Biogeography of global drylands

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Contents

Summary

Despite their extent and socio-ecological importance, a comprehensive biogeographical synthesis of drylands is lacking. Here we synthesize the biogeography of key organisms (vascular and non-vascular vegetation and soil microorganisms), attributes (functional traits, spatial patterns, plant-plant and plant-soil interactions) and processes (productivity and land cover) across global drylands. These areas have a long evolutionary history, are centers of diversification for many plant lineages and include important plant diversity hotspots. This diversity captures a strikingly high portion of the variation in leaf functional diversity observed globally. Part of this functional diversity is associated with the large variation in response and effect traits in the shrubs encroaching dryland grasslands. Aridity and its interplay with the traits of interacting plant species largely shapes biogeographical patterns in plant-plant and plant-soil interactions, and in plant spatial patterns. Aridity also drives the composition of biocrust communities and vegetation productivity, which shows large geographical variation. We finish our review discussing major research gaps, which include: i) studying regular vegetation spatial patterns, ii) establishing large-scale plant and biocrust field surveys assessing individual-level trait measurements, iii) knowing whether plant-plant and plant-soil interactions impacts on biodiversity are predictable and iv) assessing how elevated CO_2 modulates future aridity conditions and plant productivity.

Key words: macroecology, diversity, spatial pattern, biological soil crusts, woody encroachment, functional traits, plant-soil interactions, plant-plant interactions

I. Introduction

Drylands, areas characterized by Aridity Index (mean annual precipitation/mean annual potential evapotranspiration) values below 0.65, cover ~41% of the terrestrial surface (Cherlet *et al.*, 2018) and include 35% and 20% of the global diversity and plant diversity hotspots, respectively (White & Nackoney, 2003; Davies *et al.*, 2012). They play key roles regulating the global carbon (Ahlström *et al.*, 2015), nitrogen (Tian *et al.*, 2020) and water (Wang *et al.*, 2012) cycles, and are thus fundamental for sustaining life on Earth. Drylands are also crucial to achieve the sustainability of our planet because they host ~38% of the global human population, including most of the fastest-growing population areas in the world, ∼44% of global cropland areas and ∼50% of global livestock (Davies *et al.*, 2016; Cherlet *et al.*, 2018). Drylands are typically divided into hyperarid (AI < 0.05), arid (0.05 < AI < 0.20), semi-arid (0.20 < AI < 0.50) and dry sub-humid (0.50 < AI < 0.65) areas, which occupy 6.6%, 10.6%, 15.2% and 8.7%, respectively, of global land area (Fig. S1).

The study of drylands and their vegetation has a long history. Classical authors such as the Roman naturalist Gaius Plinius Secundus (AD 23/24 – 79) or the Greek geographer Strabo (BC 63/64 – AD 24) compiled the natural history and uses of many dryland plants in the Mediterranean Basin (Serrano Luque, 2018). During the XXth Century, detailed studies of the distribution of vegetation were conducted in drylands from multiple continents (e.g., Shreve, 1942; Soriano, 1956; Keast *et al.*, 1959), and studies of the ecology of dryland vegetation and their interactions with humans, soils, microorganisms and abiotic factors have grown exponentially over the past two decades (Greenville *et al.*, 2017).

Despite the growing interest in drylands, a comprehensive biogeographical synthesis of key organisms, ecosystem attributes and processes characterizing these ecosystems is still lacking. Such a synthesis could identify those factors that shape their current distribution patterns. This is important for accurately forecasting what drylands will look like in the future and for designing more efficient restoration and conservation actions. Here, we combined a literature review with the analyses of global standardized databases and remote sensing products to synthesize our current understanding of the biogeography of dryland vegetation, its spatial and productivity patterns, and the functional traits that shape them at the global scale. Crucial for understanding these patterns are those of plant-plant and plant-soil interactions, which shape community structure and functioning at the local scale but that have scarcely been explored across large geographical scales in drylands (Soliveres *et al.*, 2014; Ochoa-Hueso *et al.*, 2018). We also address the biogeography of biocrusts, another fundamental biotic component of drylands whose biogeography has been little studied (García-Pichel *et al.*, 2013; Bowker *et al.*, 2016), and that of the response and effect traits of woody species that are encroaching in herbaceous communities. This major vegetation change occurring in drylands has important implications for their structure and functioning worldwide (Eldridge *et al.*, 2011). Finally, we briefly discuss important knowledge gaps that need to be addressed to better understand the biogeography of global drylands. We do not, however, provide an in-depth coverage of key topics such as the importance of climatic attributes as drivers of the structure and functioning of dryland ecosystems or their responses to global environmental change drivers because they have been reviewed elsewhere (e.g. Austin *et al.*, 2004; Maestre *et al.*, 2016; Collins *et al.*, 2014). Our review addresses major gaps and key questions, and provides novel syntheses and analyses that both summarize the state-of-the-art in our knowledge and serve as hypotheses to guide future work in dryland biogeography (Fig. 1).

II. Geographical patterns of plant diversity are linked to the long history of dryland biomes and their plants

To understand current plant diversity patterns and the distribution of different plant lineages in drylands, we need to start with their origin. The earliest establishment of arid conditions was asynchronous in different continents. In Africa and South America, dryland ecosystems appeared in the Paleocene (66 – 56 Ma) (Partridge, 1993; Graham, 2010), in central Asia by the end of the Eocene (34 Ma) (Sun & Windley, 2015), and in Australia in the Middle Miocene (16 to 11.6 Ma) (Byrne *et al.*, 2008). The Namib, arguably the oldest desert in the world, has experienced continuous arid conditions since at least the beginning of the Late Cenozoic (33.9 Ma, Lancaster, 1984), whereas the southwestern deserts of the USA, or the Atacama Desert and the Caatinga in South America, are more recent (De Oliveira *et al.*, 1999, Thompson & Anderson, 2000). In Central Asia, the semi-arid Loess Plateau began to appear around 8 Ma likely due to global precipitation changes triggered by the second phase of the uplift of the Tibetan Plateau, which had a major role in the expansion of C4 grasses (Pagani, 1999). During the Last Glacial Period, Central Asia went through a cold arid stage that allowed the spread of steppes dominated by species of the *Asteraceae* (*Artemisia* spp.) and *Poaceae* families (Lioubimtseva, 2004). The semi-arid climate became widespread in Australia during the Pliocene (5.3-1.8 Ma), featuring open woodlands, arid shrublands, and grasslands (Martin, 2006). Later, during the glacial-interglacial cycles of the

Quaternary, glacial periods featured a cool-arid climate, while interglacials were warm and slightly wetter. The Last Glacial Period brought an extreme arid climate featuring large areas of mobile dunes, now stabilized by woodlands, in western Australia between 25 and 12 ka BP (Kershaw *et al.*, 1991).

Molecular clocks have confirmed that the long history of global drylands is coupled with the history of its major plant lineages, and that major dryland clades diversified more or less in synchrony during the interval between the Late Miocene (11.63 – 5.33 Ma) and the Early Pliocene (5.3 to 3.6 Ma). This is the case of the *Aizoaceae* family inhabiting the Succulent Karoo in South Africa and Namibia, the *Agavaceae* and *Cactaceae* now living in North American deserts, and members of the *Camphorosmeae* family in Australia, among many others (Arakaki et al., 2011; Wu et al., 2018). However, a striking exception to this pattern is the long-lived phreatophyte *Welwitschia mirabilis*. This monotypic taxon differentiated from other genera of the division Gnetopsida (*Gentum* and *Ephedra*) before the opening of the Equatorial Atlantic Gateway between Africa and South America during the Early Cretaceous (145 - 100 Ma). Today, the remainder of a past larger distribution is restricted to the Kaokoveld Desert between Namibia and Angola (Jacobson & Lester, 2003).

The long history of dryland ecosystems across all continents, and their role as the origin of many unique plant lineages, makes them an important host to a diverse flora featuring important diversity hotspots in Southern Africa, the Mediterranean basin, Western and Central Asia, North and South America, and Oceania (Fig. 2, Table S1).

The tropical dry forests of southern Africa (Miombo and Mopane woodlands) host a remarkable plant diversity (Frost, 1996; Maquia *et al.*, 2019). Another important center of plant diversification in southern Africa is the Cape Floristic Region, formed by sclerophyll shrublands and heathlands (also named *fynbos*) hosting ~6,000 endemic species (Goldblatt & Manning, 2000). Finally, among the most idiosyncratic plant diversity hotspots in drylands worldwide is the Succulent Karoo, a coastal band in Namibia and South Africa with ~5,000 plant species, of which 40% are endemic (Table S1). About 1,750 of these species are dwarf succulents belonging to the *Aizoaceae* family, *Crassulaceae*, and annual plants of the *Asteraceae* family (Hilton-Taylor, 1996). Hyperarid areas of northern Africa are less diverse, though areas such as the Algerian Sahara are inhabited by at least 1200 plant species (Ozenda, 2004).

The Mediterranean drylands of southern Spain and northern Morocco and Algeria are also among the richest drylands of the world (Médail & Quézel, 2001), and share many sclerophyllous trees (e.g., *Quercus suber*, *Q. Ilex*, *Olea europaea*, and *Pinus halepensis*) accompanied by understory shrubs dominated by species like *Cistus* spp., *Rosmarinus officinalis* and *Genista* spp. The Irano-Anatolian biogeographic region, featuring steppes dominated by the perennial *Prosopis farcta* (FAO, 2019), is the center of taxonomic diversification of annual legumes, and particularly of the genus *Astragalus* spp., with around 1,500 species (Ehrman & Cocks, 1996). This region also had an important role in the diversification of the families of halophytic succulents such as *Chenopodioidea* and *Zygophyllaceae* (Wu *et al.*, 2018).

The dryland belt of Northern Eurasia, the largest continuous set of drylands in the world, encompasses from the Great Hungarian Plain (Hungary, Serbia, Croatia, and Romania) to the Manchurian mixed forests in northeastern China (Groisman *et al.*, 2018). Its hyperarid areas are the contiguous Taklimakan Desert, Qaidam Basin semi-desert, and Alashan Plateau semi-desert in northwestern China. Their shifting sand dunes are devoid of vegetation, but more stable areas are colonized by the small halophytic tree *Haloxylon ammodendron* and the perennial shrub *Reaumuria songarica* (Gong *et al.*, 2019). The permanent Tarim River crosses the Taklimakan, creating the conditions for well-developed riparian forests of *Populus euphratica* and *P. pruinosa* (Thomas & Lang, 2021). The dryland belt of Northern Eurasia also includes important arid and semi-arid areas. For example, the Kazakh semi-desert is a large *Artemisia* spp. shrubland that limits in the north with the Kazakh steppes, rich in *Stipa* spp. and *Festuca* spp. The Central Asian and Eastern Gobi deserts are, respectively, xeric shrublands dominated by *Haloxylon persicum* and *H. ammodendron*, and extensive steppes and shrublands dominated by the endemics *Caragana bungei* and *C. leucocephala*, *Potaninia mongolica* and *Nitraria sibirica* (Thomas *et al.*, 2000) The Qinghai-Tibetan Plateau (4000 m.a.s.l) has been identified as a center of diversification of genera such as *Pedicularis* spp., *Rhododendron* spp., and *Primula* spp., among many others (see Wen *et al.*, 2014 for further details).

