

Lichen traits responding to aridity

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Summary

1. Climate change is expected to cause several impacts at the global scale, and drylands will be amongst the most affected areas. Thus, investigating how these changes will affect the composition, structure and functioning of dryland ecosystems has become a priority. From an ecological indicator point of view, several works have shown that functional diversity is better than species richness to understand ecosystem functioning or response to environmental factors. However, most of these works focus on plants, while those of other organisms remain largely unknown. Lichens are amongst the ecosystem components more sensitive to climatic changes due to several physiological and ecological characteristics. Their poikilohydric nature (therefore highly dependent on the atmosphere for water supply) and their ubiquity on terrestrial ecosystems underlie their potential as indicators of climate. Nonetheless, works specifically aiming to identify lichen functional traits that respond to aridity remain poorly explored, particularly in drylands.

2. We proposed to identify lichen functional traits and respective functional groups responding to aridity in a Mediterranean drylands ecosystem.

3. Lichen diversity was sampled in open holm oak woodlands along an aridity gradient in SW Europe (Iberian Peninsula). Lichen functional traits that could be easily identified and related to water uptake were selected to be tested: type of photobiont, growth form and reproduction strategy.

4. Lichen species composition was related to the aridity gradient. The three traits chosen were related with the community's response to aridity, but with contrasting responses in different functional groups. More specifically crustose and fruticose lichens, isidiate species and the ones with *Trentepohlia* as photobiont were related to the less arid part of the gradient. Foliose species and cyanolichens, on the contrary, were associated with the most arid areas.

5. Synthesis. We were able to identify lichen traits responding to aridity. Type of photobiont was particularly responsive, with *Trentepohlia* and cyanobacteria functional groups, responding clearly in contrasting ways to aridity in this drylands ecosystem. This work emphasizes functional diversity role on understanding and assessing the response to environmental factors, namely to climate. It also highlights the potential use of lichen functional groups as ecological indicators of climate change.

Key-words: determinants of plant community diversity and structure, drylands, functional response groups, growth form, photobiont type, reproduction type, semi-arid

Introduction

Drylands cover 41% of terrestrial ecosystems (Reynolds *et al.* 2007) and concentrate around 38% of world population (IPCC 2007). Within dryland ecosystems, semi-arid and dry-subhumid together share 29.7% of world population representing 23.9% of land surface (IPCC 2007), with dryland rangelands accounting for 50% of the world's livestock (MEA 2005). These extremely important socio-ecological

areas (Maestre, Salguero-Gómez & Quero 2012) are highly susceptible to climate change (IPCC 2007). For this reason, research on how global change will affect the composition, structure and functioning of dryland ecosystems and how in turn these changes will impair the wide range of services they provide (as the example given for livestock) and which support people livelihood and well-being has been considered a priority by scientific community (IPCC 2007).

From an ecological indicator perspective, several works have shown that functional diversity is better than species richness to understand ecosystem functioning or response to

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environmental factors, as it takes into account the redundancy of species in ecosystems and includes the information of species functional traits (Lavorel *et al.* 2011). Functional traits are characteristics of an organism considered to be relevant to its response to the environment and/or its effects on ecosystem functioning and its value and range in a given ecosystem are, by definition, a measure of its functional diversity (Díaz & Cabido 2001). Functional diversity is currently regarded as a crucial component within the ones affecting ecosystem services provision (Díaz *et al.* 2006; de Bello *et al.* 2010). In fact, a framework linking response and effect traits – the response–effect framework – has been used to predict changes in ecosystem services (Lavorel & Garnier 2002). However, much of these promising results have been focusing on functional characteristics of plants, while those of other organisms remain largely unknown (Lavorel 2013).

