



Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands



Alice Nunes^{a,b}, Melanie Köbel^a, Pedro Pinho^{a,c}, Paula Matos^{a,b}, Francesco de Bello^d,
Otilia Correia^a, Cristina Branquinho^{a,*}

^a Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, C2, Piso 5, 1749-016 Lisboa, Portugal

^b Departamento de Biologia e CESAM – Centre for Environmental and Marine Studies, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

^c CERENA- Centro de Recursos Naturais e Ambiente, Universidade de Lisboa, Instituto Superior Técnico, Av. Rovisco Pais, 1049-001 Lisboa, Portugal

^d Institute of Botany, Czech Academy of Sciences, CZ-37982 Trebon, Czech Republic

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ABSTRACT

Aridity acts as a strong environmental filter to plants, limiting major ecosystem processes. Climate change models predict an overall increase of aridity in drylands. This could lead to changes in plant communities, particularly in the dominance and range of plant functional traits, which largely determine ecosystem functioning. However, to study how changes in aridity may affect plant functional metrics, a critical decision needs to be taken: the choice of the functional traits to be studied. Previous studies related plant functional traits and aridity, however mostly focusing on a single facet of functional diversity and primarily on perennial species. Hence, the response of plant traits to aridity quantifying different functional metrics at the whole-community level (considering also annual species) is not well established in drylands.

Here, we use a high-resolution aridity gradient along a Mediterranean dryland ecosystem of Holm-oak woodlands to identify plant functional traits responding to aridity at the community-level (comprising annual and perennial species). We studied how the community-weighted-mean and functional dispersion of 13 traits related to plant establishment, growth, reproduction, dispersal and persistence changed with aridity.

Nine plant functional traits varied with aridity. Aridity acted as an environmental filter on community-weighted-means, increasing the dominance of annual species, particularly rosettes, and plants with lower maximum height, shorter flowering duration, and increased anemochorous dispersal. Higher aridity was associated to an overall decrease in functional dispersion, particularly for life cycle, specific leaf area, onset of flowering, dispersal strategy and seed persistence traits, probably due to a lower niche differentiation under more arid conditions. The changes in community-weighted-means and in functional dispersion due to aridity are likely to negatively affect major ecosystem functions such as biomass production and nutrient cycling.

Our results fill an important knowledge gap by quantifying how the functional structure and dispersion of 13 plant traits change with aridity at the whole-community level, providing an important basis for the selection of key functional traits to be used in trait-based studies in drylands.

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1. Introduction

The study of functional traits of organisms in addition to a solely taxonomic approach to diversity is becoming more and more common in ecological studies (Díaz et al., 2016; Kunstler et al., 2016). This is because functional traits may be linked to ecosystem functions, thus providing a more mechanistic understanding of species response to environmental factors, and can also help predict the

* Corresponding author.

E-mail addresses: amanunes@fc.ul.pt (A. Nunes), mkobatista@fc.ul.pt (M. Köbel), paplopes@fc.ul.pt (P. Pinho), psmatos@fc.ul.pt (P. Matos), fradebello@ctfc.es (F.d. Bello), odgato@fc.ul.pt (O. Correia), cmb Branquinho@fc.ul.pt (C. Branquinho).

effect of species on ecosystem processes (e.g., primary productivity, nutrient cycling) (Cadotte et al., 2011; Lavorel and Garnier, 2002; Mason and de Bello, 2013; Tobner et al., 2014). The functional structure and diversity of a community are most commonly defined as the mean value and range of species functional traits in that community (Díaz et al., 2007a; Lavorel et al., 2008).

Whatever the objective of the use of functional diversity may be, there is a critical decision to be taken: the choice of the functional traits to be studied at the community-level. Traits should be selected according to their responsiveness to a certain factor or to their effect on ecosystem processes. Measuring species traits is often laborious and time consuming, hence many trait-based studies addressed at the community-level rely on trait data retrieved from scientific literature or trait databases (Díaz et al., 2016; Kattge et al., 2011; Kunstler et al., 2016). Many functional traits may not vary independently but rather co-vary, reflecting patterns of resource allocation or trade-offs among plant strategies, and different combinations of traits may be adopted by species under different environments to maximize their performance (Maire et al., 2013; Volis and Bohrer, 2013; Costa-Saura et al., 2016; Díaz et al., 2016). However, to assess which functional traits are affected by a certain driver and check if and how they co-vary, it is indispensable to begin with an individual evaluation of each trait.

The functional traits of a biological community are most commonly described by two complementary community-level metrics (Díaz et al., 2007a; Lavorel et al., 2008). One is functional structure or the so-called community-weighted-mean (CWM), which reflects the dominant traits in a community (Garnier et al., 2007). It is based on the mass ratio hypothesis, according to which dominant species exert a key effect on ecosystems (Grime, 1998). CWM enables to quantify community shifts in mean trait values due to environmental selection for certain functional traits, associated to the replacement of dominant or subdominant species with particular traits by other(s) with different traits. The other component is trait range or functional dispersion (FDis), which reflects the degree of functional dissimilarity among the community, and can be expressed through various metrics (Laliberté and Legendre, 2010; Mason et al., 2005; Villeger et al., 2008). Functional dispersion may be used to quantify the decrease or increase in trait dissimilarity along ecological gradients compared to a random expectation (i.e. trait convergence or divergence, respectively). Communities characterized by a high functional dispersion lead to a more complete utilization of resources, and thus to increased ecosystem functions, such as biomass accumulation or decomposition, according to the niche complementary hypothesis (Tilman et al., 1997; Tobner et al., 2014). Both community-level functional metrics (CWM and FDis) were reported to respond to major environmental filters such as climate, disturbance regime or biotic interactions, and to affect major ecosystem processes like primary productivity or decomposition rates (De Bello et al., 2010; Díaz et al., 2007a; Mouillot et al., 2013, 2011; Valencia et al., 2015).