North America holds a vast array of dryland ecosystems, from the Sonoran Desert to the northernmost drylands of the world, the conifer taiga forests of Canada. The family *Cactaceae*, with *Carnegiea gigantea* as its most conspicuous representative, reaches its maximum levels of diversity in the southern United States and Mexico (Shreve, 1942). The Colorado Plateau and the Canyonlands region is dominated by *Pinus ponderosa* and *P. edulis* forests, and by *Juniperus* spp.

In open areas between the trees, shrubs like *Artemisia tridentata* and *Cercocarpus montanus*, an important number of *Astragalus* spp. and cacti such as *Echinocereus* spp. find their place to thrive (Shreve, 1942).

South America has a large surface of important dry forests mainly located in the Gran Chaco, the Maranhão Babaçu, and the Caatinga, the driest forest of South America that features a xeric shrubland with succulents and thorny trees with a high level of endemism (Fernandes *et al.*, 2020). The Caatinga is also an important center of diversification of the *Cactaceae* family, along with the southwestern Andes (Ortega-Baes & Godínez-Alvarez, 2006).

Australia features 28 arid ecoregions inhabited by 23,436 plant species, ranging from the 8,625 species of the temperate forests of Southeast Australia, to the 650 of the Hampton mallee and woodlands, located in the coast of Southern Australia (GBIF.org 2020; Dinerstein *et al.*, 2017). The broadleaved forests of Oceania include 803 species of the *Eucalypteae* tribe (genera *Angophora*, *Corymbia*, and *Eucalyptus*) in wetter areas, and 994 species of *Acacia* in drier areas (GBIF.org 2020). The quintessential Hummock Grasslands are located in the arid and hyperarid regions of the Australian outback and are typified by *Triodia* spp., which occupy a vast proportion of the continent (Keast *et al.*, 1959). The Tussock grasslands of Northern Australia are rich in endemic tufted grasses, such as *Dichanthium sericeum* and *Astrebla* spp. (Keast *et al.*, 1959).

III. The functional paradox of drylands

The morphological, physiological and phenological characteristics of species −functional traits− relate to how they acquire, conserve and release resources (Díaz *et al.*, 2016). They are increasingly used to explore how species assemble within communities and respond to their environment, and how changes in communities feedback on ecosystem functioning (Suding *et al.*, 2008). Strong environmental constraints such as high aridity conditions, scarce and unpredictable rainfall, and low soil nutrient contents should reduce plant functional diversity, as predicted by the environmental filtering theory (Keddy, 1992). However, drylands contradict these theoretical predictions and exhibit a strikingly high diversity of plant forms and functions (Notes S1, Fig. S2), perhaps precisely because of plants´ response to such unpredictable conditions.

We used data on leaf morphology and physiology (Maire *et al.*, 2015; Wright *et al.*, 2017) to evaluate the functional diversity of drylands, and to quantify their overlap with that of remaining terrestrial ecosystems (Fig. 3). The dataset used includes trait data for 1,502 species distributed worldwide, and offers a relatively well-balanced representation of dryland species compared with other trait databases (e.g., Kattge *et al.*, 2020). We found that leaf functional diversity from drylands largely overlaps with that observed across the rest of terrestrial ecosystems. Moreover, the variance in dryland trait distributions is as large, and sometimes larger, than that observed across other terrestrial ecosystems. These results illustrate what we define as the functional paradox of drylands**,** i.e. the higher than expected functional diversity in dryland plants compared to those from less environmentally-constrained environments. They contrast with what has been recently observed in other harsh biomes such as the cold tundra, wherein species occupy a constrained subset of the global functional trait space (Thomas *et al.*, 2020). The high variance observed in leaf size and leaf economic traits across drylands reflects the remarkable phenotypic diversity of their plants (Figs. 1 and S2), which allows them to cope with the environmental constraints of these areas. For instance, prostrate shrub species characterized by small leaves often co-occur with long-leaved tussock grass species and large trees (e.g. Frost, 1996). Also, stress-tolerant species often coexist with species with succulent leaves, and with stress-avoidant species with thin and summer-deciduous leaves, which may explain the wide variety of leaf forms and functions observed in drylands (Noy-Meir, 1973; Gross *et al.*, 2013). Furthermore, species characterized by small leaves, with low specific leaf area and high photosynthetic capacity per unit of leaf surface are over-represented in drylands (Noy-Meir, 1973). This likely helps them to cope with water shortage (Notes S1). It is also remarkable that drylands exhibit leaf-trait distributions characterized by lower kurtosis than communities from the rest of the world (Fig. 3). In other words, drylands host a high plant functional diversity of plant species that are more evenly represented than in other biomes.

The high functional diversity of drylands observed at the global scale is also evident at the local scale. A maximization of local plant functional diversity in drylands has been recently documented (Gross *et al.*, 2017), even under prevailing environmental filtering (Le Bagousse-Pinguet *et al.*, 2017). Such a pattern likely results from co-occurring species exhibiting distinct strategies to cope with the environmental conditions found in these areas (Notes S1), from spatio-temporal storage effects (Noy-Meir, 1973) and from positive and intransitive interactions (e.g., Butterfield & Briggs, 2011; Saiz *et al.*, 2019), discussed in section VII below.

IV. Productivity of dryland vegetation: drivers, trends and patterns

The high taxonomic and functional plant diversity observed in drylands plays a major role in maintaining the functioning of these ecosystems and the stability of their productivity (García-Palacios *et al.*, 2018; Le Bagousse-Pinguet *et al.*, 2019). The productivity of vegetation, which provides essential ecosystem services, including food production, soil fertility and climate regulation (Ahlström *et al.*, 2015; Maestre *et al.*, 2016; Cherlet *et al.*, 2018), is typically measured across large geographical scales using satellite measurements such as the normalized difference vegetation index (NDVI; Smith *et al.*, 2019). While in areas with low vegetation canopy cover, such as drylands, the soil background can significantly influence NDVI estimates (Smith *et al.*, 2019), this index shows good correlations with vegetation productivity measured *in situ* across drylands (e.g., Paruelo *et al.*, 1997; Tian *et al.*, 2017).

Vegetation productivity in drylands not only responds to biotic attributes, but also to abiotic ones. Indeed, productivity patterns closely match the aridity gradients found naturally across global drylands (Figs. 3a and S1). The mean (standard deviation) NDVI of dryland vegetation during the period 2001-2019 was 0.06 (0.03), 0.09 (0.06), 0.18 (0.1) and 0.26 (0.11) in hyper-arid, arid, semi-arid and dry-sub humid environments, respectively (Fig. 4a). However, there is substantial variation within aridity classes driven by both the biotic attributes mentioned above (plant richness and functional traits) and by other factors (e.g., topography, climatic variability, herbivory, soil type or land use; Collins *et al.*, 2014; Maestre *et al.*, 2016; Venter *et al.*, 2018; Burrell *et al.*, 2020).

The most abundant land cover types in drylands are grasslands, followed by areas with less than 10% vegetation cover and shrublands (Fig. 4b). Savannas and forests, including deciduous, evergreen and mixed forests, occupy ∼11% and <5% of global dryland area, respectively. It must be noted, however, that the remote sensing products typically used to quantify land cover, such as MODIS (Friedl & Sulla-Menashe, 2019), have insufficient resolution to adequately quantify discontinuous forest stands such as those found in many drylands. Recent global estimates using high resolution imagery indicate that 1327 million hectares of drylands had more than 10% tree-cover, and 1079 million hectares comprised forest in 2015 (Bastin *et al.*, 2017). A major feature of land cover in drylands, the sparse, discontinuous vegetation cover with isolated trees and shrubs (Fig. S2), is also not captured properly by most remote sensing data currently available. However, this is beginning to change as high-resolution remote sensing products become more widely available. For example, Brandt *et al.* (2020) found ~1.8 billion individual trees (crown size > 3 m^2) over 1.3 million km^2 in drylands of West Africa, with canopy cover ranging from 0.1% (0.7 trees per hectare) in hyper-arid areas to 13.3% (47 trees·$hectare^{-1}$) in dry sub-humid areas. Although previously ignored, isolated trees play a key role in drylands by capturing and re-distributing resources, providing habitat and refugia for fauna and flora, and producing goods and services crucial for local human populations, including timber, food and forage (FAO, 2019).

From 1982 to 2009, the global increase in vegetation productivity observed (Zhu *et al.*, 2016), is also apparent in many drylands. An updated analysis (Fig. S3; Notes S2) indicates that 26 million km^2 show positive trends in vegetation productivity (greening) during the 2001-2019 period. Greening increased with reductions in aridity across global drylands (e.g., 66% of hyper-arid areas experienced greening vs. 84% of dry sub-humid areas; Fig. S3). A recent analysis of greening trends in global drylands (Burrell *et al.*, 2020) indicates that their major drivers were increases in soil moisture and water use efficiency associated with a CO_2 fertilization effect, followed by land use and climate change. Climate variability and land use were, however, major greening drivers in the Sahel, India, China and Australia (Burrell *et al.*, 2020). Despite the overall greening trend observed, a total of 6 million km^2 of drylands showed significant negative trends in vegetation productivity (browning) between 2001 and 2019 (Fig. S3). Browning varied also with the degree of aridity, and ranged from 34% in hyper-arid areas to 16% in dry sub-humid areas. A recent analysis of browning trends in global drylands (Burrell *et al.*, 2020) indicates that land use was the most important browning driver, followed by climate change and climate variability. Multiple drivers often act together to amplify browning trends, as found in areas of Central Asia and the semi-arid Caatinga of Brazil (climate change and land use) or in South America (climate change and variability) (Burrell *et al.*, 2020).

