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Structure and functioning of dryland ecosystems in a changing world

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Abstract

Understanding how drylands respond to ongoing environmental change is extremely important for global sustainability. Here we review how biotic attributes, climate, grazing pressure, land cover change and nitrogen deposition affect the functioning of drylands at multiple spatial scales. Our synthesis highlights the importance of biotic attributes (e.g. species richness) in maintaining fundamental ecosystem processes such as primary productivity, illustrate how N deposition and grazing pressure are impacting ecosystem functioning in drylands worldwide, and highlight the importance of the traits of woody species as drivers of their expansion in former grasslands. We also emphasize the role of attributes such as species richness and abundance in controlling the responses of ecosystem functioning to climate change. This knowledge is essential to guide conservation and restoration efforts in drylands, as biotic attributes can be actively managed at the local scale to increase ecosystem resilience to global change.

Keywords

climate; abiotic factors; land use change; biotic attributes; drought; biodiversity

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1 Introduction

Drylands, regions with an Aridity Index (i.e., the ratio of mean annual precipitation to mean annual potential evapotranspiration) below 0.65 (Safriel & Adeel 2005), have a climate characterized by infrequent, highly variable, rainfall and intense solar radiation (Whitford 2002). Consequently, these areas experience conditions of chronic water shortage, and, unlike mesic ecosystems, do not sustain a continuous cover by vascular plants (Whitford 2002). Given the role of water as the main limiting resource for biological activity in drylands, it is not surprising to find that a high proportion of research has focused on understanding how rainfall amount and frequency affect ecological processes in these ecosystems (e.g., Reynolds et al. 2004, Schwinning et al. 2004, Collins et al. 2014). The importance of climatic factors as drivers of the structure and functioning of drylands is widely accepted. Nevertheless, there is an emerging body of literature showing that biotic attributes, such as species richness, diversity and abundance, drive key functions in these ecosystems, such as aboveground net primary productivity (ANPP) and nutrient cycling (Maestre et al. 2012a, Gaitán et al. 2014a, Jin et al. 2015, Delgado-Baquerizo et al. 2016a), and modulate the effects of abiotic factors on ecosystem functioning (Maestre et al. 2013).

Alterations in climate, land cover and use are major global change drivers that are particularly important in drylands because they cause desertification (Asner et al. 2004, MEA 2005, Xu et al. 2011, D'Odorico et al. 2013), defined as a reduction or loss of biological or economic productivity of land resulting from climatic factors and human activities (MEA 2005). Understanding how drylands might respond to these drivers is extremely important for global sustainability because they occupy 41% of Earth's land surface, and support over 38% of its human population (Safriel & Adeel 2005). It is estimated that severe ecosystem degradation has occurred in 10-20% of drylands, and its consequences affect ~250 million people in the developing world (Reynolds et al. 2007). These values are likely to increase with climate change and current rates of human population growth (Safriel & Adeel 2005), as the most recent climatic projections suggest an increase in the extent of global drylands by 11-23% by the end of this century (Huang et al. 2016).

Understanding dryland responses to global change is challenging due to the complex, dynamic interactions among multiple trophic levels and ecosystem functions (Figure 1). To unravel this complexity, we should focus on understanding how biotic attributes interact with abiotic factors to ultimately drive ecosystem functioning (Schlesinger et al. 1990, D'Odorico et al. 2013). In this review, we synthesize the literature on the drivers of ecosystem functioning in drylands, paying particular attention to structural biotic attributes such as species abundance, diversity and spatial pattern at multiple trophic levels. We will not, however, reiterate some important topics, such as the role of rainfall pulses, as these have been the subject of recent reviews (McCluney et al. 2012, Collins et al. 2014). We discuss the emergence of major global change drivers in drylands, and the ways in which they interact with abiotic factors and biotic attributes to influence the simultaneous provision of multiple ecosystem functions (multifunctionality, Hector & Bagchi 2007). We use a number of datasets from different regions to assess the impacts of biotic attributes (such as species richness) and major global change drivers (climate change, increases in grazing pressure,

land cover change and N deposition) on the functioning of drylands. Finally, we briefly discuss the importance of considering the interactions between structural biotic attributes and ecosystem functioning when monitoring desertification processes and designing restoration actions.

