental conditions identified (Chozas et al. 2015), [ii] mesoscale environmental gradients, i.e., macroecological constraints *sensu* (Guisan and Rahbek 2011), and [iii] the individualistic responses of keystone species to these mesoscale gradients, i.e., habitat suitability *sensu* (Guisan and Rahbek 2011). First, keystone species were identified by calculating their indicator value (IndVal; Legendre and Legendre 1998, Wood 2006) then, their realized environmental niches were modelled using ENFA (Chefaoui et al. 2005) and, finally, the potential distributions of these species were calculated by means of Mahalanobis distance (MD; Farber and Kadmon 2003). 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). Finally, to evaluate whether there is any structure in the co-occurrence of indicator species in the studied communities, I calculated the checkerboard score (C-score; Stone and Roberts 1990).

Distribution, environmental niche and diversification patterns in Stauracanthus *Link*

Seven hundred and forty presence records of the three *Stauracanthus* species—*S. boivinii, S. genistoides* and *S. spectabilis*—were collected from herbaria, literature and Flora-on database[1] (Pereira et al. 2016). Thirty-nine topographic and climatic variables were extracted from the WorldClim interpolated map database (Hijmans et al. 2005) and from the EDIT Geoplatform[2]. Then, those variables with high correlations were excluded, resulting in a second set of 14 potentially explanatory variables. To characterize the environmental requirements of *Stauracanthus* species in the Iberian Peninsula, the bioclimatic niche and the potential distribution of the *Stauracanthus* species were estimated using ENFA (Ecological Niche Factor Analysis; Hirzel et al. 2002)) and Generalized Linear Models (GLMs; McCullagh and Nelder 1989). The environmental niche overlap was assessed using Schoener's index. Data provided by Pardo et al. (2008) for 19 different populations of *Stauracanthus* species in the Iberian Peninsula and north-western Africa were used to assess the genetic distance between *Stauracanthus* populations. The pairwise distance between all individuals was calculated using the module available at GenalEx for haploid SSRs (Peakall and Smouse 2006, 2012).

Results and Discussion

A conceptual model of xerophytic shrub communities on stabilized dune dynamics

I found that both local and regional factors drive the distribution of xerophytic shrub communities on the stabilized dunes of SW Portugal (Chozas et al. 2015). Species composition and abundance varied mainly according to changes in soil organic matter 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. Moreover, variations in aridity discriminate between sites with or without *Juniperus navicularis* (Fig. 1). I propose a conceptual model reflecting a "classical" plant community succession where changes in plant composition result of autogenic changes in resource availability, mainly light, nutrients and water (see e.g., Grime 1977). Although I did not assess the effect of species interaction directly, data are consistent with a successional model 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 incorpora-

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1 http://flora-on.pt/#/1Stauracanthus+genistoides; last accessed 4 June 2015
2 http://edit.csic.es/GISdownloads.html; last accessed 19 October 2013