V. A single size does not fit all: biogeography of vegetation spatial patterns

The relatively low productivity of dryland vegetation prevents it from covering all the soil surface. Instead, drylands are spatially heterogeneous environments, wherein vegetation tends to form islands, or "patches", surrounded by bare soil (Aguiar & Sala, 1999; Tongway *et al.*, 2001). This discontinuous vegetation is characterized by multiple spatial configurations, including fairy circles and irregular, regular, spotted, stripped or labyrinth patterns (Fig. S4; Deblauwe *et al.*, 2008; Berdugo *et al.*, 2017, 2019b; Getzin *et al.*, 2019). These spatial patterns have fascinated ecologists, geographers, mathematicians and physicists alike since their discovery after the second world war (see Tongway *et al.*, 2001 and references therein). They have also been associated with ecosystem functioning (Pringle *et al.*, 2010; Berdugo *et al.*, 2017), and have been proposed as potential early warning signals for the onset of land degradation and desertification (Rietkerk *et al.*, 2004; Kéfi *et al.*, 2007) in drylands. Thus, their study is not only relevant to our understanding of the structure and functioning of dryland ecosystems, but also for the monitoring of degradation processes affecting them.

The spatial patterns of dryland vegetation can be broadly classified into two major types (regular and irregular), which are not evenly distributed across global drylands (Fig. 5). Regular patterns occur when a certain spatial configuration of plants and bare soil is periodically repeated through the landscape (Fig. S4). They tend to resemble patterns observed on animal coats, such as tiger stripes or "brousse tigree" (see Tongway *et al.*, 2001 and references therein), and are characterized by a typical patch size (Kéfi *et al.*, 2010). Fairy circles, which manifest as an arrangement of bare soil circles surrounded by vegetation, and are therefore a special case of regular patterns, have been reported from the Namib and Australia (Getzin *et al.*, 2019). Irregular patterns occur when patches of a broad range of sizes occur across the landscape (Fig. S4; Kéfi *et al.*, 2007).

Although external factors such as soil or resource spatial heterogeneity and vegetation growth form affect vegetation spatial patterns (e.g., Couteron *et al.*, 2014), they have been shown to result largely from plant-plant and plant-soil interactions (Lefever & Lejeune, 1997; Kéfi *et al.*, 2010). Mechanisms of vegetation pattern formation have been identified using theoretical models (e.g., Lefever & Lejeune, 1997; von Hardenberg *et al.*, 2010) and are supported by field observations from different environments (e.g., Barbier *et al.*, 2008; Berdugo *et al.*, 2017; Getzin *et al.*, 2021). Irregular patterns emerge when plant facilitation processes occur at a much smaller spatial scale than competitive processes (e.g., von Hardenberg *et al.*, 2010). In turn, regular patterns result from a dominance of competitive mechanisms, whose spatial scale determines the regular distancing between patches (von Hardenberg *et al.*, 2010). The formation of fairy circles is controversial, as they can be explained by either plant allelopathic interactions, an interaction with mound-forming termites and plant competition, or by the role of grasses as ecosystem engineers of soil water diffusion and infiltration (see Tarnita *et al.*, 2017; Getzin *et al.*, 2019, 2021 and references therein).

In the same way as for plant productivity, aridity is the most important predictor of the occurrence of regular vegetation patterns, followed by mean temperature of the wettest quarter (Deblauwe *et al.*, 2008). High (> 24ºC) or low to medium (2-6ºC) temperature seasonality also favored the formation of regular spatial patterns. Other studies have shown that the shape of regular patterns (bands, stripes, gaps, spots) is driven by the combination of rainfall and the slope of the terrain (Deblauwe *et al.*, 2012). Gaps are more likely to occur in drylands where annual rainfall is higher (~500 mm per year), followed by labyrinths (400-450 mm) and spots (<400 mm). Bands become increasingly more frequent as slope increases (Tongway *et al.*, 2001).

A biogeographical analysis of dryland vegetation patterns (Berdugo *et al.* 2019b) indicates that they tend to shift from irregular to regular as aridity increases, coinciding with the collapse of positive plant-plant interactions under the most arid conditions (Aridity Index < 0.3; Berdugo *et al.*, 2019a). Aridity and plant-plant interactions are not, however, the sole drivers of changes in plant spatial patterns. Indeed, vegetation type strongly modulates the importance of abiotic drivers of vegetation patterns (e.g. precipitation seasonality and soil texture are important drivers in grasslands and shrublands, respectively), and contrasting mechanisms of facilitation (soil amelioration in shrublands vs. percentage of facilitated species in grasslands) operate to form irregular patterns (Berdugo *et al*., 2019b).

Different plant growth forms (trees, shrubs or grasses) often display different spatial patterns in drylands, even at small spatial scales (Fig. S4). For example, trees might be regularly patterned whereas grasses are often irregular. Moreover, the drivers of the overall vegetation pattern formation can involve multi-scale patterning (patterns within the patterns) due to multiple mechanisms of ecological self-organization at different scales, as it occurs with fairy circles (Tarnita *et al.*, 2017). Addressing these mechanisms in the field has remained an elusive task so far due to the difficulty of measuring plant-plant interactions within and across these hierarchical spatial scales.

VI. Biogeography of biocrusts, the "living skin" of drylands

In addition to vascular plants, the functioning of dryland ecosystems worldwide is largely determined by the presence, cover and composition of biological soil crusts (biocrusts), diverse communities composed of lichens, bryophytes and other soil microorganisms (such as cyanobacteria, algae, and fungi) coexisting in the uppermost soil layers (Weber *et al.*, 2016). They are typically found in plant interspaces and under plant canopies that are not covered by litter (Fig. S5), and their global distribution results from climate and edaphic characteristics interacting at multiple spatial and temporal scales (Weber *et al.*, 2016; Bowker *et al.*, 2017).

In particular, aridity, temperature and gypsum content are important drivers of broad patterns of biocrust composition in drylands (García-Pichel *et al.*, 2013, Bowker *et al.*, 2017). For example, biocrusts in hyper-arid regions are commonly dominated by cyanobacteria, together with other microscopic components (e.g., bacteria, fungi; Büdel *et al.*, 2016; Figs. 6a, S5 and S8). Cyanobacteria are also an important feature in arid and semi-arid regions of North America, Southern Africa, Eastern Asia and Australia (Figs. 6b-d, S5 and S6). Major functional roles played by cyanobacteria in such regions are nitrogen fixation, run off modulation and soil stabilization by creating an extracellular matrix (Büdel *et al.*, 2016; Eldridge *et al.*, 2020).

In deserts under maritime influence such as the Namib, biocrusts can be dominated by lichens, sometimes representing the most abundant ground cover (e.g., Lalley & Viles, 2005; Figs. 6c and S6). In arid and semi-arid drylands, greater moisture availability allows lichens to develop extensive ground covers (Fig. S5). They dominate biocrusts in semi-arid drylands of Western North America, Portugal, Spain, China, Argentina, Southern Africa and Australia (Figs. 6 and S6), and are particularly diverse and abundant in gypsum soils (Bowker et al., 2017). Lichens are important contributors to carbon fixation, sediment trapping and microbial activity regulation in these areas (Bowker *et al.*, 2017; Eldridge *et al.*, 2020).

Bryophyte-dominated biocrusts can be found from hyper-arid to arid and semi-arid habitats of North America, China and Australia (Seppelt *et al.*, 2016; Figs. 6b, 6d, 6e and S6), where they influence carbon fixation, germination and emergence of vascular plants, habitat provision and the regulation of soil surface microclimate (Weber *et al.*, 2016; Bowker *et al.*, 2017). These biocrusts also become more abundant with increasing water availability (Bowker et al., 2006; Li *et al.*, 2017; Fig. S6) and are particularly sensitive to climate change, which can seriously reduce their distribution and functional roles in drylands (Ferrenberg *et al.*, 2017). Algae and liverworts are important biocrust constituents in Chinese deserts, calcareous drylands in Australia and siliceous and sandy drylands in South Africa, also contributing to carbon fixation and soil stabilization in these regions (Seppelt *et al.*, 2016; Büdel *et al.*, 2016).

VII. Environmental conditions and functional traits drive variations in plant-plant and plant-soil interactions

The interactions between different plant species, and between plants and the soils beneath them, are not only fundamental drivers of vegetation patterns (section V) but can also shape biogeographical patterns (reviewed in Godsoe *et al.*, 2017). Plant-plant and plant-soil interactions are involved in macro-ecological processes, including range expansions (e.g., Zhang *et al.*, 2020), or plant evolution (e.g., Thorpe *et al.*, 2011) in many biomes worldwide. However, no previous study has specifically evaluated how plant-plant or plant-soil interactions (the latter including soil microbes and soil physico-chemical attributes) shape the biogeography of dryland ecosystems. Plant-plant and plant-soil interactions are sensitive to climate, soil type and land use (e.g., Mazía *et al.*, 2016; Van der Putten *et al.*, 2016), and, therefore, are expected to shape dryland´s diversity patterns. Plant-plant interactions are also influenced by the biogeographic patterns of herbivores and the co-evolution between them (Stebbins, 1981), a topic beyond the scope of this review.

A quarter of dryland plant species seem to depend on positive plant-plant interactions (facilitation; Soliveres & Maestre, 2014; Vega-Alvarez *et al.*, 2019). These patterns hold particularly true for those species less adapted to dry conditions (Valiente-Banuet *et al.*, 2006; Berdugo *et al.*, 2019a), which also greatly benefit from associations with symbiotic microbes like mycorrhiza. This influence has allowed, for example, the continuation of Mediterranean plant lineages that evolved during the wetter conditions of the Tertiary to today´s harsher conditions (Valiente-Banuet *et al.*, 2006), and could be a potential explanation of the high functional diversity observed in drylands (Section III). Plant-associated microbes are a fundamental driver of the colonization of plants into new habitats (e.g., Delavaux *et al.*, 2019). Conversely, if plant species manage to disperse far enough as to escape their soil antagonists, they can outcompete their neighbors and successfully invade new habitats (Zhang *et al.*, 2020). Thus, existing empirical evidence leaves little doubt about the importance of plant-plant and plant-soil interactions in shaping species´ niches, and therefore influence dryland biodiversity and biogeographical patterns.

Latitudinal gradients in biodiversity are less apparent in drylands than in other ecosystems (e.g., Ulrich *et al.*, 2014). Similarly, plant-plant interactions do not show clear relationships with latitude in drylands (Fig. 7). For example, although the positive effects of trees on grass biomass peak near the tropics, this pattern is overridden by prevailing conditions of aridity or tree functional traits (Mazía *et al.*, 2016). Indeed, positive plant-plant interactions are stronger and more prevalent in arid and semi-arid environments than in lower latitude tropical biomes (Gómez-Aparicio, 2009). Latitudinal patterns are not evident in plant-soil interactions either (Ochoa-Hueso *et al.*, 2018; but see Delavaux *et al.*, 2019; Steidinger *et al.*, 2019). Instead of following latitudinal gradients, macroecological patterns in plant-plant and plant-soil interactions are largely driven by variation in environmental conditions and their interaction with the functional traits of the interacting plant species. However, the interactions between vegetation and environment as drivers of plant-plant interactions may themselves exhibit biogeographical patterns, as shown by the large shared variance explained by vegetation, environment and geography, and the large importance of latitude and longitude as predictors of these interactions across global drylands (Fig. 7).

