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Biogeography of global drylands

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68 **Summary**

Despite their extent and socio-ecological importance, a comprehensive biogeographical synthesis
70 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-
72 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
74 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
76 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
78 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,
80 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
82 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
84 elevated CO₂ modulates future aridity conditions and plant productivity.

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

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94 **I. Introduction**

96 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
98 & 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
100 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-
102 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
104 (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.
106 S1).

The study of drylands and their vegetation has a long history. Classical authors such as the
108 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
110 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;
112 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
114 decades (Greenville *et al.*, 2017).

Despite the growing interest in drylands, a comprehensive biogeographical synthesis of key
116 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
118 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
120 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
122 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
124 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
126 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
128 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
130 (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
132 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
134 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
136 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).

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

140 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
142 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
144 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
146 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
148 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
150 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
152 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
154 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

156 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
158 dunes, now stabilized by woodlands, in western Australia between 25 and 12 ka BP (Kershaw *et*
al., 1991).

160 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
162 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
164 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;
166 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
168 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
170 past larger distribution is restricted to the Kaokoveld Desert between Namibia and Angola
(Jacobson & Lester, 2003).

172 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
174 diversity hotspots in Southern Africa, the Mediterranean basin, Western and Central Asia, North
and South America, and Oceania (Fig. 2, Table S1).

176 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
178 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).
180 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
182 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).
184 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).

186 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
188 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.
190 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
192 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
194 *Chenopodioidea* and *Zygophyllaceae* (Wu *et al.*, 2018).

The dryland belt of Northern Eurasia, the largest continuous set of drylands in the world,
196 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
198 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
200 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,
202 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
204 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
206 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*
208 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
210 such as *Pedicularis* spp., *Rhododendron* spp., and *Primula* spp., among many others (see Wen *et*
al., 2014 for further details).

212 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*,
214 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
216 Canyonlands region is dominated by *Pinus ponderosa* and *P. edulis* forests, and by *Juniperus* spp.

218 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).

220 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
222 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
224 with the southwestern Andes (Ortega-Baes & Godínez-Alvarez, 2006).

Australia features 28 arid ecoregions inhabited by 23,436 plant species, ranging from the
226 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).
228 The broadleaved forests of Oceania include 803 species of the *Eucalyptae* tribe (genera
Angophora, *Corymbia*, and *Eucalyptus*) in wetter areas, and 994 species of *Acacia* in drier areas
230 (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
232 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).

234 **III. The functional paradox of drylands**

The morphological, physiological and phenological characteristics of species –functional traits–
236 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
238 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
240 low soil nutrient contents should reduce plant functional diversity, as predicted by the
environmental filtering theory (Keddy, 1992). However, drylands contradict these theoretical
242 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.

244 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
246 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

248 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,
250 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
252 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
254 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
256 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
258 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
260 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
262 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-
264 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
266 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.

268 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
270 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
272 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.,
274 Butterfield & Briggs, 2011; Saiz *et al.*, 2019), discussed in section VII below.

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

276 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-
278 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
280 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
282 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.*,
284 2019), this index shows good correlations with vegetation productivity measured *in situ* across
drylands (e.g., Paruelo *et al.*, 1997; Tian *et al.*, 2017).

286 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
288 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-
290 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
292 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).

294 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,
296 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
298 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
300 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
302 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,
304 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 m²)
306 over 1.3 million km² 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
308 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
310 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.*,
312 2016), is also apparent in many drylands. An updated analysis (Fig. S3; Notes S2) indicates that
26 million km² show positive trends in vegetation productivity (greening) during the 2001-2019
314 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
316 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 CO₂ fertilization effect,
318 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
320 greening trend observed, a total of 6 million km² of drylands showed significant negative trends in
vegetation productivity (browning) between 2001 and 2019 (Fig. S3). Browning varied also with
322 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
324 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
326 and the semi-arid Caatinga of Brazil (climate change and land use) or in South America (climate
change and variability) (Burrell *et al.*, 2020).

328 **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.
330 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
332 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;
334 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
336 (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
338 warning signals for the onset of land degradation and desertification (Rietkerk *et al.*, 2004; Kéfi *et al.*,
et al., 2007) in drylands. Thus, their study is not only relevant to our understanding of the structure

340 and functioning of dryland ecosystems, but also for the monitoring of degradation processes
affecting them.

342 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
344 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
346 tiger stripes or “brousse tigrée” (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
348 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
350 patterns occur when patches of a broad range of sizes occur across the landscape (Fig. S4; Kéfi *et*
al., 2007).

352 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
354 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
356 (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
358 *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
360 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
362 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
364 of soil water diffusion and infiltration (see Tarnita *et al.*, 2017; Getzin *et al.*, 2019, 2021 and
references therein).

366 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
368 (Deblauwe *et al.*, 2008). High (> 24°C) or low to medium (2-6°C) temperature seasonality also
favored the formation of regular spatial patterns. Other studies have shown that the shape of regular
370 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
372 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).

374 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
376 positive plant-plant interactions under the most arid conditions (Aridity Index < 0.3; Berdugo *et al.*,
et al., 2019a). Aridity and plant-plant interactions are not, however, the sole drivers of changes in
378 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
380 grasslands and shrublands, respectively), and contrasting mechanisms of facilitation (soil
amelioration in shrublands vs. percentage of facilitated species in grasslands) operate to form
382 irregular patterns (Berdugo *et al.*, 2019b).