Lichens are amongst the most sensitive organisms to environmental changes, signalling it before other less sensitive components of the ecosystems (Pinho *et al.* 2009, 2011, 2014). For that reason, they have long been used as ecological indicators. The use of lichen sensitivity to map air pollution (De Sloover & LeBlanc 1968), or to estimate SO₂ deposition (Hawksworth & Rose 1970) and the first signs of SO₂ decay (Rose & Hawksworth 1981), are just some of the striking examples of its historical use as ecological indicators of air pollution. Currently, works have also shown that they respond to global warming (Aptroot & Van Herk 2007; Ellis *et al.* 2007; Colesie *et al.* 2014). This sensitivity is related to their physiological characteristics. Lichens are a symbiotic association between a fungus and a photosynthetic partner and exist in a variety of land ecosystems, ranging from Antarctica to the deserts. These organisms are poikilohydric, meaning that they cannot regulate their water content, which fluctuates to be in equilibrium with the surrounding environment (Green, Sancho & Pintado 2011). This external water dependence ultimately regulates their physiological activity, as wet environmental conditions hydrate and activate them, while under dry environmental conditions, they become inactive (Green, Sancho & Pintado 2011). Even though they are usually considered as slow-growing organisms, this dependence on the atmosphere enables them to respond to a climate shift on a time interval as short as 5 years placing them within the most sensitive responding to climate change (Aptroot & Van Herk 2007), which usually considers a time-scale of around 30 years. Nonetheless, although some works have been carried out in cold regions (Antarctica mainly) relating temperature gradients with species richness of lichens and other poikilohydric organisms (hepatics and bryophytes) (Green *et al.* 2011) or using lichenometry (Sancho, Allan Green & Pintado 2007) under the current context of climate change, very few works have used them specifically as indicators of macro and microclimate (Giordani & Incerti 2008; Pinho, Máguas & Branquinho 2010; Marini, Nascimbene & Nimis 2011; Giordani *et al.* 2012, 2013; Colesie *et al.* 2014). However, works specifically aiming to identify lichen functional traits that respond to aridity remain poorly explored, particularly in drylands.

The objective of this work was to identify lichen key functional traits and respective functional groups that respond to aridity in a drylands ecosystem. We focused on how lichen composition varied along an aridity gradient, and how lichen functional diversity responded to this environmental driver, trying to identify the most relevant response traits to this response [a set of organisms sharing similar responses to the environment (Díaz & Cabido 2001)]. This was performed by sampling epiphytic lichens in south-west Mediterranean Europe along an aridity gradient within the semi-arid and on the border of its transition to the dry–subhumid.

Materials and methods

STUDY AREA

The study was carried out in SW Europe (Iberian Peninsula), comprising 54 sampling sites distributed along Portugal and Spain. Lichen diversity was always sampled in open holm oak woodland, known as *Montado* in Portugal or *Dehesa* in Spain. Montado is a man-shaped savanna like ecosystem (agro–forestry–pastoral system) with a sparse tree cover (30–100 trees per ha) dominated by evergreen oaks (holm oak, *Quercus ilex* L., and/or cork oak, *Quercus suber* L.) (Pereira & Da Fonseca 2003; Bugalho *et al.* 2011). Grasslands, fallows and cereal crops compose its understorey and are sometimes scattered with mixed shrub formations (Pereira & Da Fonseca 2003; Bugalho *et al.* 2011). Sampling was performed along an aridity gradient across the semi-arid and up to the dry–subhumid climate (Fig. 1). We considered the aridity index (AI) of the United Nations (Atlas 1992), representing the ratio of mean annual precipitation to mean annual potential evapotranspiration. According to the UNEP classification, drylands are tropical and temperate areas with an AI < 0.65 and subdivided into four classes: hyper-arid (AI < 0.05), arid (0.05 < AI < 0.20), semi-arid (0.20 < AI < 0.50) and dry–subhumid (0.50 < AI < 0.65). The gradient in our work was established within the semi-arid and ranged between 0.3 and 0.5.

SAMPLING

Lichen epiphyte communities were sampled on holm oak (*Q. ilex* L.) trees following a standard protocol (Asta *et al.* 2002). In each of the 54 sampling sites, a plot was established of c. 50 m radius and a minimum of 1 and a maximum of 10 trees were sampled (according to the number of suitable phorophytes found at each plot), with a total of 345 trees. A 10 cm × 50 cm grid divided in 4 10-cm squares was placed on the four main aspects of the trunk (N, E, S, W), and all lichen species occurring in the quadrats were identified, and the number of quadrats where each species appeared was registered as its frequency. The uppermost part of the sampling grid was placed at 1.5 m from the ground following a standard protocol (Asta *et al.* 2002) and that height was adjusted to a maximum of two metres height when the trunk at the desired height was not suitable for sampling. When the identification was not possible in the field, samples were collected and taken to the laboratory for identification.