2 Determinants of Ecosystem Functioning in Drylands

Abiotic factors, including the frequency and amount of individual rainfall events, together with temperature, drive multiple ecological processes in drylands, including the activity of organisms (Collins et al. 2014), ANPP (Sala et al. 1988), nutrient cycling (Austin et al. 2004), the transfer of energy between trophic groups (Mesarve et al. 2015) or species interactions and coexistence (McCluney et al. 2012). Other abiotic factors, such as geomorphology and soil texture, largely modulate the effects of climate on the functioning of these ecosystems (see Supplemental Appendix 1). Their climatic features, and the fact that their scarce resources limit biological activity for most of the year, make the processes driving the functioning of drylands rather unique compared to other ecosystems. For example, litter decomposition is controlled by climate, litter quality and soil biota in most biomes (Parton et al. 2007), but this process is mostly driven by photodegradation in drylands (Austin 2011).

Biotic forces, ranging from cover, diversity and spatial patterning of plants and microbial communities, to the influences of grazing animals, also influence the functioning of drylands. Studies conducted at multiple spatial scales (from local to global) have reported a positive relationship between the cover of vascular plants and key ecosystem functions and services, such as ANPP and soil fertility (Martínez-Mena et al. 2002, Delgado-Baquerizo et al. 2013, Gaitán et al. 2014a). For example, large tree canopies in South African savannas not only reduce incident light, increase soil organic matter and pump-up water to the upper soil layers through hydraulic lift (Ludwig et al. 2003), but also attract seed-disperser birds, bats and mammals, which alter nutrient inputs and water infiltration into the soil and generate positive feedbacks on nutrient cycling and vegetation community structure (Dean et al. 1999). A biotic component typical of drylands is the soil surface communities dominated by cyanobacteria, lichens, and mosses (biocrusts). This component functions as an alternative primary producer community in addition to plants, and largely drives processes like erosion resistance, nutrient cycling and hydrology (Belnap 2006, Maestre et al. 2011). Consequently, biocrust cover has been reported to promote multifunctionality in drylands worldwide (Bowker et al. 2013, Delgado-Baquerizo et al. 2016b). These positive effects of cover of both plants and biocrusts are thus caused by their ability to: i) capture and cycle resources such as water and nutrients, and ii) attract a range of biota with a disproportionate effect on ecosystem attributes and functions.

Experiments and observations conducted at local (e.g., Flombaum & Sala 2008), regional (Conti & Díaz 2013, Gaitán et al. 2014a) and global (Maestre et al. 2012a) scales have reported positive relationships between plant species richness and key ecosystem functions (e.g. ANPP) and multifunctionality in drylands. Similar results have been observed by studies focusing on biocrusts (Maestre et al. 2012b, Bowker et al. 2013) and soil microbial communities (Jing et al. 2015, Delgado-Baquerizo et al. 2016a). However, these effects of

species richness may not be independent of factors such as climate (Jing et al. 2015) or land use (Zhou et al. 2006), emphasizing the need for understanding the interactions among biotic and abiotic drivers of ecosystem functioning. The richness of dryland plant communities is linked to other biotic attributes such as species interactions. Soliveres & Maestre (2014) found that over 25% of the plant species present in 137 dryland communities worldwide were more closely spatially associated with nurse plants than expected by chance, illustrating the importance of positive plant–plant interactions for maintaining plant species richness in these environments. To date, there is little evidence that species interactions within the same trophic level, such as plant–plant facilitation, directly impact ecosystem functioning (Maestre et al. 2010). However, there is a growing recognition of the important role that multitrophic interactions among plants, biocrusts and microorganisms play as drivers of ecosystem functioning in drylands (see Supplemental Appendix 2).