At the core of plant-plant and plant-soil interactions in drylands is the "fertility island" phenomenon, which refers to the higher contents in organic matter and available nutrients, coupled with cooler and moister environments, typically found beneath plant patches compared with adjacent open areas without vegetation (Schlesinger & Pilmanis, 1998; Aguiar & Sala, 1999). Vegetated patches in drylands capture air-borne particles, contributing to nutrient input and conservation beneath them (Schlesinger & Pilmanis, 1998; Gonzales *et al.*, 2018). They also intercept water and nutrients from surface run-off after rainfall events, thus altering the soil and microclimatic conditions underneath them. Macro-ecological patterns in the fertility island effect across global drylands are determined by: (i) environmental conditions, including aridity and grazing pressure, (ii) soil properties, including soil parent material and age, which determine soil texture and pH, and (iii) the structure and composition of plant communities, including their functional traits (Allington & Valone, 2014; Ochoa-Hueso *et al.*, 2018; Fig. S7; section VIII). Plant patches are comparatively more fertile than adjacent bare soils when soils are more alkaline, have greater sand content, under semiarid climates or when grazed (Allington & Valone, 2014; Ochoa-Hueso *et al.*, 2018).

Aridity is a major driver of the structure and functioning of drylands (e.g. Maestre *et al.*, 2016; Berdugo *et al.*, 2020; sections IV and V), and thus of plant-plant and plant-soil interactions there (e.g., Maestre & Soliveres 2014; Ochoa-Hueso *et al.*, 2018). Increases in aridity such as those forecasted by the end of XXIth century (Huang *et al.*, 2017) drastically alter the structure and function of the soil microbiome in drylands (Berdugo *et al.*, 2020; Delgado-Baquerizo *et al.*, 2020). For example, Berdugo *et al.* (2020) identified an important aridity threshold associated with a transition from semiarid to arid ecosystems (Aridity Index = 0.2), wherein small increases in aridity dramatically increased the proportion of fungal pathogens and reduced that of plant fungal symbionts. This could partly explain why the fertility island effect, tightly linked to these fungal communities, is less pronounced under arid than under semi-arid conditions (Ochoa-Hueso *et al.*, 2018). These findings also suggest that climate change could shift the balance between positive and negative plant-soil interactions, negatively impacting the fitness of plant communities in drylands. Even without further aridification, drylands may have generally weaker or more negative plant-soil interactions than more mesic environments. This is due to a greater proportion of plant antagonists, compared with decomposers or symbionts, in drylands than in other terrestrial ecosystems (Fig. S8, Notes S3), or to the lower abundance of soil microorganisms observed as aridity increases (Maestre *et al.*, 2015). Aridity also accounts for a substantial proportion of the variation in the effects of plant-plant interactions on the structure and composition of drylands (~50% for biomass [Mazía *et al.*, 2016] ~29% for biodiversity [Soliveres & Maestre, 2014]). Considered collectively, existing research suggests that the effects of plant-plant interactions tend to become more positive for biomass and for biodiversity in tree- or annual-dominated ecosystems when aridity increases (Mazía *et al.*, 2016; Rey *et al.*, 2016; Berdugo *et al.*, 2019a). Therefore, in these cases, and contrary to expectations for plant-soil interactions, plant-plant interactions should become more positive, and perhaps more important in shaping dryland biodiversity and productivity patterns, under future climatic scenarios.

The effects of plant-plant interactions on biodiversity across aridity gradients are far less consistent in grass- or shrub-dominated ecosystems than in savannas or annual-dominated communities (Soliveres & Maestre, 2014; Rey *et al.*, 2016). In these cases, it is more likely that the traits of the interacting species play a greater role in modulating the outcome of plant-plant interactions than environmental conditions *per se* (Soliveres *et al.*, 2014). Nurse and beneficiary traits are a crucial driver of the outcome of plant-plant interactions in drylands (Gómez-Aparicio, 2009; Butterfield & Briggs, 2011; Al Hayek *et al.*, 2015; Mazía *et al.*, 2016). Existing evidence suggests that woody species are generally better nurses than grasses (Gómez-Aparicio, 2009; Soliveres *et al.*, 2014), particularly if they are N-fixers (e.g., Mazía *et al.*, 2016) or have open and large canopies (Al Hayek *et al.*, 2015). These traits are also those behind more pronounced fertility island effects and can alter the abundance of fungi and bacteria beneath plant canopies (Ochoa-Hueso *et al.*, 2018). Tall woody species are more efficient at capturing airborne particles (Gonzales *et al.*, 2018) and redistribute nutrients and water *via* their highly developed and deep root systems (Prieto *et al.*, 2012). Such features of root systems are also important determinants of the association of plants with microbial symbionts such as mycorrhizae (Schenk & Jackson, 2002). This could explain why woody plants are better facilitators than grasses. In addition, population growth rates in soil microbes increase more strongly after rainfall pulses in tree- than in grass-dominated ecosystems (Fierer *et al.*, 2003), which may cause a higher sensitivity of plant-microbe interactions to changes in rainfall amount and frequency expected under future climate scenarios in grasslands than woodlands. Whether or how plant functional traits drive plant-microbe interactions in drylands, and how they interact with aridity, is still poorly understood, mainly because of the short duration and highly species-specific responses often reported in the few existing studies (Van der Putten *et al.*, 2016).

VIII. Tradeoffs between traits of encroaching woody plants have a biogeographical basis

Woody encroachment, perhaps the most dramatic form of dryland vegetation cover change, continues to increase over large dryland areas of the United States (Archer *et al.*, 2017), Africa (Venter *et al.*, 2018), Australia (Fensham *et al.*, 2005), South America (Rosan *et al.*, 2019) and Europe (Maestre *et al.*, 2009). The causes of encroachment are many and complex, but generally relate to altered intensities of land-use (e.g., overgrazing and changes in fire regimes) and increases in atmospheric carbon dioxide, all of which give woody plants a competitive advantage over herbaceous vegetation (see Archer *et al.*, 2017 and references therein). This global phenomenon summarizes well the importance of plant-plant and plant-soil interactions to shape the structure and functioning of drylands. Although the ecosystem consequences of encroachment have been extensively studied (e.g., Eldridge *et al.*, 2011; Maestre *et al.*, 2016; Archer *et al.*, 2017), we still have relatively poor appreciation of the biogeography of the main encroaching species.

Many of the more than 100 woody species that are known to encroach (Eldridge *et al.*, 2011; Ding and Eldridge, 2019) share common traits, so a trait-based assessment of their biogeography can help us to understand their global distribution and impacts on dryland ecosystems. We did so by combining global databases of woody encroachment (Eldridge *et al.*, 2011), woody plant removal following encroachment (Ding *et al.*, 2020) and woody plant functional traits (Ding *et al.*, 2020). These combined datasets (315 independent studies of 100 species) included traits that are related to the effects of woody plants on ecosystem functioning (i.e. how they affect functional outcomes such as nutrient cycling, hydrological function or habitat quality). For the purposes of our analyses, we separated them into traits linked to their morphology (structural traits) and to their physiology and phenology (functional traits). Our structural traits related to size (plant height), canopy shape (v-shaped to round), root type (mixed to surface roots) and foliage contact with the soil surface. The five functional traits related to whether plants were deciduous, allelopathic, resprouting, palatable, or nitrogen fixers. These traits have previously been ranked according to whether they increase or reduce ecosystem functions (Ding *et al.*, 2020). After assigning a numerical value to each of these traits, these data were standardized such that a higher value corresponded to a greater function (see Ding *et al.* 2020 for details).

Encroaching woody plants from North American and African drylands were significantly taller (7.8 – 9.9 m) than those from South American, Asian or Australian drylands (1.3 – 1.5 m; Fig. S9). Encroaching woody plants from Africa were more likely to have tap roots, foliage that touches the ground, and fix nitrogen. Woody plants encroaching in Australia were more likely to be palatable, evergreen, tap-rooted, resprouting species, whereas encroaching species from North America were less likely to resprout or fix nitrogen. Encroaching species from Asia were more likely to have tap roots, and those from Africa more likely to be v-shaped than expected by chance. Finally, species from Europe were more likely to have fibrous roots but less likely to be allelopathic.

Average values of structural and functional traits at the continental scale reveal that sites encroached by woody plants with high value of functional traits tend to have low values of structural traits, and *vice versa* (Fig. 8). For example, African woody plants had high values of function but relatively low structure, whereas North America exhibited the opposite, with generally higher structural values but low values of functional traits. Europe and to a lesser extent Australia and Asia, had average values of structural and functional plant traits.

Our synthesis shows the tradeoffs between structural and functional trait values of woody plants that encroach in drylands. It also demonstrates that the idiosyncratic portfolio of traits that confer functional outcomes have a biogeographical basis. For example, the larger than expected number of nitrogen-fixing shrubs from Australia may reflect a competitive advantage of these species in Australia's soils, which have low nitrogen contents compared to other drylands (Eldridge *et al.*, 2018). Similarly, taller shrubs in Africa may be an evolutionary advantage under higher levels of vertebrate browsing, compared with continents such as South America or Australia, which have long been dominated by vertebrate herbivores such as camelids or macropods, respectively (Dantas & Pausas, 2013).

IX. Concluding remarks and future research directions

Drylands host a diversity of plants that capture a surprisingly large portion of the variation in foliar traits observed globally. This extraordinary functional diversity opens up relevant questions for future research, including: i) Could the high-functional diversity of drylands confer them a greater resistance or resilience to climate change compared with other biomes?, ii) How does plant functional diversity correlate with soil microbial diversity and soil-borne pathogens?, and iii) Does the phenotypic variability expressed at the individual level (intraspecific trait variability) play an important role for the functioning of drylands at the global scale? To address these questions, however, we need to better characterize the functional traits of dryland plants, which are largely underrepresented in global databases (Kattge *et al.*, 2020; Thomas *et al.*, 2020). A significant challenge is therefore the development of large-scale trait databases comprising *in situ* individual-level measurements directly coupled with environmental and soil data. The development of such databases would provide key insights into how plant functional diversity regulates ecosystem functioning and help to develop sound conservation and restoration strategies aimed at enhancing their capacity to provide essential ecosystem services.