Different plant growth forms (trees, shrubs or grasses) often display different spatial
384 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
386 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
388 (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
390 spatial scales.

VI. Biogeography of biocrusts, the “living skin” of drylands

392 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
394 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
396 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
398 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
400 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

402 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,
404 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
406 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
408 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
410 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
412 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
414 (Bowker *et al.*, 2017; Eldridge *et al.*, 2020).

Bryophyte-dominated biocrusts can be found from hyper-arid to arid and semi-arid habitats
416 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
418 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;
420 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
422 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
424 these regions (Seppelt *et al.*, 2016; Büdel *et al.*, 2016).

426 **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,
428 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
430 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
432 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.
434 Plant-plant and plant-soil interactions are sensitive to climate, soil type and land use (e.g., Mazia
et al., 2016; Van der Putten *et al.*, 2016), and, therefore, are expected to shape dryland's diversity
436 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.

438 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
440 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
442 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
444 (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
446 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
448 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
450 shaping species' niches, and therefore influence dryland biodiversity and biogeographical patterns.

Latitudinal gradients in biodiversity are less apparent in drylands than in other ecosystems
452 (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
454 peak near the tropics, this pattern is overridden by prevailing conditions of aridity or tree functional
traits (Mazia *et al.*, 2016). Indeed, positive plant-plant interactions are stronger and more prevalent
456 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
458 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
460 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
462 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
464 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”
466 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
468 adjacent open areas without vegetation (Schlesinger & Pilmanis, 1998; Aguiar & Sala, 1999).
Vegetated patches in drylands capture air-borne particles, contributing to nutrient input and
470 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
472 microclimatic conditions underneath them. Macro-ecological patterns in the fertility island effect
across global drylands are determined by: (i) environmental conditions, including aridity and
474 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
476 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
478 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.*,
480 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
482 forecasted by the end of XXIth century (Huang *et al.*, 2017) drastically alter the structure and
484 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
486 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
488 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.*,
490 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
492 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

494 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
496 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
498 (~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
500 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
502 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
504 productivity patterns, under future climatic scenarios.

The effects of plant-plant interactions on biodiversity across aridity gradients are far less
506 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
508 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
510 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
512 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
514 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-
516 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
518 (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).
520 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-
522 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
524 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
526 because of the short duration and highly species-specific responses often reported in the few
existing studies (Van der Putten *et al.*, 2016).

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

Woody encroachment, perhaps the most dramatic form of dryland vegetation cover change,
530 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
532 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
534 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
536 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
538 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.

540 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
542 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
544 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
546 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
548 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),
550 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,
552 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
554 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).

556 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;
558 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
560 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
562 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
564 allelopathic.

Average values of structural and functional traits at the continental scale reveal that sites
566 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
568 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
570 and Asia, had average values of structural and functional plant traits.

Our synthesis shows the tradeoffs between structural and functional trait values of woody
572 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
574 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
576 *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
578 have long been dominated by vertebrate herbivores such as camelids or macropods, respectively
(Dantas & Pausas, 2013).

580 **IX. Concluding remarks and future research directions**

Drylands host a diversity of plants that capture a surprisingly large portion of the variation in foliar
582 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
584 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
586 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,
588 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
590 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
592 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
594 their capacity to provide essential ecosystem services.

New remote sensing techniques, such as solar-induced fluorescence, near infrared
596 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
598 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.
600 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
602 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
604 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
606 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
608 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 CO₂
610 (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).
612 There is also considerable uncertainty in our projections of future aridity, depending on whether
the effects of elevated CO₂ on vegetation are considered or not (see Huang *et al.*, 2017 and Lian *et al.*
614 *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
616 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

618 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
620 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
622 elevated CO₂ 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
624 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
626 components into them, could provide important insights into these important questions.

Despite impressive advances in biocrust research over the past few decades, our knowledge
628 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
630 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
632 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
634 (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
636 functioning of dryland ecosystems, and to develop sound management, conservation and
restoration strategies that account for these important communities. The collection of standardized
638 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
640 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-
642 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
644 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
646 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
648 us to better link biotic interactions with ecosystem structure and functioning in drylands, and to

650 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
652 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
654 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,
656 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).
658 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.

660 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
662 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,
664 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
666 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
668 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
670 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
672 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
674 (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
676 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
678 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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698 **Author contribution**

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

Data Accessibility

702 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
704 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
706 either public datasets or other published studies, and can be accessed from the links and
references provided.

708

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1144 **Supporting Information**

Additional Supporting Information may be found online in the Supporting Information section at
1146 the end of the article.

Notes S1. Adaptations to aridity of dryland vascular vegetation.

1148 **Notes S2.** Assessing greening and browning trends across global drylands.

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

1150 **Notes S4.** Estimating the global distribution of positive plant-plant interactions.

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

1152 **Notes S6.** Mapping the distribution of biocrust communities across global drylands.

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

1154 **Table S2.** Examples of international/global networks of experiments and observations focusing on
the ecology and biogeography of dryland ecosystems.

1156 **Figure S1.** Distribution of dryland areas worldwide.