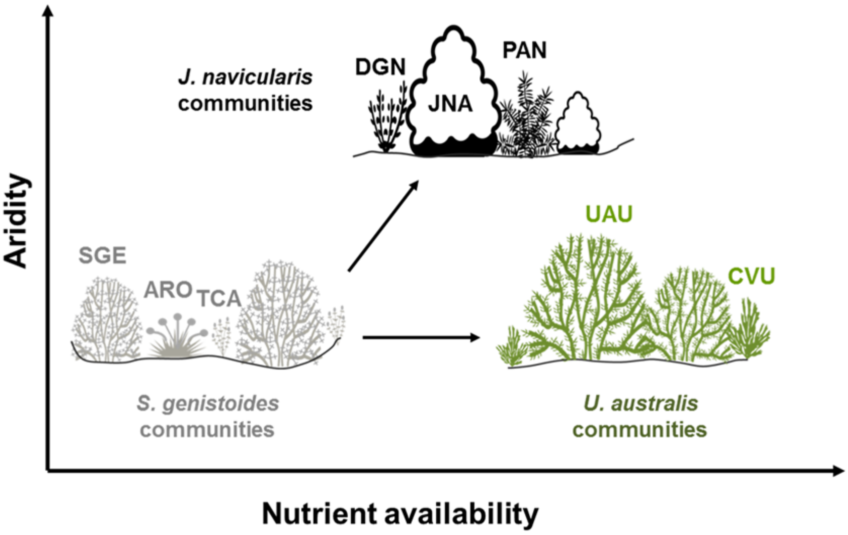

Figure 1. Conceptual model of the xerophytic shrub community dynamics on stabilized dunes of the southwestern Iberian Peninsula. I propose that scrub dynamics in Alentejo coast and Peninsula of Setúbal are mainly determined by the soil nutrient matter content, driven by successional processes, and water 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*.

tion into the soil, thereby enhancing light and nutrient competition eliminating colonizer species. This model is also supported by the substitution of *Ulex australis* communities by *S. genistoides* communities described by Neto (2002) on highly disturbed sandy loam soils and on sandy soils with the presence of a hardpan layer improving humid edaphic conditions (Neto et al. 2004).

These community changes in the studied system also involve a turnover in key functional traits (Chozas et al. 2017b) and imply variations in species richness, trait dynamics and functional diversity, 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, mainly determined by the presence and dominance of a reduced number of pioneer species shaped by early stage environmental conditions, such as high radiation and low nutrient availability. The transitional stage between *S. genistoides* and *U. australis* is dominated by drought avoiders together with species from both communities, resulting in higher species and functional richness and functional divergence. *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. 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.

I found a remarkable consistency 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. Performed models clearly identified the substitution of *S: genistoides* by *U. australis* along the environmental gradients (Fig. 2), despite the factors driving this successional gradient changing regionally. 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 SSW 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 ex-