How the spatial organization of vegetation affects the functioning of drylands is a topic being studied by both modelers and field ecologists. Empirical studies have shown that, for a given level of total cover, changes in spatial pattern affect water and soil losses via runoff and erosion (Bautista et al. 2007). Plant patches also tend to be aligned parallel to the contours in dryland hillslopes, increasing their ability to trap runoff water generated in bare ground areas, which is critical to sustain plant growth (Puigdefábregas et al. 1999). Mathematical models have also shown that biomass, water and sediment yields from hillslopes with spatially structured vegetation can be higher than that from alternative situations with spatially uniform distributions (von Hardenberg *et al.* 2001, Boer & Puigdefábregas 2005). Moreover, the concentration of scarce resources into fertile patches sustains perennial vegetation in environments where it would be unsustainable if resources were distributed uniformly across the landscape (Noy-Meir 1973, Rietkerk et al. 2002, Kéfi et al. 2010a). Similarly to plants, the spatial features of biocrust patches also affect ecosystem functioning; for example, a greater frequency of small to medium sized patches leads to greater accumulation and cycling of C than many very small patches (Bowker et al. 2013).

Livestock grazing is the most widespread land use in drylands, where it supports the livelihoods of many people worldwide (Asner et al. 2004, Safriel & Adeel 2005). Grazing has important effects on ecosystem structure and functioning in these areas (Milchunas & Lauenroth 1993, Fleischner 1994, Adler et al. 2001, Hanke et al. 2014). For example, a meta-analysis of 7615 published records across Australia showed that livestock grazing substantially reduced plant cover and biomass, animal richness and abundance and litter cover, and that negative effects on structural and functional variables were more pronounced in drier environments (Eldridge et al. 2016). Interactions between climate and grazing are, indeed, a fundamental driver of ecosystem functioning in drylands (e.g., Milchunas and Lauenroth 1993, Asner et al. 2004, Ruppert et al. 2015), and have major implications for their management (Safriel and Adeel 2005). In addition, grazing effects also vary with i) the intensity of grazing and the composition of herbivore assemblages (Riginos & Grace 2008, Eldridge et al. 2016), ii) the shared evolutionary history of plants and herbivores (Milchunas & Lauenroth 1993), or iii) the ecosystem variable being investigated. For example, grazing has generally a stronger effect on plant or soil attributes than on animals (Eldridge et al.

2016), and has a greater influence on resilience (plant recovery after drought) than resistance (reduction in plant productivity during drought, Ruppert et al. 2015).

The different examples discussed above highlight the multiplicity of factors affecting ecosystem processes in drylands, and the importance of positive (e.g. facilitation) and negative (e.g. grazing) biotic interactions as determinants of the structure and functioning of these ecosystems. How abiotic and biotic features interact to determine future changes in drylands, and the relative importance of multiple drivers of ecosystem functioning in these environments are discussed further in the following sections.

3 Ecosystem Structure and Functioning of Drylands Under Global Change

3.1 Climate change

There is a consensus that the future climate of drylands will be characterized by: i) higher temperature, up to 4°C in some areas, ii) shifts in the seasonal rainfall regime and a greater frequency of extreme events (such as droughts and heatwaves), and iii) an increase in the degree of aridity (IPCC 2013, Collins et al. 2014, Fu & Feng 2014, Cook et al. 2015). These changes will affect the size, frequency, intensity and timing of rainfall events, which largely determine the structure and functioning of drylands (reviewed by McCluney et al. 2012 and Collins et al. 2014). Understanding how dryland biota adapts to drought, a prevalent climatic feature of drylands, has been a classical research topic (Goodall 1976, Whitford 2002). Observations indicate that the frequency, duration, and severity of droughts have increased in many dryland regions during the 1951–2010 period (Spinoni et al. 2014). Climatic projections point to a greater risk of facing severe droughts during the second half of this century in many drylands worldwide (IPCC 2013), which may lead to unprecedented drought conditions in areas such as the Southwest and Central Plains of Western North America (Cook et al. 2015). It is thus imperative to expand research on drought beyond its effects on the physiology and evolution of organisms to understand how this phenomenon impacts the functioning of whole ecosystems. Using more than 300 sites scattered all over Patagonia (Argentina), Gaitán et al. (2014b) found that increases in plant species richness and shrub cover dampened the reductions in ANPP during a drought year. Ruppert et al. (2015) used a database consisting of 174 long-term datasets from more than 30 dryland regions to quantify the resistance and recovery of ANPP to drought. They found that annual and perennial systems showed the same rate of response to increasing drought intensity, but annual systems were ~27% less resistant to drought. However, areas with an herbaceous layer dominated by annuals had substantially higher postdrought recovery, particularly when grazed. These studies point to the importance of biotic attributes such as species composition and richness for better understanding how drylands will respond to the forecasted intensification in drought frequency and severity.