New remote sensing techniques, such as solar-induced fluorescence, near infrared reflectivity, thermography, hyperspectral imaging and lidar (reviewed in Smith *et al.*, 2019), coupled with the use of high-resolution satellite images allowing the characterization identification of individual shrubs and trees characteristics across large regions (Brandt *et al.*, 2020) are substantially improving our ability to monitor vegetation across multiple spatio-temporal scales. Such technological developments offer great promise to better characterize vegetation patterns in drylands, and to further advance our understanding of their functioning and productivity. Our knowledge of the biogeography of vegetation patterns in drylands, occurring mostly from studies in Africa, North America and Australia, is more advanced for regular than irregular patterns. The latter, however, comprise the vast majority of vegetation spatial patterns across global drylands (Fig. 5), and are the next frontier for studying their biogeography. There is also a paucity of experiments about mechanisms of vegetation pattern formation in drylands, a gap that should be addressed by future studies. Understanding the uncertainty about whether vegetation greening observed in recent decades will be maintained under future climates is a priority for future research. This uncertainty is due to contrasting effects of greater water efficiency, through elevated CO_2 (Walker *et al.*, 2020) on vegetation productivity, which will likely be offset by negative effects due to increased evapotranspiration and reduced soil moisture (Huang *et al.*, 2017; Soong *et al.*, 2020). There is also considerable uncertainty in our projections of future aridity, depending on whether the effects of elevated CO_2 on vegetation are considered or not (see Huang *et al.*, 2017 and Lian *et al.*, 2021). Understanding the impacts of future aridity conditions on vegetation productivity is essential, as productivity has been found to decline abruptly in drylands worldwide when aridity index exceeds values of 0.46, leading to multiple cascading, non-linear effects on key structural and functional ecosystem attributes (see Berdugo *et al.*, 2020 for details). Furthermore, it has been suggested that total dryland gross primary production will increase by 123% relative to the 2000–2014 baseline, largely due to the expansion of drylands into formerly more productive ecosystems by 2100 (Yao *et al.*, 2020). However, forecasted changes in primary production also show large regional variations and important declines across drylands worldwide (Yao *et al.*, 2020). How elevated CO_2 and other factors may modulate future aridity conditions and their impacts on ecosystem productivity in drylands is thus a key, yet unsolved, question with major implications for the global carbon cycle and climate change mitigation actions. The use of ecosystem models parameterized across a wide variety of drylands, and the inclusion of biocrust and soil microbial components into them, could provide important insights into these important questions.

Despite impressive advances in biocrust research over the past few decades, our knowledge of biocrust biogeography is still limited, particularly in regions such as Central Eurasia, North Africa, Mexico and South America. Similarly, despite the increasingly available information on ecological and trait information for mosses and liverworts at regional scales (e.g., Bernhardt-Römermann *et al.*, 2018), we still lack comprehensive databases of a wide range of biocrust species and associated functional traits at the global scale. Increases in aridity linked to climate change are expected to result in considerable shifts in the abundance and distribution of dryland biocrusts (Rodríguez-Caballero *et al.*, 2018). Thus, renewed efforts to examine the biogeography of biocrusts would allow us to better understand current patterns and predict future changes in the structure and functioning of dryland ecosystems, and to develop sound management, conservation and restoration strategies that account for these important communities. The collection of standardized spatio-temporal data on the abundance of multiple biocrust components and associated traits (e.g., tissue nutrient content, albedo, hydrophobicity) and ecosystem functions across a wide range of drylands remains as one of the next major challenges in dryland research.

Nurse plants enhance both phylogenetic and functional diversity in drylands (e.g., Valiente-Banuet *et al.*, 2006; Butterfield & Briggs, 2011). Our understanding of the extent to which these nurse plant effects are consistent across environments or among different components of biodiversity (e.g., taxonomic, functional or phylogenetic; but see Vega-Alvarez *et al.*, 2019) is still in its infancy. Both plant-plant and plant-soil interactions are crucial determinants of spatial and biodiversity patterns in drylands, yet we ignore their relative importance, in comparison to environmental factors such as climate, in shaping these patterns. Addressing these issues can help us to better link biotic interactions with ecosystem structure and functioning in drylands, and to establish a mechanistic understanding of the biogeographical patterns of their vegetation. Although not free of limitations, which are discussed in Notes S4, the map and the analyses shown in Fig. 7 also serve as a working hypothesis to further explore the biogeography of plant-plant interactions in drylands and elsewhere. A better knowledge of plant-plant and plant-soil interactions can also help, for example, to aid in the restoration of degraded drylands by helping us to select species with traits that enhance ecosystem functioning (Gross *et al.*, 2017; Le Bagousse-Pinguet *et al.*, 2019). Bottom-up community approaches may also be successful for dryland restoration. For example, inoculating the soil with fungal species that create densely connected networks of hyphae may help plants to tolerate water stress and capture scarcely available soil nutrients (Collins *et al.*, 2008). Thus, studying plant-plant and plant-soil interactions in drylands will provide us with information that is relevant to restoration goals using nature-based solutions.

Despite our fascination with drylands and the renewed research efforts over the past few decades, we still have a relatively poor understanding of their biogeography at the global scale compared with other ecosystems such as tropical forests (e.g. Primack & Corlett, 2004). However, there is a growing interest in drylands, as evidenced by a burgeoning dryland research community, with its increasing network of coordinated dryland research studies across the globe (Table S2). Given the extent of drylands, and their contrasting evolutionary histories, environmental conditions and habitat types, their responses to environmental changes or biotic factors can only be properly understood through systematic and coordinated research efforts conducted worldwide. Such global collaborative efforts have proven fruitful, and have provided key insights into the biogeography and functioning of dryland vegetation and associated ecosystem processes, and how they respond to major climate change drivers (e.g., Maestre *et al.*, 2012; Ulrich *et al.*, 2014; Gross *et al.*, 2017; Berdugo *et al.*, 2019b). Networks of scientists working together are now in a position to test experimentally some of the major paradigms related to the biogeography and functioning of drylands under different global environmental change scenarios, to collect much-needed field data (e.g. plant functional traits and biocrusts) and to set up *in situ* temporal monitoring programs of vegetation and ecosystem processes across global drylands. These are major challenges for such networks and a priority theme for future research. We hope that this review will serve to stimulate future research on, and discussion of, dryland biogeography, so that we all have a better understanding of the fate of drylands, one of Earth's most important biomes, as we move to a warmer and more unpredictable world.

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Author contribution

FTM planned the review. All authors contributed to data synthesis, analysis, and mapping. All authors contributed to the writing of the review.

Data Accessibility

The data used to make Figure 1 are available at Zenodo (**https://doi.org/10.5281/zenodo.4252661**). The data used to run the variance partitioning analyses shown in Figure 7 are available at Figshare (https://doi.org/10.6084/m9.figshare.14237702). The rest of data used in our analyses come from either public datasets or other published studies, and can be accessed from the links and references provided.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1. Adaptations to aridity of dryland vascular vegetation.

Notes S2. Assessing greening and browning trends across global drylands.

Notes S3. Analyzing and mapping major soil fungal groups across global drylands.

Notes S4. Estimating the global distribution of positive plant-plant interactions.

Notes S5. Credits for species and ecosystem pictures shown in Figure 2.

Notes S6. Mapping the distribution of biocrust communities across global drylands.

Table S1. Values of plant species richness from selected drylands.

Table S2. Examples of international/global networks of experiments and observations focusing on the ecology and biogeography of dryland ecosystems.

Figure S1. Distribution of dryland areas worldwide.

Figure S2. Examples of the vegetation types and plant life forms that can be found across global drylands.

Figure S3. Dryland areas showing increasing (greening) and declining (browning) productivity during the period 2001-2019.

Figure S4. Examples of vegetation spatial patterns typically found in global drylands.

Figure S5. View of biocrust habitats and detail of typical biocrust communities that can be found across global drylands.

Figure S6. Distribution of biocrust community cover across global drylands.

Figure S7. Fertile island effect for soil functions associated with the carbon, nitrogen, and phosphorus biogeochemical cycles by aridity class (a) and conceptual representation of the main ecological drivers of fertile island formation in drylands (b).

Figure S8. Global distribution of essential soil fungal groups for plant communities (a, plant pathogens; b, decomposers and c, mycorrhizal fungi) across global drylands.

Figure S9. Mean (± SE) values for average structural and functional traits for woody plant species that are encroaching across drylands worldwide.

Figure S10. Relation between predicted and observed values for the percentage of positive plant-plant interactions (A). Relative importance of the geographical, climatic and vegetation predictors used to perform the random models (B).

Figure captions

Figure 1. Interdependence of the different sections of the review (central box), showing how they link fundamental research questions about dryland biogeography (yellow boxes) and main review outputs (green boxes).

Figure 2. Plant species richness of the world's dryland ecoregions and examples of plant species and vegetation types that can be found in drylands worldwide. Plant richness was computed as the number of species in the GBIF *Plantae* dataset located on ecoregions with a mean aridity index lower than 0.65 (GBIF.org, 2020). Please note that the boundaries of the ecoregions presented in the map do not fully match those of drylands presented in the rest of maps within this review. Aridity values and ecoregions were obtained from Trabucco and Zomer (2019) and Dinerstein *et al.* (2017), respectively. Picture credits are available in Notes S5. See Fig. S2 for additional examples of major dryland vegetation types.

Figure 3. The diversity of leaf forms and functions in global drylands (areas with an aridity index < 0.65, orange) and in the rest of the terrestrial ecosystems (grey). We show the biome-scale distributions (mean [M], variance [V], skewness [S] and kurtosis [K]) of six leaf morphological

and chemical traits related to nutrient acquisition and conservation and photosynthetic activity. The data used come from Wright *et al.* (2017) for leaf area and from Maire *et al.* (2015) for specific leaf area, light-saturated photosynthetic carbon assimilation per unit leaf mass (Amass), light-saturated photosynthetic carbon assimilation per unit leaf area (Aarea), leaf nitrogen content (LNC) and leaf nitrogen content per unit leaf area (Narea). The overlap between trait distributions was calculated with the package "overlap" in R (Ridout & Linkie, 2009). The overlap index ranges from 0 to 1. A high overlap among distributions indicates a similar level of trait diversity between drylands and the rest of terrestrial ecosystems.

Figure 4. Normalized difference vegetation index (NDVI, a) and land cover types (b) across global drylands. The data shown in panel a represent average NDVI data for the period 2001-2019 obtained from the MODIS MOD13Q1 Version 6 product (https://lpdaac.usgs.gov/products/mod13q1v006/). The data shown in panel b represent the main land cover types in 2019 obtained from the MODIS MCD12Q1 Version 6 product (https://lpdaac.usgs.gov/products/mcd12q1v006/). The Others class in panel b includes urban areas, those covered by snow/ice and water bodies.