Figure S2. Examples of the vegetation types and plant life forms that can be found across global
1158 drylands.

Figure S3. Dryland areas showing increasing (greening) and declining (browning) productivity
1160 during the period 2001-2019.

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

1162 **Figure S5.** View of biocrust habitats and detail of typical biocrust communities that can be found
across global drylands.

1164 **Figure S6.** Distribution of biocrust community cover across global drylands.

1166 **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).

1168 **Figure S8.** Global distribution of essential soil fungal groups for plant communities (a, plant pathogens; b, decomposers and c, mycorrhizal fungi) across global drylands.

1170 **Figure S9.** Mean (\pm SE) values for average structural and functional traits for woody plant species that are encroaching across drylands worldwide.

1172 **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).

1176 **Figure captions**

1178 **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).

1182 **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.

1190 **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

1194 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
1196 leaf area, light-saturated photosynthetic carbon assimilation per unit leaf mass (A_{mass}), light-
saturated photosynthetic carbon assimilation per unit leaf area (A_{area}), leaf nitrogen content (LNC)
1198 and leaf nitrogen content per unit leaf area (N_{area}). The overlap between trait distributions was
calculated with the package “overlap” in R (Ridout & Linkie, 2009). The overlap index ranges
1200 from 0 to 1. A high overlap among distributions indicates a similar level of trait diversity between
drylands and the rest of terrestrial ecosystems.

1202
Figure 4. Normalized difference vegetation index (NDVI, a) and land cover types (b) across global
1204 drylands. The data shown in panel a represent average NDVI data for the period 2001-2019
obtained from the MODIS MOD13Q1 Version 6 product
1206 (<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
1208 (<https://lpdaac.usgs.gov/products/mcd12q1v006/>). The Others class in panel b includes urban
areas, those covered by snow/ice and water bodies.

1210
Figure 5. Distribution of major vegetation spatial patterns across global drylands. Dark brown
1212 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
1214 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
1216 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
1218 (<https://lpdaac.usgs.gov/products/mod44bv006/>). See Fig. S4 for examples of these spatial
patterns.

1220
Figure 6. Distribution of biocrust communities across global drylands. Different colors indicate
1222 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,

1224 diamonds) and Chen *et al.* (2020, circles). See additional methodological details in Notes S6 and
1226 Fig. S6 for a companion map of the global distribution of biocrust cover.

1226
Figure 7. Distribution of positive plant-plant interactions (facilitation) across global drylands and
1228 variation partitioning analysis showing the relative proportion of variation explained from major
1230 predictors of these interactions. Geographical predictors include latitude and longitude; vegetation
1232 predictors include the cover and dominance of grasses, shrubs and trees; and environmental
1234 predictors include 19 climatic variables, elevation, soil carbon, pH and sand content. The scale
1236 represents the percentage of positive interactions (in %). See Notes S4 for an explanation of the
1238 methodology used to obtain the map and of the variation partitioning analyses and Fig. S10 for
1240 additional details on the performance of the model used and on the relative importance of predictors
1242 used to obtain this map.

1236
Figure 8. Biogeography of structural (a) and functional (b) traits of woody plants that have
1238 encroached into former grasslands across global drylands. Structural traits are plant size (average
1240 height), shape (v-shaped to round), root type (mixed to surface roots) and foliage contact with the
1242 soil surface (contact vs. no contact). The functional traits are whether or not plants are deciduous,
1244 allelopathic, resprouters, palatable, or nitrogen fixers. Values represent the average (standardized)
1246 values assigned to different traits (see Ding & Eldridge, 2019) according to whether they increase
1248 or reduce structure or function. A larger value equates with greater structure or function.

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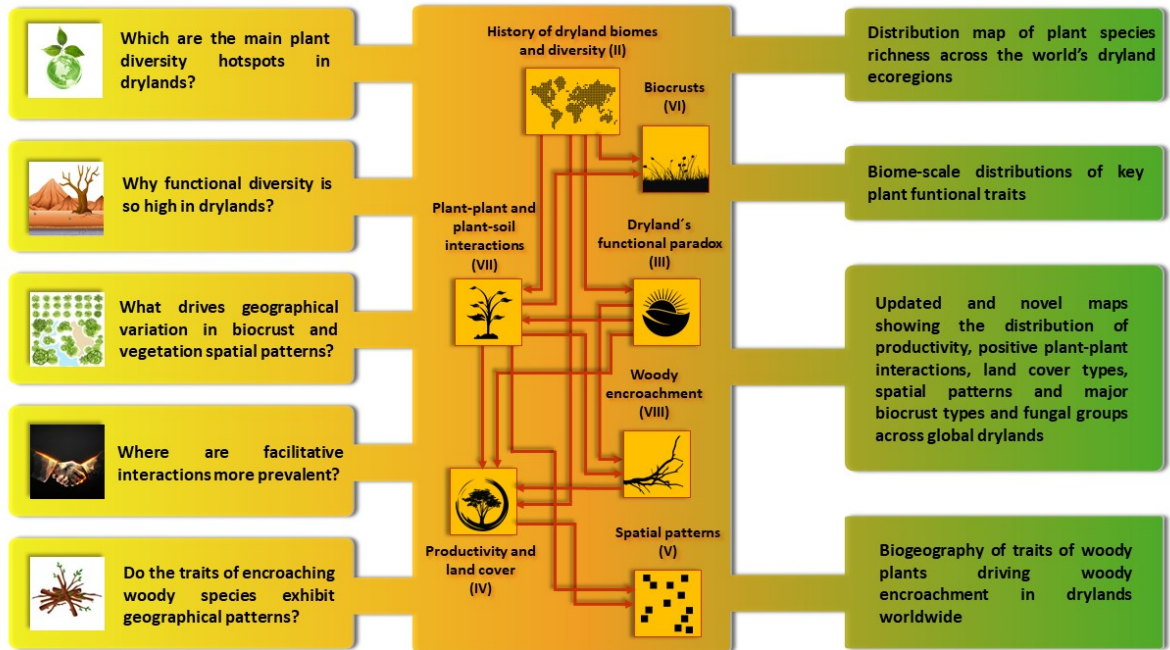