LICHEN DIVERSITY

A total of 161 species were identified and classified according to three traits (see Table S1 in Supporting Information). In Southern Europe, most works based their functional groups classification on the

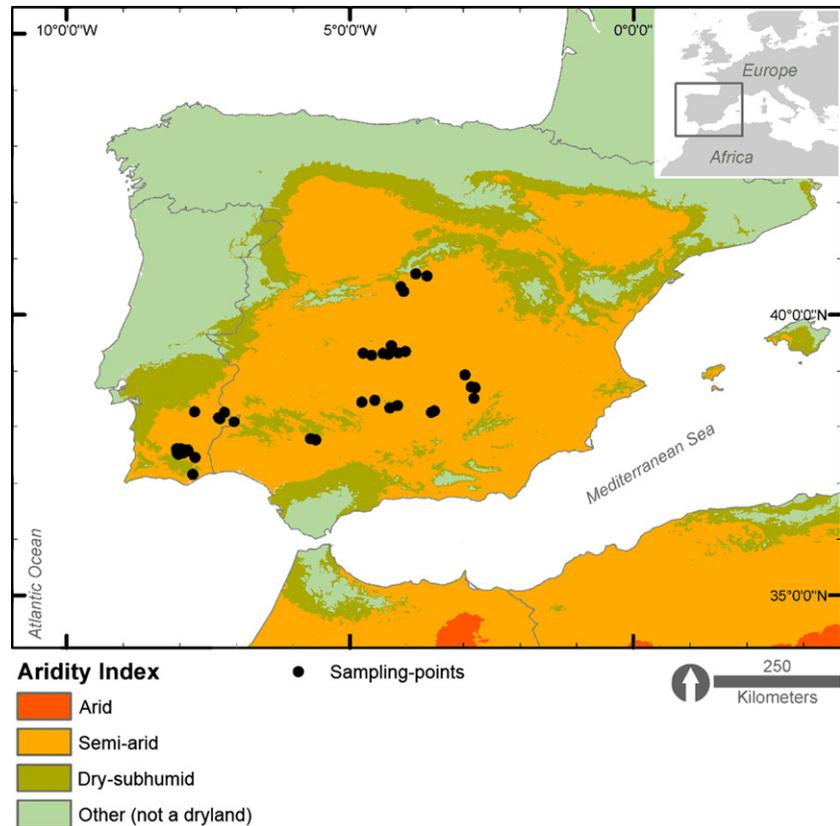


Fig. 1. Map of the study area showing sampling sites and the aridity index (AI) gradient.

Italian data base (Nimis & Martellos 2008), as there is no international data base with lichen species traits as in the case of plants (Kattge *et al.* 2011). This data base classifies species into response traits (e.g. eutrophication tolerance or light preferences) according to expert knowledge based on ecological performance and has been shown to work well for responses to nitrogen (Pinho *et al.* 2011). However, as it is a national data base, not all species of Europe are included. For this reason, to make trait analysis independent of expert judgment assessment and geographical area, we selected photobiont type, growth form and main type of reproduction (Table 1). These are easily measurable lichen traits, that do not need identification to the species level, an important feature when there is a need for universal ecological indicators. Trait classification for each species was retrieved from the Italian lichen data base (Nimis & Martellos 2008). Information on species not present in this data base was taken from the Iberian Lichen Flora (Llop 2007; Giralt 2010; Carvalho 2012) and from The Lichens of Great Britain and Ireland (Smith *et al.* 2009).

Data were used to calculate the LDV index (Lichen Diversity Value) that accounts for species frequency (Asta *et al.* 2002), and it is presented as the mean value for each species of all the trees sampled per sampling site (sampling sites \times species LDV). This species abundance measure was combined with species trait data to obtain the community-level weighted mean (CWM) (Lavorel *et al.* 2008) (see Table 1 for traits and respective functional groups). This index represents the mean trait value (i.e. mean for each of its respective functional groups) in the community, weighted by the abundance of species having those values (Lavorel *et al.* 2008). It is actually the same as relative LDV calculated for groups of species sharing the same trait value. The 'dbFD' function implemented in the FD package (Laliberté & Legendre 2010) of CRAN software R (R Core Team 2013) was used to calculate the CWMs indexes.