Among the many influences that increases in aridity and drought frequency have on biotic composition are alterations in the dominance of plant forms (e.g. grasses and shrubs; Soliveres et al. 2014a), shifts in plant species interactions, which influence diversity and spatial patterning in drylands (Kéfi et al. 2007, Soliveres & Maestre 2014), and reductions in total plant cover (Delgado-Baquerizo et al. 2013). Because functions such as nutrient cycling, carbon sequestration and litter decomposition are influenced by these biotic

attributes (Figure 1), ecosystem functioning is likely to decline with increasing aridity. Using a global survey conducted at 224 dryland sites, Maestre et al. (2012a) showed that temperature was a major driver of multifunctionality, which declines as temperature increases. Additional analyses of the same database revealed that increasing aridity reduces soil organic C and total N, independently of its negative effect on plant abundance (Delgado-Baquerizo et al. 2013). Concurrently, physically regulated elements such as phosphorus (P) become dominant as aridity increases; as a result, increasing aridity imbalanced soil nutrient stoichiometry in global drylands. Such imbalances with increasing aridity have also been recently reported in Chinese drylands (Jiao et al. 2016).

Increases in aridity will also likely alter belowground communities in drylands. Dryland soils host bacterial and fungal communities dominated by *Actinobacteria* and *Ascomycota* (Maestre et al. 2015), in contrast to soils from more humid ecosystems, which are typically dominated by *Acidobacteria*/*Proteobacteria* and *Basidiomycota* (Tedersoo et al. 2014, Ramirez et al. 2014). Despite the important role that the abundance and diversity of soil microbes play in maintaining ecosystem functioning in terrestrial environments (Bardgett & van der Putten 2014), little is known about how they will respond to forecasted increases in aridity. A survey of 80 drylands from all continents except Antarctica revealed linear declines in the diversity and abundance of soil bacteria and fungi with increases in aridity (Maestre et al. 2015). This response was mainly driven by the negative impacts of aridity on variables such as soil organic C, which positively affected the abundance and diversity of both bacteria and fungi. Aridity also promoted increases in the relative abundance of *Chloroflexi* and α -*Proteobacteria* and decreases in that of *Acidobacteria* and *Verrucomicrobia*. Using this global database, Delgado-Baquerizo et al. (2016a) reported positive effects of the diversity of soil microbial communities on multifunctionality, which were particularly driven by the diversity of soil fungi. We used these data to further explore how these changes in microbial communities may affect ecosystem functioning. We found that the diversity and abundance of both bacteria and fungi were positively related to surrogates of C, N and P cycling and storage, such as the activity of the enzymes β -glucosidase and phosphatase, soil available N and the N transformation rate, and to multiple proxies of soil C availability (Supplemental Table 1). Similar results were found when evaluating the relationships between these variables and the relative abundance and diversity of phyla such as *Acidobacteria*, which are considered oligotrophs that may promote soil C sequestration (Trivedi et al. 2013), and *Verrucomicrobia*, which contain an important array of genes supporting organic matter decomposition (e.g. hemicellulose and cellulose degradation, Trivedi et al. 2013). Although these correlative analyses do not allow us to establish cause and effect relationships, they are consistent with results from Jing et al. (2015), who reported positive effects of soil microbial communities on multifunctionality in drylands from the Tibetan Plateau.