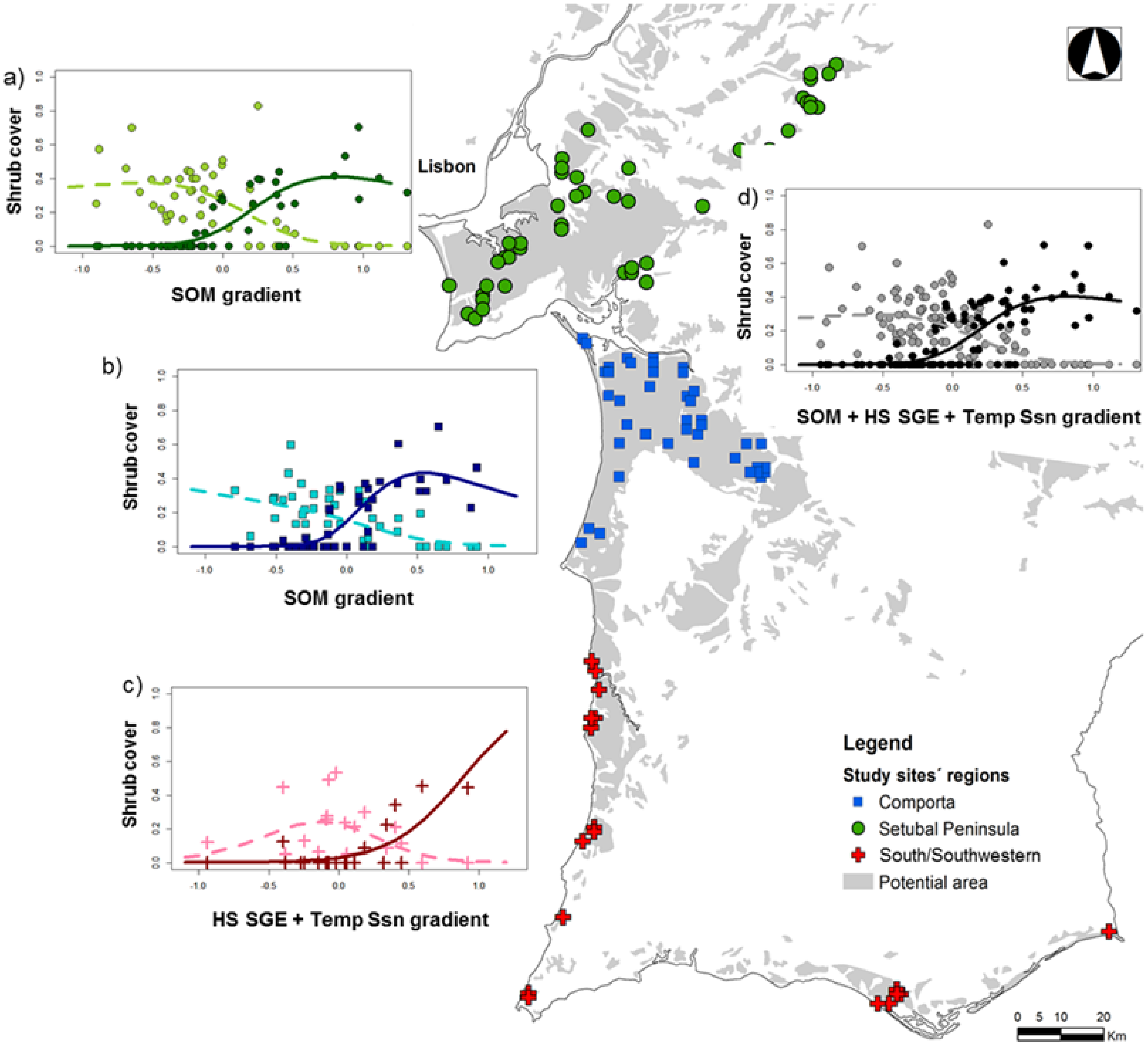

Figure 2. Relationships between the cover of *Stauracanthus genistoides* (in pale dashed lines) and *Ulex australis* (in dark continuous lines) and the environmental gradients defined by the first axis of the ordination based on scrub cover in **(a)** Setúbal Peninsula region, circles, **(b)** Comporta region, squares, **(c)** South/southwestern region (SSW), crosses and **(d)** all sites. The main trends of the relationships were identified by Generalized Additive Models of the binomial family. SOM: Soil organic matter; HS SGE: Habitat suitability of *S. genistoides*; and Temp Ssn: Temperature seasonality.

plaining 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 regulate the relevance of the main factors determining the transition between different successional stages, mainly climatic and historical. In fact, the factors determining successional dynamics change between Setúbal and Comporta regions and the SSW 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). 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). As a consequence of the importance of environmental constraints for the occurrence of these species, *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.

Distribution, environmental niche and diversification patterns in the genus Stauracanthus *Link*

The three *Stauracanthus* species show remarkably similar responses to climatic conditions. This supports that this recently-diversified clade retains common adaptations to climate, thereby explaining the existence of high levels of climatic niche overlap. This contrasts with the diverse edaphic requirements of *Stauracanthus* species. *S. genistoides-spectabilis* clade grows on Miocene and Pliocene fine-textured sedimentary soils while *S. boivinii*, the species genetically more distant, occurs on older and more coarse-textured sedimentary substrates. These patterns of diversification are consistent with a stochastic process of geographic range expansion and fragmentation coupled with niche evolution in the context of spatially complex environmental fluctuations. I concluded that the evolution and current distribution of *Stauracanthus* species has been shaped by edaphic and climatic requirements, as well as by historical events (Chozas et al. 2017a).

Concluding remarks

To summarize, I propose a successional model including the main community dynamics between the three shrub habitats studied. This model is supported by the analyses of the variation of both drivers and functional diversity along the successional community gradients. I also found that drivers of community dynamics in xerophytic shrubs vary across regions. However, species turnover and community stages are remarkably consistent, probably due to the individualistic responses of the species to the drivers and to intrinsic community mechanisms such as facilitation and competition. Additionally, I found that the combined analysis of the distribution, environmental niche and phylogeographic relationships allows integrating the biogeographical, ecological and evolutionary processes driving the evolution of species adaptations and how they determine their current geographic ranges.

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