Figure 1

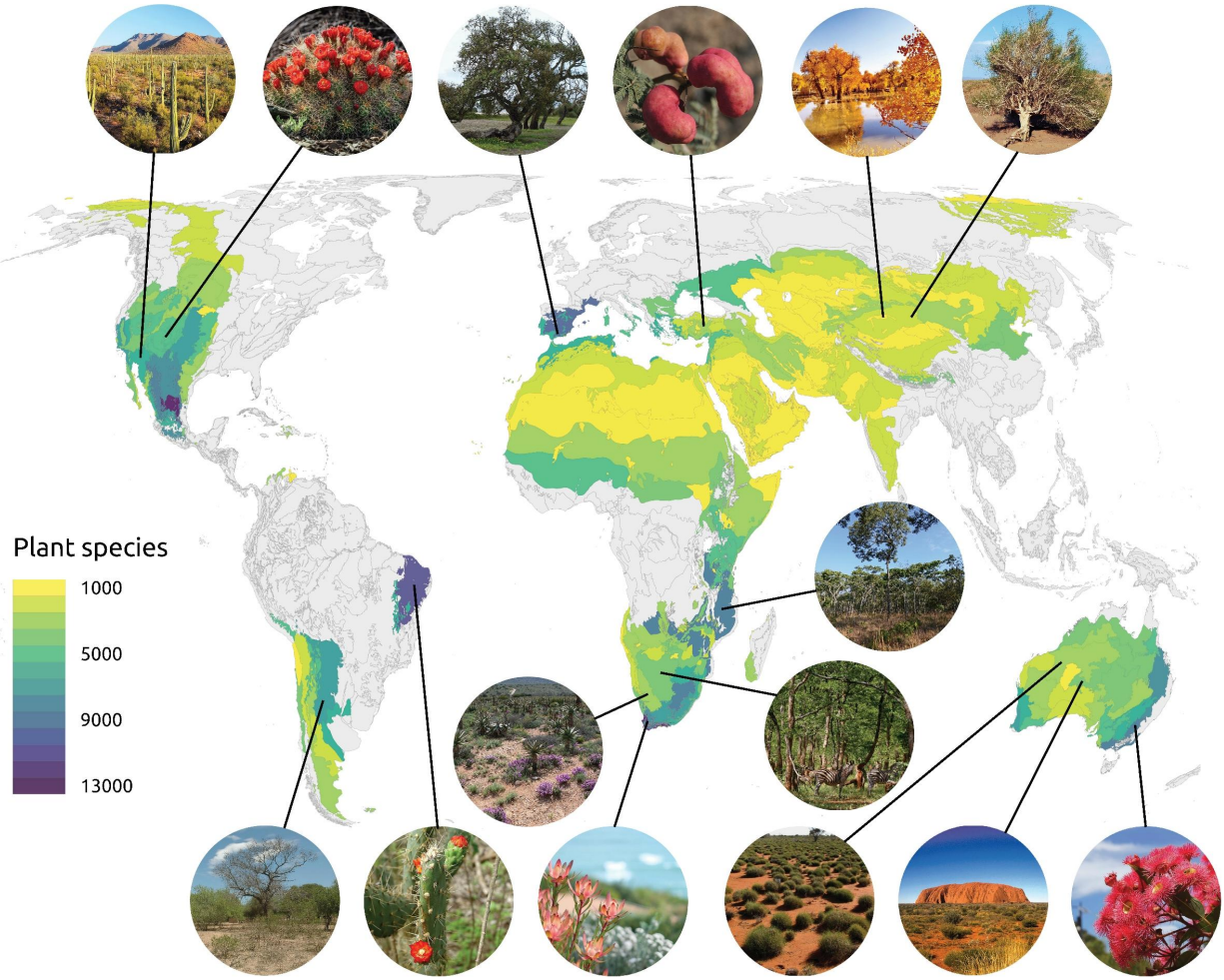


Figure 2