Climate change will also promote important changes on biocrust communities. Compositional surveys of biocrust-associated cyanobacteria across the Southwestern US revealed a latitudinal change in the dominance of *Microcoleus vaginatus*, which was replaced by *M. steenstrupii* as aridity increased (Garcia-Pichel et al. 2013). Ferrenberg et al. (2015) evaluated the response of biocrust communities to 10 years of altered precipitation (increases in small summer rainfall events) and experimental warming (2-4 °C above

ambient) in the Colorado Plateau. Five years after the beginning of this experiment, warming considerably reduced moss and lichen cover relative to control plots, and increased the cover of cyanobacteria. Altered precipitation frequency exerted similar effects on mosses and cyanobacteria, but these were noted soon after the treatments started. Experiments conducted in Central and SE Spain revealed that a 2–2.5 °C warming significantly decreased the diversity and cover of well-developed lichen-dominated biocrusts (Escolar et al. 2012, Maestre et al. 2013). Another experiment conducted in South Africa revealed that a 2.1–3.8 °C warming dramatically reduced the photosynthetic effective quantum yields of four biocrust-forming lichens (Maphangwa et al. 2012). These changes in the composition, abundance and performance of biocrust constituents have dramatic cascading effects on multiple ecosystem processes. In the Spanish experiments, Maestre et al. (2013) reported significant increases in soil CO₂ efflux with warming from biocrust-dominated soils, an effect that was not observed in areas with low biocrust cover. Further, warming reduced C fixation in biocrust-dominated microsites (Ladrón de Guevara et al. 2014) and increased the temperature sensitivity (Q_{10}) of soil respiration in these areas (Escolar et al. 2015), suggesting that higher temperatures may result in a reduced capacity for biocrusts to act as a C sink. Similar responses were found in the Colorado Plateau, as warming promoted CO₂ loss from biocrust-dominated soils (Darrouzet-Nardi et al. 2015).

Together, available evidence suggests that climate change will reduce the capacity of drylands to provide ecosystem services such as the maintenance of soil fertility and C sequestration because these are largely regulated by biocrusts and soil bacteria and fungi, whose abundance, composition and diversity will likely change under future climatic scenarios (Maestre et al. 2013, 2015, Ferrenberg et al. 2015, Jing et al. 2015). These effects can feedback upon other forecasted impacts of increased aridity, such as the reduction of plant productivity (Brookshire & Weaver 2015) and the imbalance in the C, N and P cycles (Delgado-Baquerizo et al. 2013, Jiao et al. 2016), further diminishing the ability of drylands to provide life-supporting ecosystem services under climate change.

3.2 Nitrogen deposition

Nitrogen inputs from human activities have already doubled the total amount of N fixed naturally by terrestrial and aquatic ecosystems, with current global annual rates of N deposition of about 120 Tg N·year⁻¹ (Dentener et al. 2006, Schlesinger 2009). Impacts from N enrichment can be particularly deleterious in drylands because N is, after water, the main factor limiting plant production and organic matter decomposition (Schlesinger & Bernhardt 2013). These impacts include reductions in native plant diversity, changes in plant species composition, soil acidification, increased aluminium toxicity and alterations in N cycling, among others (reviewed in Ochoa-Hueso et al. 2011). Delgado-Baquerizo et al. (2016c) demonstrated that human impacts linked to N deposition are already increasing the amount of inorganic N in global drylands. They found that the biggest impacts from N deposition take place at the more mesic parts of drylands, coinciding with the highest human pressure.

To further explore the effects from N enrichment in global drylands, we used data from Maestre et al. (2012b, 2015) and Delgado-Baquerizo et al. (2016c) to evaluate the relationships between N deposition, inorganic N from global fertilizers and manure, and

multiple descriptors of ecosystem structure and functioning in global drylands (Supplemental Table 2). We found a negative correlation between N in manure and fertilizers and plant diversity ($\rho = -0.147$, $P = 0.031$), in agreement with the general notion that N additions reduce the biodiversity of terrestrial ecosystems (Bobbink et al. 2010). We also found a positive correlation between N enrichment and soil C content ($\rho = 0.283$, $P < 0.001$), as found by studies suggesting that soil C storage and plant and microbial biomass are limited by N availability in drylands (reviewed in Schlesinger & Bernhardt 2013). Moreover, the positive correlation between N in fertilizer and the fungi: bacteria ratio found ($\rho = 0.493$, $P < 0.001$) is consistent with the notion that fungal communities are often stimulated by N addition in N-limited environments (Strickland & Rousk 2010). Of special interest were the observed negative and positive correlations between N enrichment and the availability of both P ($\rho = -0.256$, $P < 0.001$) and N ($\rho = 0.175$, $P < 0.001$), respectively. The negative effect of N enrichment on P availability is also supported by the increase in the activity of phosphatase observed with overall N fertilization ($\rho > 0.192$, $P < 0.005$), as this enzyme (released by plants and microbes) transforms organic P to inorganic P (Schlesinger & Bernhardt 2013). The shift from N to P limitation is one of the most reported effects of N enrichment in terrestrial ecosystems (Ochoa-Hueso et al. 2011), and can negatively impact nutrient cycling, primary productivity and plant diversity (Bobbink et al. 2010). Available evidence, therefore, shows that N enrichment derived from human activities is already having important consequences for ecosystem functioning in drylands worldwide.