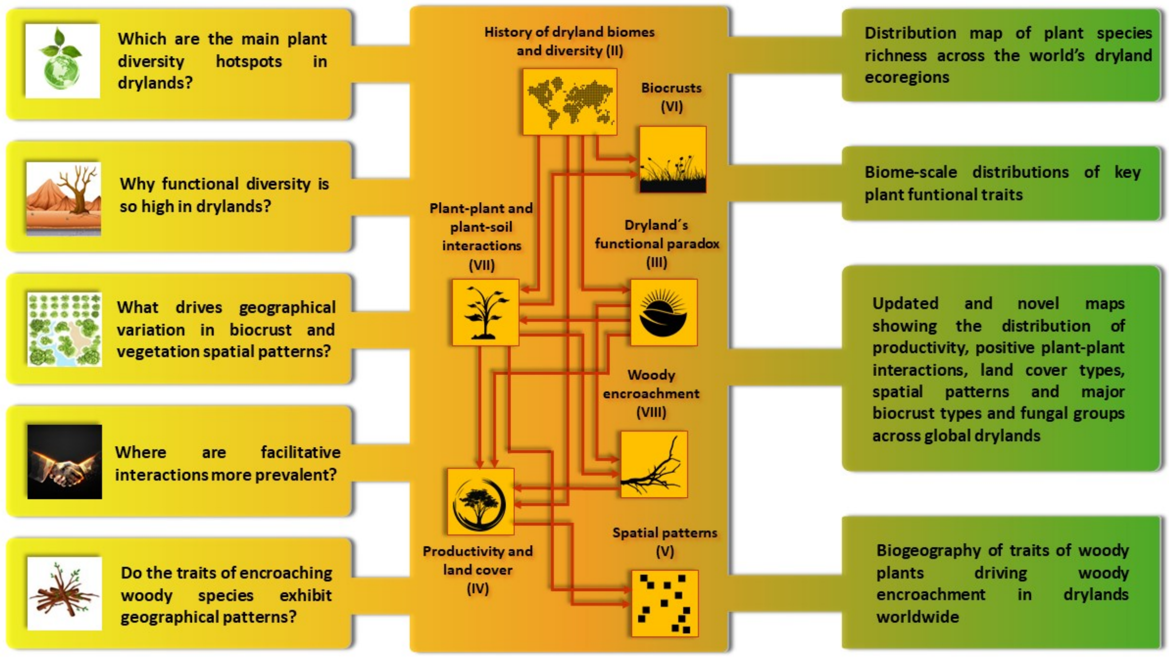
Figure 5. Distribution of major vegetation spatial patterns across global drylands. Dark brown areas are those in which vegetation cover is too low to create patterns (<5% of cover); green areas are fully covered by vegetation (>95% of cover); blue areas are those showing regular patterns as identified by Deblauwe *et al.* (2008); dark orange areas contain fairy circles (according to Juergens, 2013; Ravi *et al.*, 2017; Getzin *et al.*, 2019); light orange areas represent those where their spatial patterns remain underexplored (probably holding irregular or mixed patterns). Cover data (averaged for the period 2000-2019) were estimated using the MODIS MOD44B Version 6 product (https://lpdaac.usgs.gov/products/mod44bv006/). See Fig. S4 for examples of these spatial patterns.

Figure 6. Distribution of biocrust communities across global drylands. Different colors indicate the dominant biocrust components (i.e., cyanobacteria, hypolithic, lichens, mosses) at each study site. The data plotted come from the syntheses conducted by Rodríguez-Caballero *et al.* (2018,

diamonds) and Chen *et al.* (2020, circles). See additional methodological details in Notes S6 and Fig. S6 for a companion map of the global distribution of biocrust cover.

Figure 7. Distribution of positive plant-plant interactions (facilitation) across global drylands and variation partitioning analysis showing the relative proportion of variation explained from major predictors of these interactions. Geographical predictors include latitude and longitude; vegetation predictors include the cover and dominance of grasses, shrubs and trees; and environmental predictors include 19 climatic variables, elevation, soil carbon, pH and sand content. The scale represents the percentage of positive interactions (in %). See Notes S4 for an explanation of the methodology used to obtain the map and of the variation partitioning analyses and Fig. S10 for additional details on the performance of the model used and on the relative importance of predictors used to obtain this map.

Figure 8. Biogeography of structural (a) and functional (b) traits of woody plants that have encroached into former grasslands across global drylands. Structural traits are plant size (average height), shape (v-shaped to round), root type (mixed to surface roots) and foliage contact with the soil surface (contact vs. no contact). The functional traits are whether or not plants are deciduous, allelopathic, resprouters, palatable, or nitrogen fixers. Values represent the average (standardized) values assigned to different traits (see Ding & Eldridge, 2019) according to whether they increase or reduce structure or function. A larger value equates with greater structure or function.



Which are the main plant diversity hotspots in drylands?
Why functional diversity is so high in drylands?
What drives geographical variation in biocrust and vegetation spatial patterns?
Where are facilitative interactions more prevalent?
Do the traits of encroaching woody species exhibit geographical patterns?
History of dryland biomes and diversity (II)
Biocrusts (VI)
Plant-plant and plant-soil interactions (VII)
Dryland´s functional paradox (III)
Woody encroachment (VIII)
Productivity and land cover (IV)
Spatial patterns (V)
Distribution map of plant species richness across the world's dryland ecoregions
Biome-scale distributions of key plant funtional traits
Updated and novel maps showing the distribution of productivity, positive plant-plant interactions, land cover types, spatial patterns and major biocrust types and fungal groups across global drylands
Biogeography of traits of woody plants driving woody encroachment in drylands worldwide