DATA ANALYSIS

Statistical analyses were performed using CRAN software R (R Core Team 2013) with VEGAN package (Oksanen *et al.* 2013) (functions 'metaMDS', 'envfit' and 'protest') and STATISTICA 11 (StatSoft, Tulsa, OK, USA). Non-metric multidimensional scaling (NMDS) ordination was performed on a matrix of sampling sites by species LDV to detect prominent gradients in species composition. When using data sets that include large gradients, species LDV values may vary greatly in absolute values due to local site characteristics unrelated to the environmental gradient of interest, biasing results and impairing comparisons. To solve this problem, species LDV values were relativized prior to the analysis and were used as % of total LDV of the sample, in a similar way as CWMs are calculated. Lichenicolous fungi and species identified only to genus level and without complete information on the three traits were excluded from the analysis. For the NMDS analysis, Bray–Curtis distance measure was used, as it has been shown to be one of the most effective measures of samples of species dissimilarities, and for this reason, the one recommended for community data (McCune, Grace & Urban 2002). Data underwent 500 iterations per run, and the best (lowest stress) solution from 500 runs with real data was chosen, each run beginning with a random configuration. The strength of the results was assessed comparing our resulting ordination with the ordination of 500 runs of randomized data (data randomized by column), using the 'protest' function that tests for the non-randomness (significance) between two configurations. The coefficients of determination (r^2) between original plot distances and distances in the final ordination solution were calculated to assess how much variability in lichen community composition was represented by the NMDS axes (McCune, Grace & Urban 2002). AI and CWMs were overlaid in the NMDS ordination (McCune, Grace

Table 1. Traits and related functional groups following (Nimis & Martellos 2008)

Trait	Functional group	Description	Symbol
Type of primary photobiont	Chlorococcoid	With Chlorococcoid (Green algae)	Ch
	<i>Trentepohlia</i>	With <i>Trentepohlia</i> (Green algae)	Tr
	Cyanolichens	With Cyanobacteria	Cy
Growth form	Crustose	Firmly and entirely attached to the substrate by the lower surface	Cr
	Crustose placodioid	Like crustose but with a plate-like form	Crp
	Leprose	Like crustose but surface thallus with a granular mass appearance and always decorticated	Lp
	Squamulose	Composed of small scales	Sq
	Foliose narrow-lobed	Partly attached to the substrate with a leaf-like form and narrow lobes	Fon
	Foliose broad-lobed	Same as Foliose narrow-lobed but with broad lobes	Fob
	Fruticose	3D-like structure, attached by one point to the substrate with the rest of the thallus standing out from the surface of the substrate	Fr
	Fruticose filamentous	Same as fruticose but with filamentous form	Frf
	Type of reproduction	Asexual sorediate	Mainly with soredia or soredia-like structures
Asexual isidiate		Mainly with isidia or isidia-like structures	Ai
Sexual		Mainly sexual reproduction by spores	S

& Urban 2002), and significant correlations between community ordination and these variables were assessed using 1000 permutations (e.g. Jiménez *et al.* 2011). Correlation between individual NMDS site scores and AI and CWMs were also determined using Spearman correlations (ρ), to account for possible nonlinearity in the relationships (correlations were considered significant for $P < 0.05$).

Results

The NMDS ordination joint plot shows species distribution in Fig. 2. This analysis suggested two axes (the addition of a third axis had only a slight reduction in minimum stress) with a final stability of 15.46. Minimum stress of the ordination was lower than would be expected by chance ($P = 0.33$). Most of the variability in lichen community structure was explained by axis 1 ($r^2 = 0.42$), whereas axis 2 explained less variability ($r^2 = 0.27$, Fig. 2). First axis site scores of the NMDS showed to be significantly correlated to the AI (Spearman $\rho = 0.67$, $P < 0.001$), which is assumed to be hereafter the main driver of species ordination. Axis 2 site scores were not correlated to the AI (Spearman $\rho = 0.14$) and because this was our environmental variable of interest, axis 2 was discarded from further analysis.