3.3 Intensification of livestock grazing

The increasing global demand for the production of meat and other animal products will lead to the intensification of grazing in many dryland regions (Thornton 2010). To gain additional insights on how this phenomenon may affect ecosystem functioning, we re-analyzed the large database of published effects of livestock in Australia from Eldridge et al. (2016). By comparing all possible two-way combinations of four different grazing intensities (ungrazed, low, moderate and high grazing), we evaluated how grazing impacts soil C content and three surrogates of the capacity of the soil to cycle nutrients, resist disturbance and maintain water flow (nutrient, stability and infiltration indices, respectively; see Supplemental Appendix 3), which are critical determinants of ecosystem functioning in drylands (Whitford 2002, Tongway & Hindley 2004).

We found that, across all levels, grazing negatively impacted both C content (Figure 2), indicating average reductions in C of about 8%. Similarly, soil stability was reduced by about 8%, nutrient cycling by 11% and water infiltration by 13%. Reductions in soil C were most pronounced under the smallest (low *cf.* ungrazed: C: 23% reduction) and greatest (high *cf.* ungrazed: C: 23%) grazing contrasts, whereas the strongest (suppressive) effect of grazing on soil functional indices occurred at high grazing contrasts (ungrazed or low *cf.* high grazing; Figure 2). Grazing is known to reduce organic inputs into the soil by reducing litter cover, hence reducing litter decomposition (Daryanto et al. 2013), or the capacity of the soil surface to capture and store rainfall (Fleischner 1994) via physical surface disturbance (Whitford 2002). Secondly, and unexpectedly, C declined markedly under very low (low grazing *cf.* ungrazed) grazing conditions. This could be due to the breakdown and loss of volatile, water soluble, labile forms of C, particularly microbial biomass C, which is

sensitive to even very low levels of grazing-induced disturbances (Holt 1997). Thirdly, response ratios for C and the nutrient, stability and infiltration indices were close to neutral under intermediate grazing contrasts. The effects of grazing likely represent a balance between losses of C from soil disturbance, which could stimulate C and N mineralization and therefore respiration (Hassink 1994), and additions from dung and urine during livestock camping (Haynes & Williams 1999). Finally, the boundary between dry subhumid and semiarid areas represented the domain where the effects of grazing on C shifted from a decline to an increase with increasing aridity (Supplemental Figure 1), which has been shown to reduce plant cover and soil C and N contents in drylands worldwide (Delgado-Baquerizo et al. 2013). This scenario for Australia may represent, therefore, an idiosyncratic effect of grazing on soil C in an environment that has experienced a short evolutionary history of livestock grazing.