Figure 1

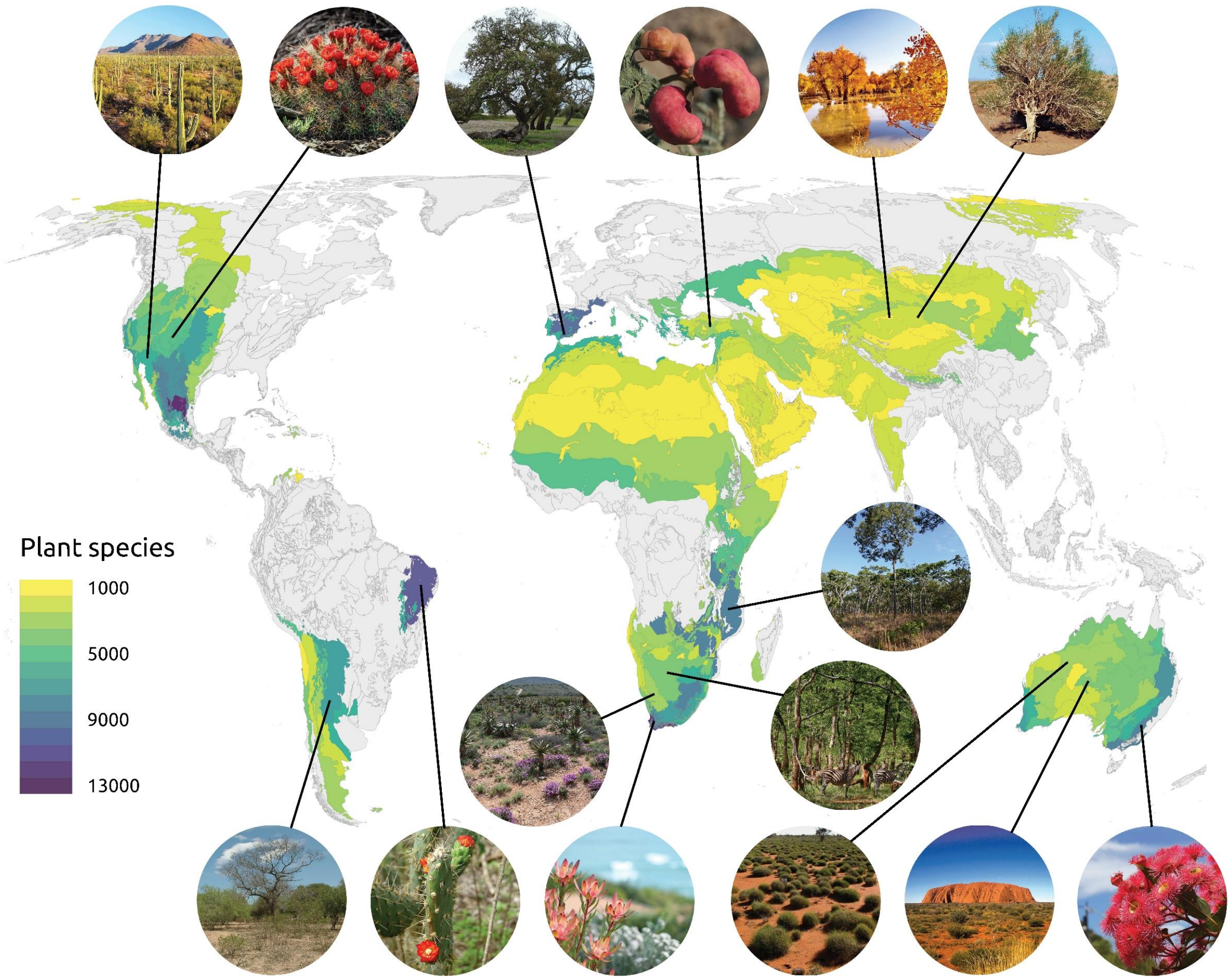


Figure 2

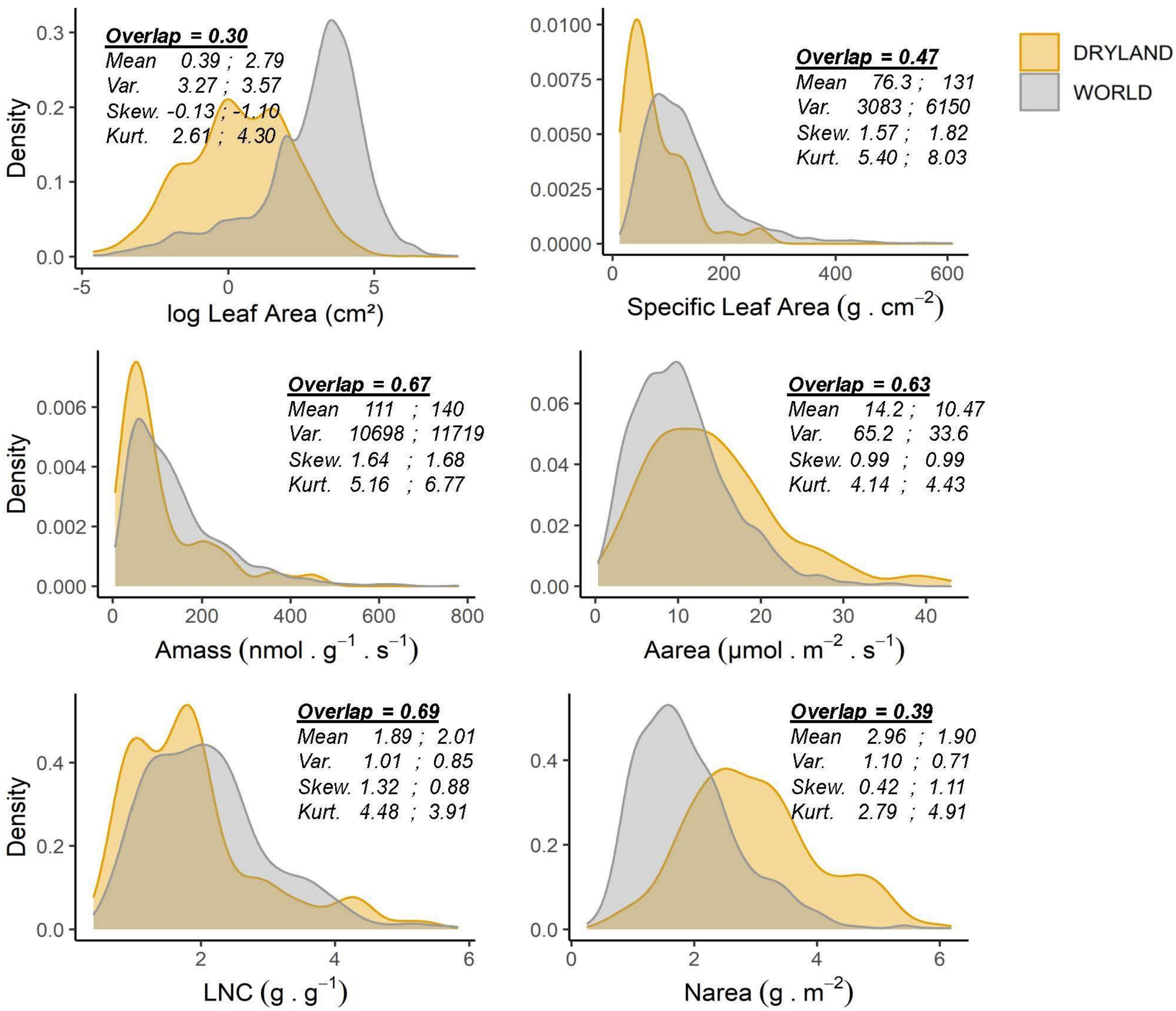

Overlap = 0.30
Mean 0.39 ; 2.79
Var. 3.27 ; 3.57
Skew. -0.13 ; -1.10
Kurt. 2.61 ; 4.30
Density
log Leaf Area (cm²)
Overlap = 0.47
Mean 76.3 ; 131
Var. 3083 ; 6150
Skew. 1.57 ; 1.82
Kurt. 5.40 ; 8.03
Specific Leaf Area (g . cm−2)
DRYLAND
WORLD
Overlap = 0.67
Mean 111 ; 140
Var. 10698 ; 11719
Skew. 1.64 ; 1.68
Kurt. 5.16 ; 6.77
Amass (nmol . g−1 . s−1)
Overlap = 0.63
Mean 14.2 ; 10.47
Var. 65.2 ; 33.6
Skew. 0.99 ; 0.99
Kurt. 4.14 ; 4.43
Aarea (µmol . m−2 . s−1)
Overlap = 0.69
Mean 1.89 ; 2.01
Var. 1.01 ; 0.85
Skew. 1.32 ; 0.88
Kurt. 4.48 ; 3.91
LNC (g . g−1)
Overlap = 0.39
Mean 2.96 ; 1.90
Var. 1.10 ; 0.71
Skew. 0.42 ; 1.11
Kurt. 2.79 ; 4.91
Narea (g . m−2)

Figure 3

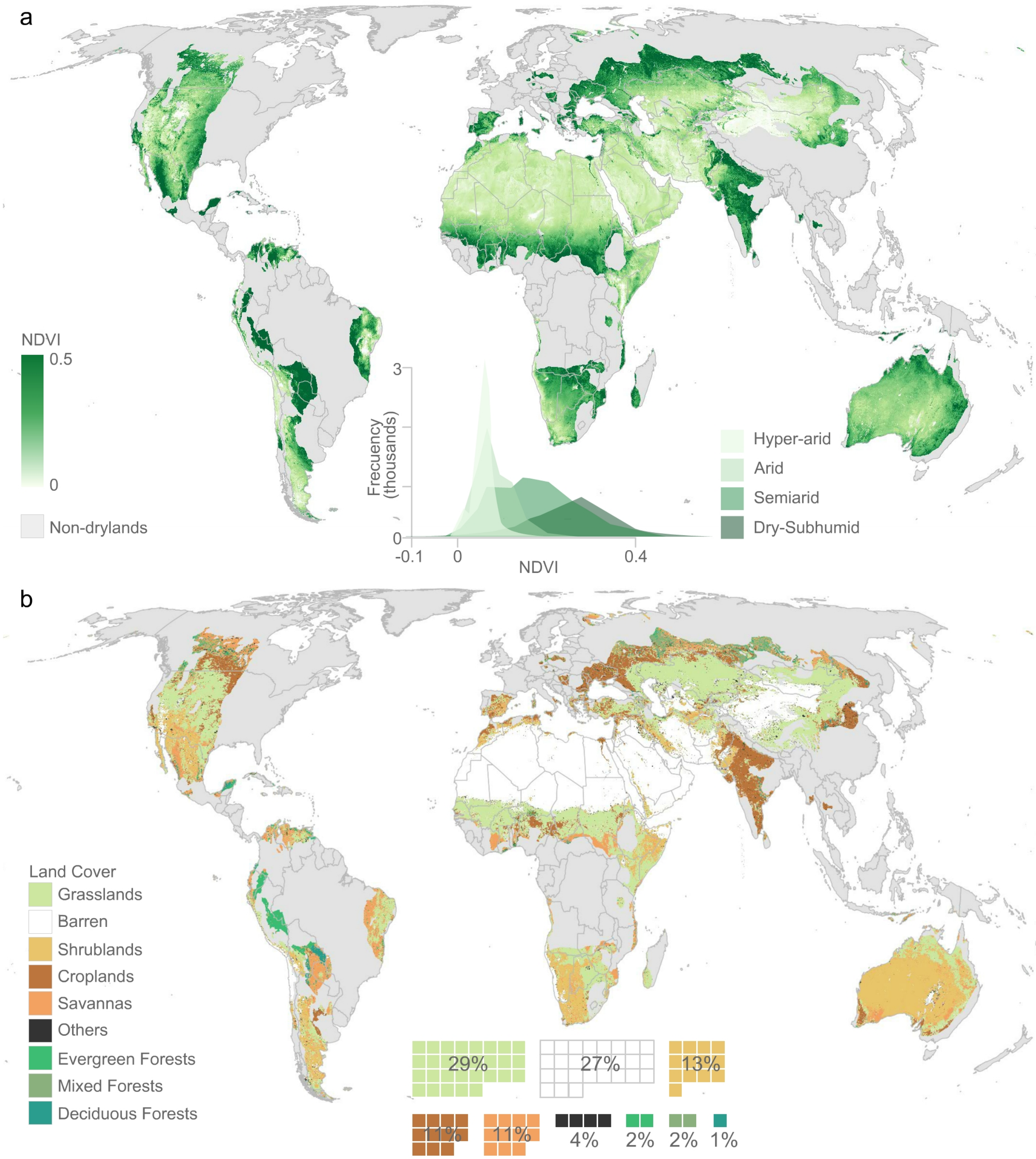

a
NDVI
0.5
0
Non-drylands
3
0
Frecuency (thousands)
-0.1
0
0.4
NDVI
Hyper-arid
Arid
Semiarid
Dry-Subhumid
b
Land Cover
Grasslands
Barren
Shrublands
Croplands
Savannas
Others
Evergreen Forests
Mixed Forests
Deciduous Forests
29%
27%
13%
11%
11%
4%
2%
2%
1%