Some functional group vectors (belonging to all the traits considered) were significantly correlated to the ordination solution and are shown in Fig. 2. Besides determining the correlation between functional groups and NMDS ordination, we also investigated the individual correlations between functional groups and NMDS axis 1 site scores, to establish the isolated effect of our main driver (Table 2). Concerning the type of photobiont, lichens with *Trentepohlia* and cyanolichens were associated to axis 1 of the ordination; the first ones associated to sites with lower aridity, while the opposite is observed for cyanolichens. Also the type of growth form responded to the gradient: crustose and fruticose species were associated to most humid area of the gradient, contrasting with foliose and squa-

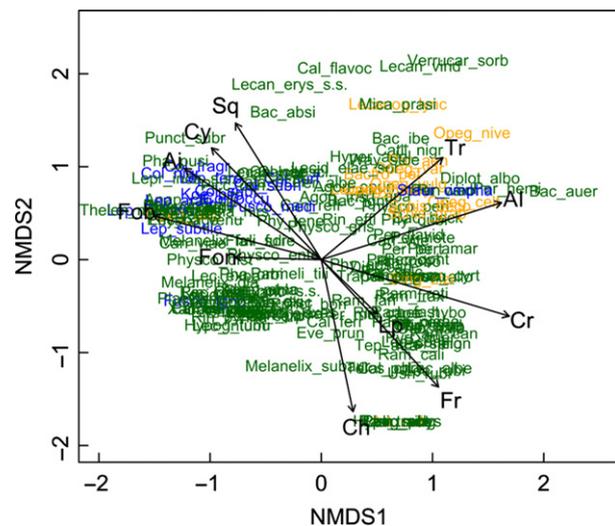


Fig. 2. Non-metric multidimensional scaling (NMDS) analysis of species composition. Vectors represent significant correlations between community composition and environmental (AI) and functional variables (community-level weighted mean). Only vectors with a significant correlation with the ordination ($P < 0.05$) and a significant Spearman correlation ($P < 0.05$) with individual axis 1 site scores (Table 2) are represented to prevent crowding: AI = Aridity index ($r^2 = 0.56$, $P = 0.001$); Tr = lichens with *Trentepohlia* ($r^2 = 0.45$, $P = 0.001$); Cy = cyanolichens ($r^2 = 0.45$, $P = 0.001$); Cr = crustose ($r^2 = 0.61$, $P = 0.001$); Fob = foliose broad-lobed ($r^2 = 0.47$, $P = 0.001$); Sq = squamulose ($r^2 = 0.52$, $P = 0.001$); Fr = fruticose ($r^2 = 0.56$, $P = 0.001$); Ai = Asexual isidiate ($r^2 = 0.47$, $P = 0.001$). Names indicate species' centroids (i.e. species scores along axes 1 and 2) and colours refer to the type of primary photobiont (Tr = orange, Gr = green, Cy = blue). (Final stress = 15.46, $rmse = 5e^{-6}$, $max\ resid = 2e^{-5}$, stress-based $R^2 = 0.98$, fit-based $R^2 = 0.89$.) First axis explains 42% of the variability and the second 27%.

mulose species which were associated to the most arid areas. Regarding the type of reproduction, species with isidia showed to be related to the most arid part of the gradient.

Table 2. Summary of Spearman correlations (ρ) between non-metric multidimensional scaling ordination axis 1 and community-level weighted mean of trait values (functional groups). $N = 54$

Traits	Functional groups	ρ	P
Type of primary photobiont	Ch	0.09	0.500
	Tr	0.52	<0.001
	Cy	-0.42	0.001
Type of growth form	Cr	0.81	<0.001
	Crp	0.22	0.120
	Lp	0.18	0.202
	Sq	-0.43	0.001
	Fon	-0.33	0.015
	Fob	-0.70	<0.001
	Fr	0.48	<0.001
	Frf	0.16	0.234
Reproduction type	As	0.14	0.327
	Ai	-0.57	<0.001
	S	0.24	0.080

Bold values represent significant correlations ($P < 0.05$).