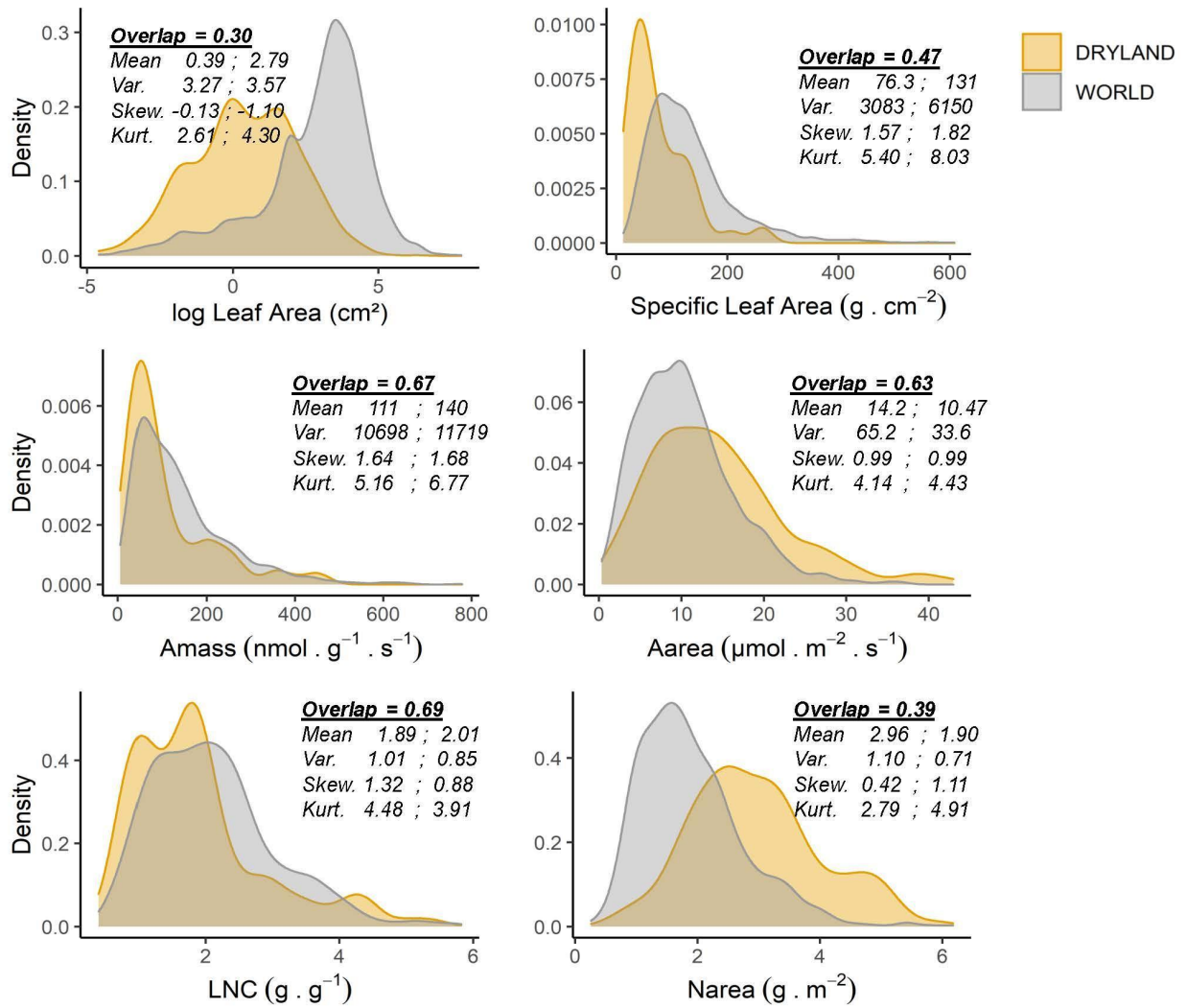


Figure 3

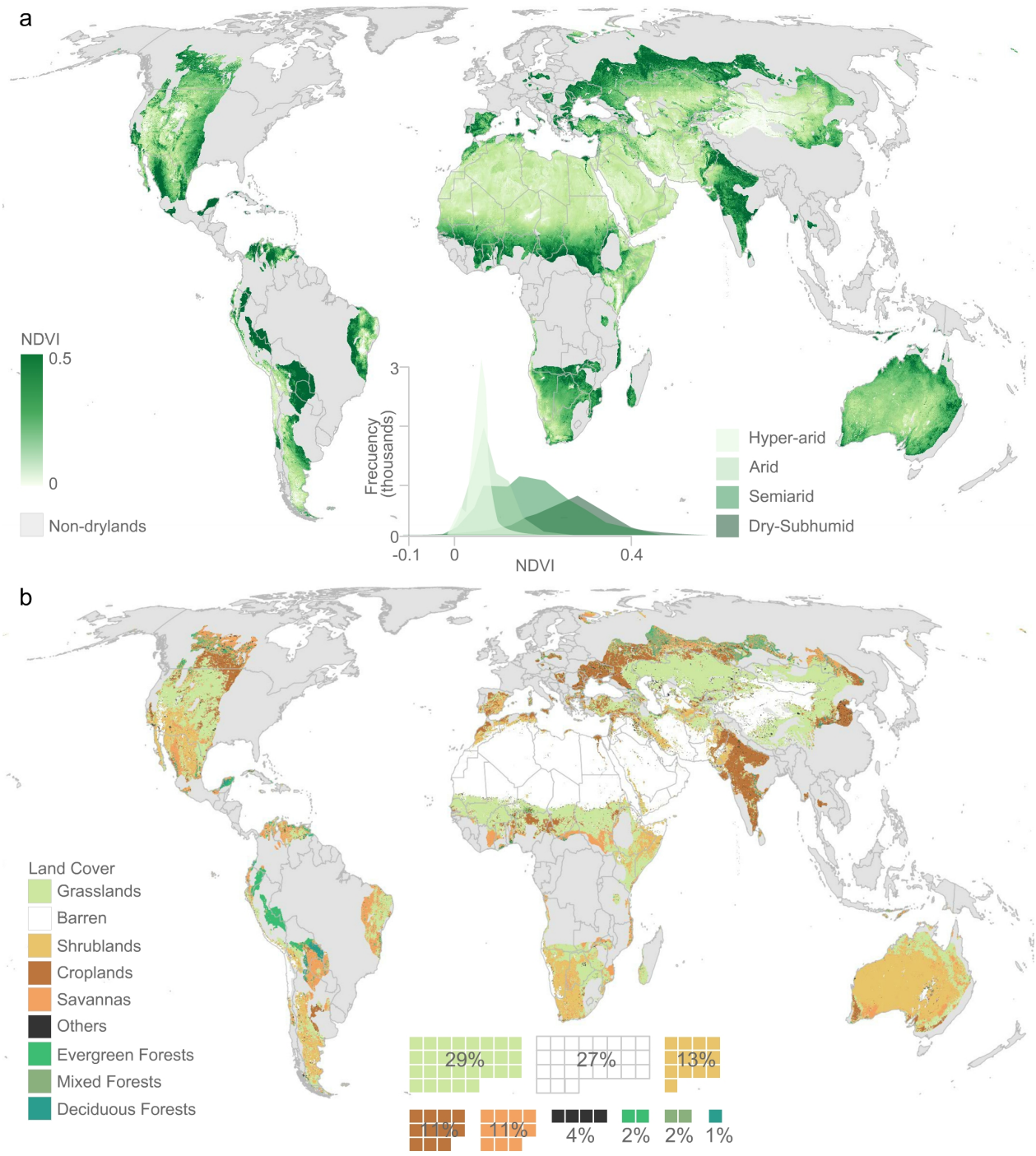