Figure 4

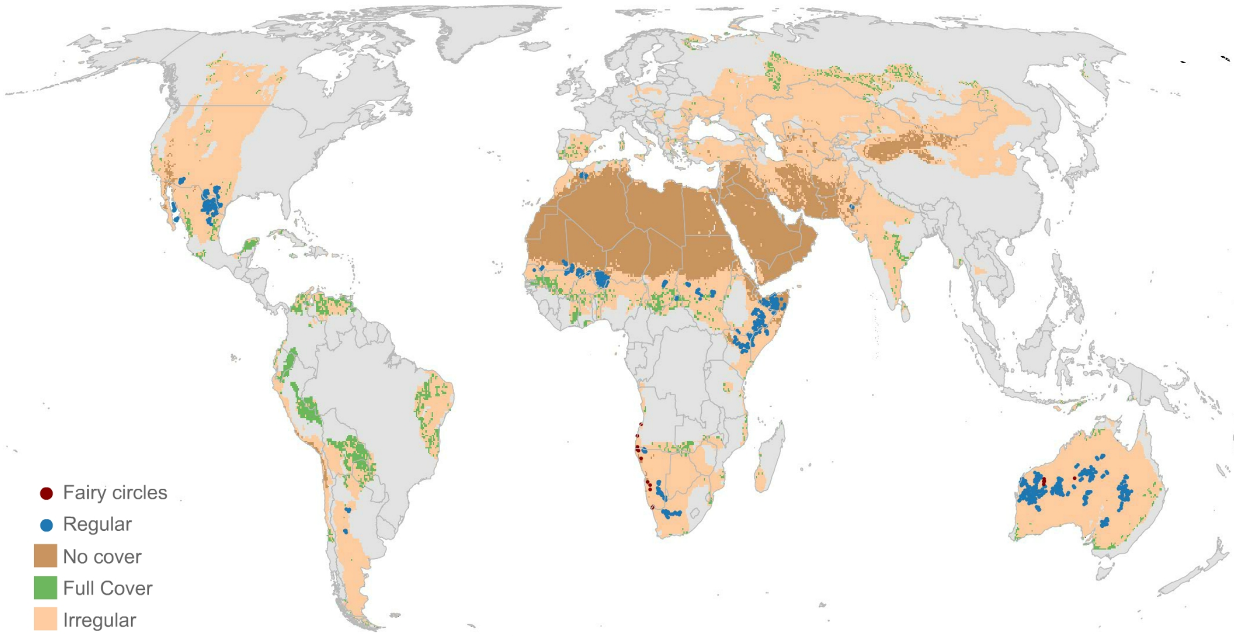
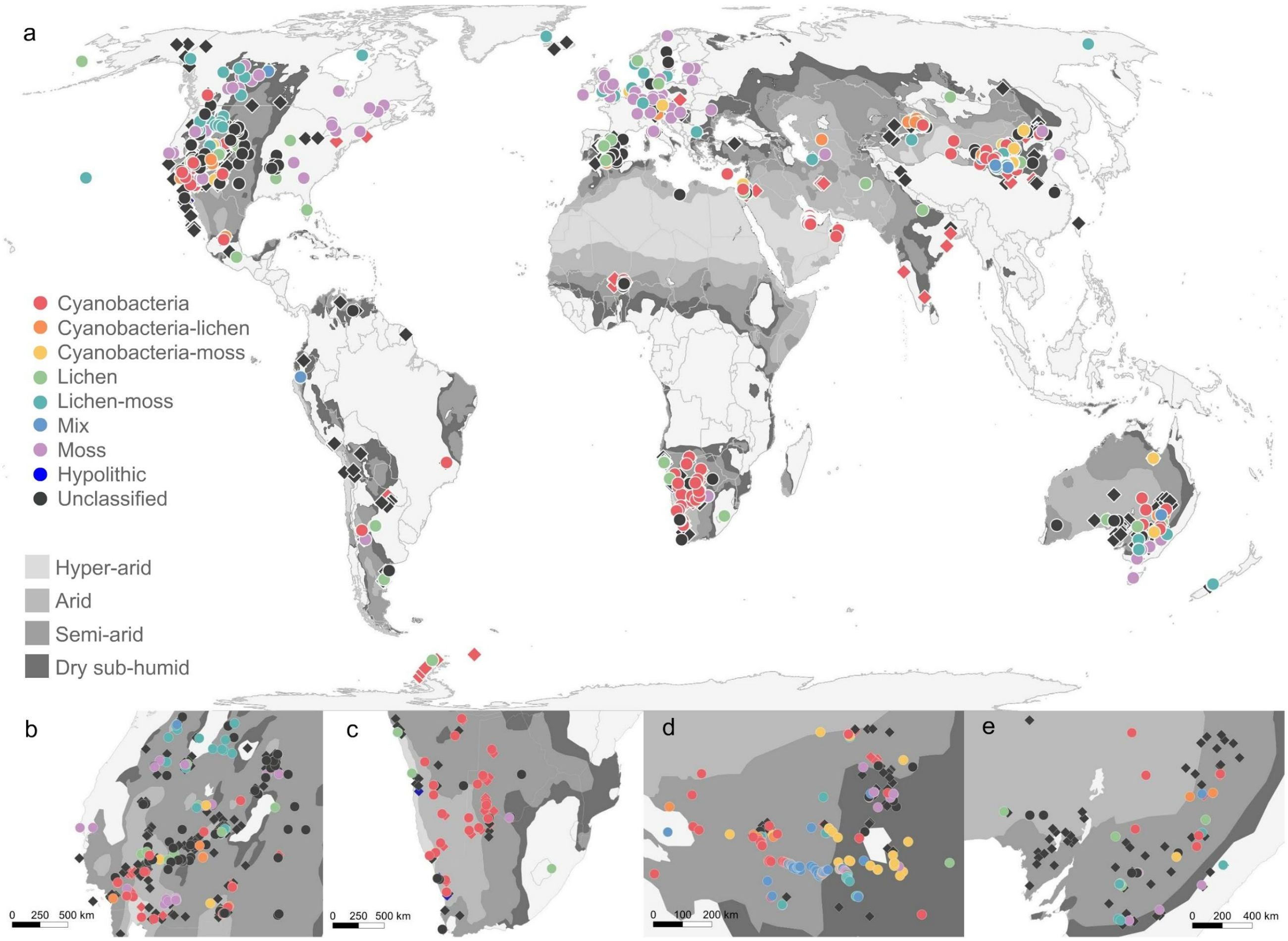


Figure 5



a
Cyanobacteria
Cyanobacteria-lichen
Cyanobacteria-moss
Lichen
Lichen-moss
Mix
Moss
Hypolithic
Unclassified
Hyper-arid
Arid
Semi-arid
Dry sub-humid
b
0 250 500 km
c
0 250 500 km
d
0 100 200 km
e
0 200 400 km

Figure 6

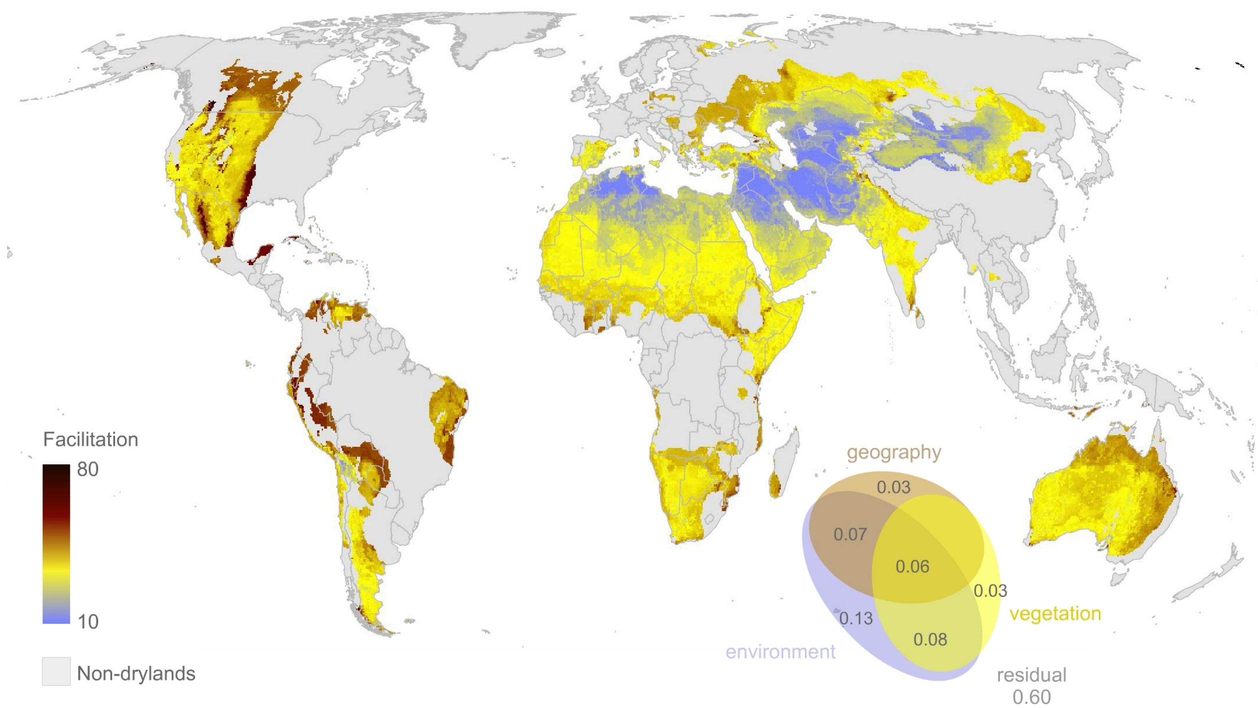

Facilitation
80
10
Non-drylands
geography
0.03
0.07
0.06
0.03
vegetation
0.13
0.08
environment
residual
0.60

Figure 7

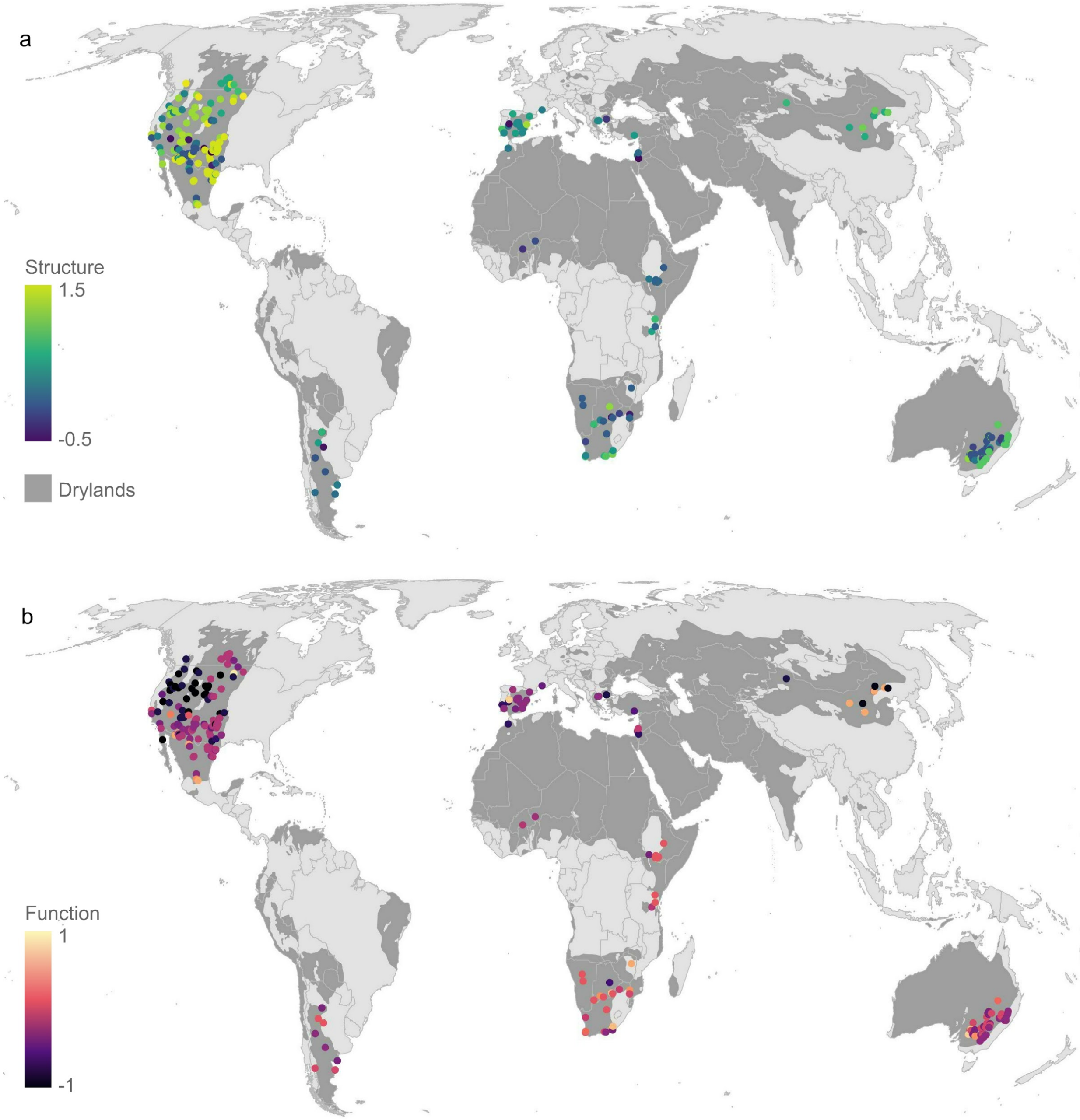


Figure 8