3.4 Land cover change: the case of woody encroachment

Woody encroachment, i.e. the increase of woody vegetation in former grasslands or open shrublands/savannas, has become a major issue in global drylands over the past century (van Auken 2000, Asner et al. 2004, Eldridge et al. 2011, Eldridge & Soliveres 2015). This phenomenon has substantial effects on ecosystem functioning due to the capacity of shrubs to buffer environmental conditions, and to increase organic matter accumulation, soil biotic activity, nutrient pools and hydrological processes (Dean et al. 1999, Asner et al. 2004, Knapp et al. 2008, Eldridge et al. 2011). However, the ecological effects of woody encroachment on ecosystem functioning have been shown to be highly contextual, as they depend on i) the prevailing land use and the extent to which landscapes are managed, with normally positive functioning-encroachment relationships dampening under livestock grazing (e.g. Eldridge et al. 2011, 2013), ii) the density of woody plants, with high density areas being less functional than those with moderate woody cover (Riginos et al. 2009, Soliveres et al. 2014a), or iii) the prevailing environmental conditions, with more arid environments showing more negative responses to woody encroachment (Knapp et al. 2008, Soliveres et al. 2014a). However, less well-known is how different woody species, and their idiosyncratic traits, affect ecosystem processes, and how these effects are mediated by forecasted increases in aridity (Eldridge & Soliveres 2015). To fill this knowledge gap, we synthesize here the effects of encroachment on a range of ecosystem attributes, and show how they varied with the traits of the encroaching plants. To do this we calculated a log response ratio (lnRR) for each of 1852 independent records from an updated global database of encroachment effects on drylands (Eldridge et al. 2012), such that a positive value of lnRR indicates an increase in the value of a given function with encroachment (Supplemental Appendix 4). We then analyzed the joint and independent effects of aridity and plant traits on five synthetic response variables (C, N, soil hydrological function, vascular plant richness, and aboveground plant biomass) using Classification and Regression Trees (CART; see Supplemental Appendix 4 for details).

We found that different plant attributes had different effects on our five response variables (Supplemental Figure 2). Aridity and shrub trait effects explained from 18% (plant richness) to 40% (soil hydrological function) of the variation found in these variables. Overall, aridity and plant height were important in four of the five response variables evaluated, with plant

shape, palatability to herbivores and deciduousness in three of them (Supplemental Figure 2). Further, aridity was involved in two or more splits of the tree for plant biomass, C and soil hydrological function (Supplemental Figure 3). As an example, aridity accounted for over half (57%) of the variance in soil hydrology, while the most influential shrub trait was dispersal mode, which accounted for 23% of this variance (Supplemental Table 3). The greatest LnRR for soil hydrological function was observed under high values for aridity (> 0.80 ; arid) and the predominant woody plants were either water or wind dispersed. Interestingly, the second largest LnRR for this function was observed when aridity was low (< 0.25 , subhumid), irrespective of woody plant height (Supplemental Figure 3). When aridity was intermediate (semiarid), short, v-shaped woody plants (shrubs) were the most functional in terms of soil hydrology (Supplemental Figure 3). These v-shaped woody plants structures are known to have a larger effect on infiltration than other plant shapes in drylands because they tend to funnel water to the centre of the plant (Whitford 2002). Plant height and N-fixation were important predictors of the LnRR for plant species richness, but this was independent of aridity (Supplemental Figure 2). Taller plants produce more litter, generally have larger canopies, and therefore likely provide more diverse surface microsites with a greater capacity to ameliorate environmental conditions, thus increasing the number of understorey plant species (Soliveres et al. 2014b). Overall, these findings highlight the importance of the attributes of encroachers, which should be explicitly considered in future studies addressing the functional consequences of woody encroachment and also when evaluating the utility of management policies aimed at woody eradication, which commonly consider every woody species to have equivalent functional consequences (see Eldridge & Soliveres 2015 for a review).

4 The Relative Importance of the Multiple Drivers of Ecosystem Functioning in Drylands

Despite decades of research and the well-known interactions between them, the relative importance of the different abiotic and biotic drivers for ecosystem functioning is surprisingly poorly studied in drylands. Most of our knowledge about the controls on ecosystem functioning at regional to global scales in these ecosystems comes from correlative analyses conducted across natural environmental gradients (e.g., Sala et al. 1988, Gaitán et al. 2014a, Maestre et al. 2012a, but see Ruppert et al. 2015). However, these studies rarely consider interrelationships among major drivers of ecosystem functioning (but see Gaitán et al. 2014a, Soliveres et al. 2014a). Grazing, climate and biotic attributes covary along natural gradients, and it is often difficult to disentangle their independent effects and the interactions between them. Structural equation modelling (SEM) provides a statistical framework to deal with the complex relationships among these different drivers of dryland functioning, giving us a more comprehensive picture of their relative importance and providing insights into the mechanisms behind their effects (Grace 2006). Using SEM, Gaitán et al. (2014a) and Soliveres et al. (2014a) showed that structural attributes of vegetation, such as cover of particular functional groups (i.e., grasses or shrubs) or species richness, were as important as climate to ecosystem functioning at regional and global scales. However, no previous study has evaluated how the intensity of grazing, aridity and biotic attributes simultaneously affect ecosystem functioning in drylands. We did so by