Figure 4

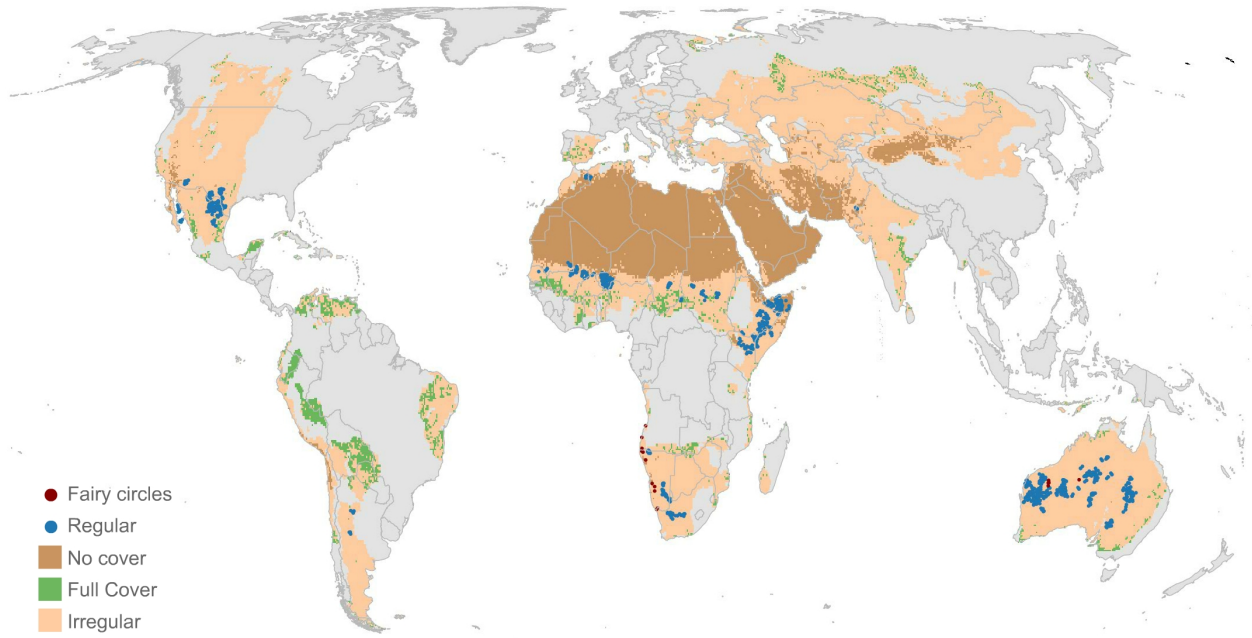


Figure 5