Aridity acts as a strong environmental filter on plant communities (e.g. determining species presence/absence) and limits major ecosystem processes such as primary productivity and nutrient cycling (Delgado-Baquerizo et al., 2013). Climate change predictions point to an overall increase of aridity in drylands worldwide (Dai, 2013; IPCC, 2007). This could lead to changes in vegetation structure and composition and alter the dominant plant traits (CWM) and the FDis of dryland communities. Increasing aridity may change the dominance of distinct life-forms in the community (Noy-Meir, 1973), and favor particular growth-forms (e.g. grasses, species with a prostrate habit) (Fay et al., 2002) that may confer higher ability to withstand dry periods. Also, aridity may select for smaller species (Gross et al., 2013), as a strategy to reduce the risk of cavitation under increased water stress (Enquist, 2002). Aridity may select for an earlier flowering onset and shorter flowering

duration (Hänel and Tielbörger, 2015; Kigel et al., 2011), as a way to reduce the risk of reproductive failure as the dry season progresses. Aridity may also affect dispersal strategies and promote higher seed mass and seed longevity (Baker, 1972; Arroyo et al., 2006; Metz et al., 2010; Arellano and Peco, 2012), thus increasing the chances of survival and persistence under dry environments (Volis and Bohrer, 2013; Gremer and Venable, 2014). Increasing aridity may favor species with a particular type of root system, more able to maximize water and nutrients acquisition during short peaks of resource availability (Schenk and Jackson, 2002) or, on the contrary, promote the coexistence of a wide variety of root systems, capable of a more complete resource utilization. Finally, for perennial species, aridity may favor stress-tolerant strategies e.g. evergreen leaves with low specific leaf area (SLA) (Ackerly et al., 2002; Costa-Saura et al., 2016). However, in the most arid conditions these species can be replaced by short-lived stress-avoidant species with semi-deciduous leaves and high SLA (Ackerly et al., 2002; Gross et al., 2013). In addition to possible changes in trait dominance, aridity may also modify community FDis of particular traits, by selecting a wider or narrower variety of coexisting functional strategies or trait values. A previous work found a higher than expected functional dispersion of leaf traits within dryland communities, attributing it to the high specialization of the flora to drought adaptation (Freschet et al., 2011). Contrastingly, other work found decreased functional dispersion of particular traits in response to aridity (e.g. plant height), suggesting that different traits may respond differently to aridity (Gross et al., 2013). Changes in community FDis may have important consequences for ecosystem functioning and resilience. This is because a high FDis is expected to lead to improved ecosystem functioning (Díaz et al., 2007a; Mouillot et al., 2011; Tobner et al., 2014). In addition, high FDis has been hypothesized to increase the resilience of dryland ecosystems to aridity (Voltaire et al., 2014), because it would enhance the chances that some species could survive under more arid conditions, thus maintaining ecosystem functioning (Díaz et al., 2007a).

Previous studies have tried to examine the relationship between plant functional traits and aridity. Although all of them contributed to partially clarify this subject, there is no clear picture about which are the main plant traits responding to aridity, particularly at the whole-community level. The main limitations of previous studies are: (i) addressing simultaneously other environmental factors interacting with aridity (Adler et al., 2004); (ii) studying only one component of functional traits, e.g. the CWM (Barboni et al., 2004); (iii) using low-resolution gradients e.g. no more than five sites under different aridity levels (De Bello et al., 2005; Frenette-Dussault et al., 2012; Lavorel et al., 2011); (iv) studying aridity impacts on particular (few) species (Hänel and Tielbörger, 2015) or only on perennial species (Gross et al., 2013; Valencia et al., 2015; Costa-Saura et al., 2016), not considering the whole plant community. The latter reason is a major shortcoming, considering that annual species constitute an important part of the diversity of dryland plant communities (Aronson et al., 1993; Noy-Meir, 1973). In addition, annuals play a critical role in ecosystem functioning, e.g. in energy flow and nutrient cycling (Baldocchi et al., 2004; Gilliam, 2007; Ramos et al., 2015). They have a faster species turnover than perennials, and thus are expected to respond more readily to environmental changes. To our knowledge, for many plant traits it remains unclear whether their community-weighted-mean and functional dispersion respond simultaneously to aridity (i.e., if both change), and, if so, if their response is similar (e.g. increasing or decreasing). Clarification could be improved if works contemplated a higher number of plant traits addressed at the whole-community level along aridity gradients with higher resolution.

In this paper, we propose to identify plant functional traits responding to aridity in a Mediterranean dryland ecosystem. To

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