Discussion

Lichen species composition reflected the aridity gradient and allowed the identification of key traits and respective functional groups responding to this driver.

Considering the photosynthetic strategy, different photobiont types showed different responses to aridity. Chlorococcoid algae lichens showed no correlation with species composition along the aridity gradient, probably due to the fact that 83% (134 species) of the species found belong to this group and can be divided into the remaining traits and almost all of its respective functional groups, thus corresponding to a variety of functional traits combination that compromises its use as an indicator group for this range of aridity. On the other hand, lichens with *Trentepohlia* were associated with the less arid areas of the gradient. These species have their optimum in shaded, warm-humid conditions, reason why they are mostly found in subtropical to tropical conditions (Nimis & Tretiach 1995). This combined sensitivity to relative air humidity and temperature may be the reason why they appeared in less arid sites. These sites are closer to the sea, under an Atlantic influence, thus characterized by higher air moisture contents, which favour *Trentepohlia* lichen species. In fact, the same pattern was found in a work that highlighted a photobiont-dependent response to climate in a large-scale pattern of epiphyte lichen species richness in Italy (Marini, Nascimbene & Nimis 2011). In their work, high species richness of *Trentepohlia* lichens was associated with warmer, wetter regions or under maritime influence, while continental areas sustained less species with this functional group, which almost disappeared in inner cold alpine regions (Marini, Nascimbene & Nimis 2011). Lichens having cyanobacteria as a photobiont were also correlated to the aridity gradient, but associated with the most arid areas. It is long known that cyanolichens need liquid water to activate photosynthesis (Lange *et al.* 1993; Green, Sancho & Pintado 2011) and also that they are regarded as highly sensitive to dry conditions

(Pinho, Máguas & Branquinho 2010). In fact, it is not difficult to find references in literature strongly relating cyanolichens occurrence to sites with elevated air moisture contents (Jovan & McCune 2004). Still, most of these were carried out in temperate zones and with a large part of the species forming this functional group characterized as foliose broad-lobed (the emblematic macro cyanolichen species). Thus, one would not expect to find them associated to more arid conditions. However, several works have shown that not only they exist, but they are also common and ubiquitous in dry lands (Belnap, Büdel & Lange 2001; Rogers 2006; Zedda *et al.* 2011; Giordani *et al.* 2013), and even increase with increasing aridity (Concostrina-Zubiri *et al.* 2014). The disparate results can be justified by the fact that cyanolichens associated to drier areas form a group of small-sized species with dark pigmentation (Zedda *et al.* 2011) that has been linked to semi-arid regions (Rogers 2006; Zedda *et al.* 2011; Giordani *et al.* 2013). In fact, a work on the three main hydration sources models for lichens (rain, dew and humid air) (Gauslaa 2014), showed forest cyanolichens responding to rain, as expected, and to a less extent to dew, this later ones corresponding spatially to arid regions. The extreme resistance of cyanobacteria to dry conditions has long been the subject of research, and even a book on the ecology *Nostoc* species, the one present in these dark coloured cyanolichens, is long known (Dodds, Gudder & Mollenhauer 1995; Seckbach 2007; Sand-Jensen & Jespersen 2012). Yet, besides the fact that the dark pigmentation can act as a protection mechanism (Gauslaa & Solhaug 2001; McEvoy, Gauslaa & Solhaug 2007) and that their lower temperature limit is around 0 °C (Green *et al.* 2011), not much is known about the reasons underlying cyanolichens capacity to withstand higher temperatures, intensive solar radiations and lower atmospheric moisture contents. Further work is needed to understand why these dark pigmented cyanolichens respond in such a different way from the non-dark pigmented ones and what traits could be involved in this different behaviour. More importantly, this work highlights the importance of considering these two functional groups of cyanolichens separately in works dealing with the influence of climate.