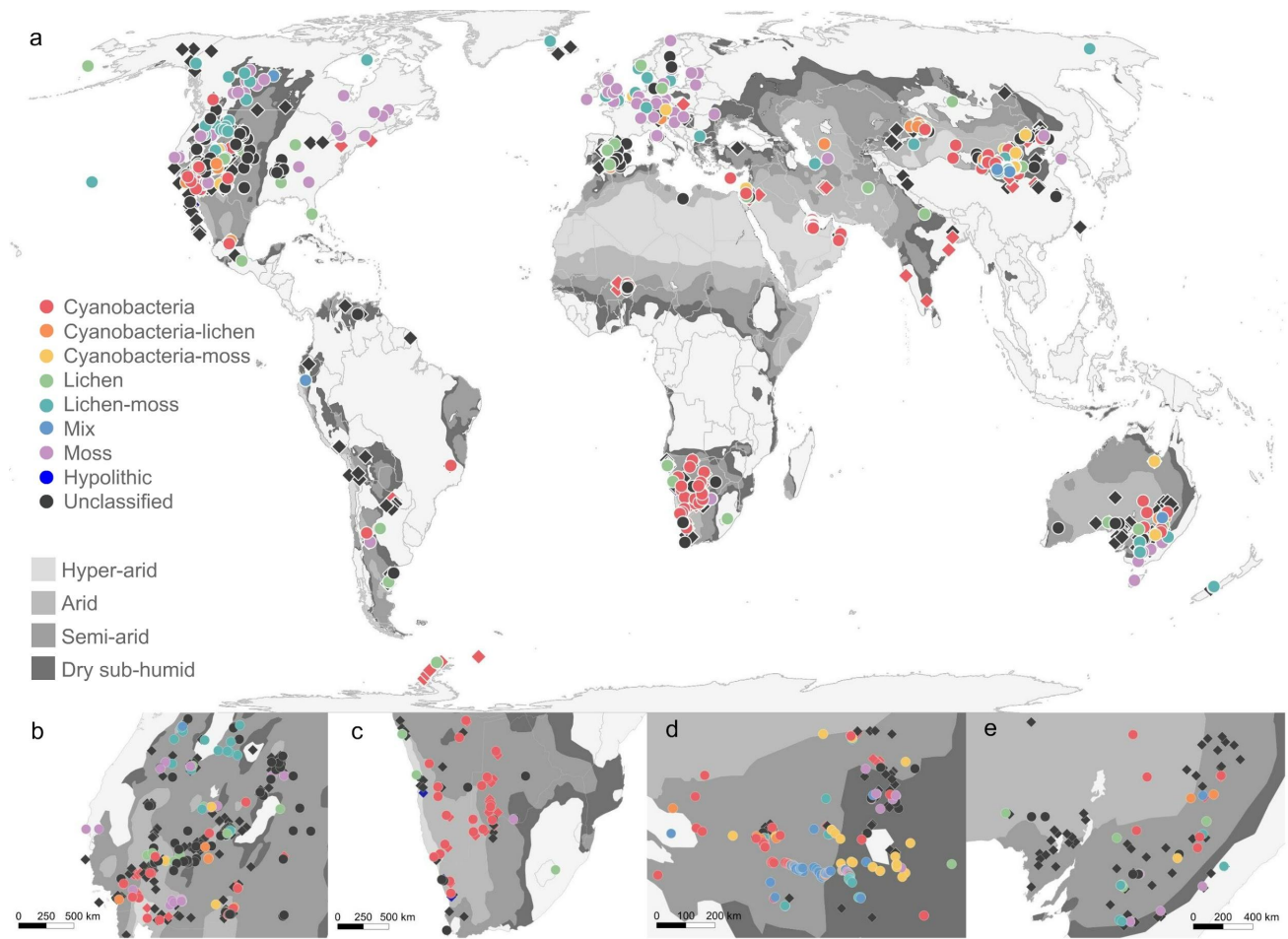


Figure 6

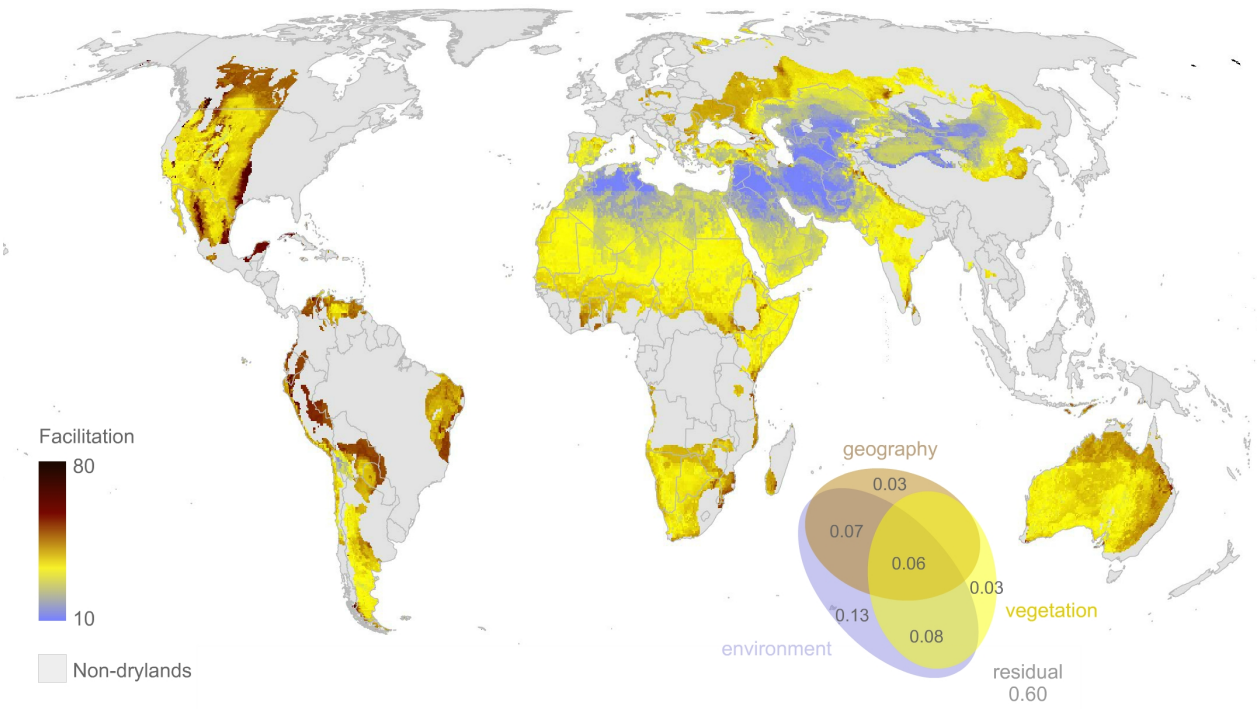


Figure 7

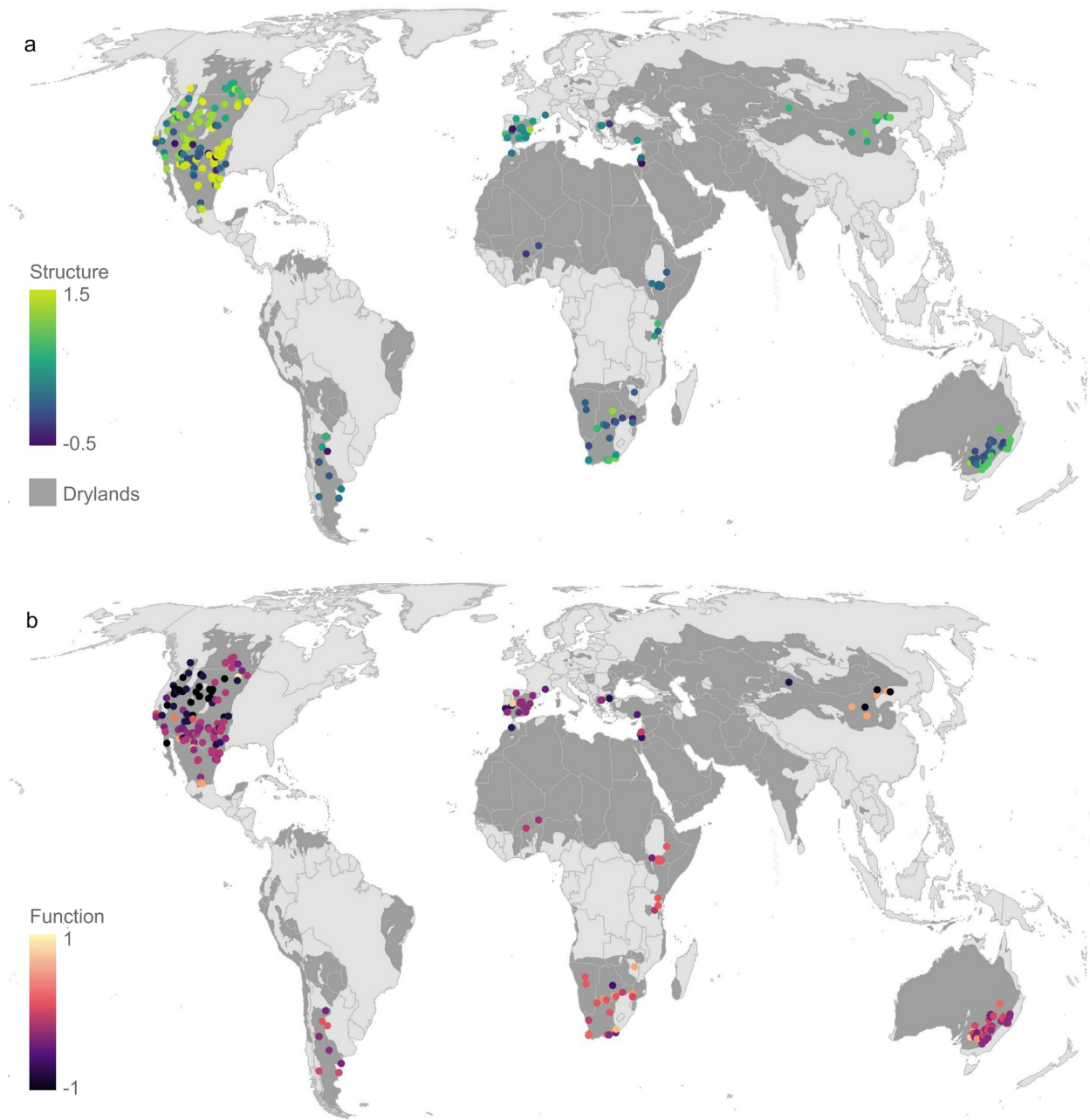


Figure 8