Regarding growth form trait, crustose and foliose functional groups were associated to the aridity gradient, the crustose preferring lower aridity and the foliose (mainly the broad-lobed but less pronouncedly the narrow-lobed ones) associated to higher aridity sites. The same pattern was found in Italy in response to rainfall gradients, where crustose species were found to be associated with plots with higher precipitation (Giordani *et al.* 2012). Also in Scotland, foliose species showed to become less frequent in stands from wetter localities, reflecting a climatic gradient across Scotland, from the wet and oceanic Atlantic seaboard to the drier and more continental north-east (Ellis & Coppins 2006). Fruticose species were associated to sites with lower aridity. This functional group is usually regarded as indicator of light-related factors caused by forest structure, like canopy openness, as light is usually their most limiting factor (Giordani *et al.* 2012; Li, Liu & Li 2013) and is commonly known to be bound to more

humid conditions (Belnap, Büdel & Lange 2001; Giordani *et al.* 2013). In our sampling sites, forest structure and thus canopy openness and light conditions were more or less even (all sites in *Montado* with similar structure). Thus, air moisture content in sites with higher aridity values (with an Atlantic influence) may be the determinant factor linking fruticose species as indicators of this part of the gradient.

Regarding the reproduction trait, only mainly asexual species with isidia showed to be associated with the aridity gradient. Isidia are corticated diaspores, variable in size and shape, whose dispersal is favoured by water run-off, as its heavy structure probably makes them less efficient for dispersal than soredia or spores (Giordani *et al.* 2013). Accordingly, most of recent genetic and population studies have focused on these species dispersal ability, establishment and survival (Scheidegger, Frey & Zoller 1995; Zoller, Frey & Scheidegger 2000). Although, to our knowledge, its relation with climate has not been directly addressed, a work with *Lobaria pulmonaria* (L.) (Martínez *et al.* 2012) showed a higher frequency and abundance of isidia upon tree trunks closer to the canopy, where microclimatic conditions are harsher (higher radiation and temperature, lower humidity). Some authors have pointed out that important changes may occur in species with a dense cover of isidia (Jahns 1984). More isidia cover could modify thallus water absorption (Rikkinen 1997) and water-holding capacity (Tretiach *et al.* 2005) in a way similar to trichomas in plants. This may be a possible explanation for why these species appear associated with the most arid areas in our gradient, as this characteristic may represent an improvement of water absorption and water-holding capacity.

In conclusion, the three traits chosen showed to be relevant to the response to aridity. Type of photobiont appears particularly promising, namely *Trentepohlia*, as seen in previous works (Aptroot & Van Herk 2007), and cyanobacteria functional groups, responding clearly in contrasting ways to aridity. This work emphasizes once again the role of functional diversity on understanding and assessing the response to environmental factors, as previous works did (Lavorel *et al.* 2011) and brings a fresh new insight to this area of research from a less known group of organisms, a gap of knowledge that had been pointed out before (Lavorel 2013). This first community-level approach based on traits that require minimum expert knowledge worked well, showing its potential to be further developed and applied in the future. Understanding key functional traits associated to aridity is a fundamental step to build up a model of ecological indicators of climate change for drylands (Maestre, Salguero-Gómez & Quero 2012). These results highlight lichen functional diversity potential for areas where shifts towards drier climatic conditions are expected to occur, opening new doors for future research in this area. Nonetheless, future work should focus on the search for other functional groups that may also be potential candidates of ecological indicators of climate change in drylands.

This work was limited to a single environmental variable, the AI, which has some limitations to its use as it does not account for other forms of precipitation such as mist, clouds, dew or fog, which could be more important in ecological

terms for this group. These sources of hydration are all known to be important for lichens and connected to the patterns of functional variation in growth form and type of photobiont, as a recent work highlighted (Gauslaa 2014). Large-scale ecological studies have to rely on the available data at a large scale, and it is widely known and accepted that the existent precipitation models are limited in terms of spatial resolution, relative air humidity models are rarely available and models for dew, mist or fog are inexistent at a global scale. This work emphasizes that even using a variable with such limitations, it is possible to explain a significant part of the functional diversity pattern observed, revealing its potential for a wide-scale use. Nonetheless, future research on other functional traits and groups responding to aridity gradients should also contemplate including, when available, other environmental variables known to be important in lichen ecology. Additionally, in this context of global change, an important challenge to future research will be to disentangle the effects of climate drivers from other major drivers of global change in drylands, such as nitrogen deposition, to access its independent effects and its interactions.

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Data accessibility

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.vn2sh> (Matos *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of lichen species and trait values.