assessing the relative importance of grazing, aridity and plant species richness as drivers of soil C contents and plant biomass/productivity using four existing datasets and SEM: the global EPES-BIOCOM database (Maestre et al. 2012a), data gathered at the continental level in Australia (Eldridge et al. 2016), a regional survey across Patagonian rangelands (Gaitán et al. 2014a), and a local survey from South Africa (Fynn 1998; see details in Supplemental Appendix 5).

We found negative effects of aridity on plant species richness (standardized path coefficient = -0.37 ± 0.1 , averaged across datasets), biomass/productivity (-0.32 ± 0.1) and soil C content (-0.50 ± 0.1). These effects were relatively consistent regardless of the different spatial scales, approaches and variables measured in each study case (Figure 3). Plant species richness was the second most important driver of dryland functioning, and had positive effects on both soil C content and biomass/productivity (Supplemental Figure 4). The average (across datasets) size of the effect of species richness on biomass/productivity was equivalent to that of aridity (0.30 vs. -0.32), although it was lower than the effect of aridity on soil C content (0.16 vs. -0.50). Grazing effects on plant biomass/productivity and soil C content varied among studies, with generally negative effects at the local scale that shifted to positive ones at broader spatial scales (Supplemental Figure 5). However, differences in the way that grazing pressure was measured among the datasets are substantial (Supplemental Appendix 5) and should be considered when interpreting these results. When significant, grazing effects were relatively similar in size to the effects of plant species richness but of opposite sign (Figure 3; Supplemental Figure 4). Overall, these results suggest that i) biotic attributes partially buffer the negative effects of aridity on dryland functioning, ii) positive effects of plant diversity dampen with increasing livestock grazing pressure, and iii) the relative importance of the different drivers of ecosystem functioning (particularly those of grazing) are scale-dependent. This scale-dependency has also been found when analyzing other key ecosystem functions in drylands. For example, studies often report declines in the relative importance of biotic attributes on infiltration with increasing spatial scale. At microsite and hillslope scales ($\text{cm}^2\text{-dam}^2$), infiltration is driven largely by soil surface components such as plant patches or biocrusts (Bhark & Small 2003, Berdugo et al. 2014), while climate, topography and land use are the dominant drivers of this process at the catchment scale (ha; Bracken & Croke 2007).

Mathematical models have also been used as an alternative to field studies to deal with the inherent difficulties of studying the joint effects of multiple drivers of dryland functioning. The interactions between vegetation attributes and climate, and between grazing and vegetation, have been tested with these models (Tietjen & Jeltsch 2007), though they rarely address the joint impacts of grazing, rainfall and vegetation attributes on ecosystem functioning (Manor & Shnerb 2008) or the effects of different herbivores (e.g., Riginos & Grace 2008, Eldridge et al. 2016). Additionally, plant attributes other than co-occurrence of particular plant functional groups, such as spatial pattern or species richness, also play a fundamental role on the functioning of dryland ecosystems, yet are rarely considered in current models. Developing more comprehensive models that consider the interplay between the major drivers of dryland functioning (climate, grazing, biocrust and plant attributes) across different spatial scales, and testing their performance with field data, will

undoubtedly help to improve our ability to forecast the response of drylands to ongoing global change.

5 The Importance of Structure-Functioning Relationships for Understanding Desertification and Restoring Degraded Drylands

Desertification is intimately linked to climate change through environmental processes (e.g., trace gas emissions to the atmosphere and dust storms; MEA 2005) and human activities (e.g., poor cultivation practices and overgrazing; Asner et al. 2004), whose effects on ecosystem functioning are modulated by biotic attributes such as plant cover, spatial patterns and species richness (Figures 1 and 4). Desertification is commonly associated with the transition between non-degraded and desertified states, where either situation could exist depending upon the balance between the intensity of drivers (e.g., grazing, climate change), changes in the spatial distribution of soil nutrients and plants, and the subsequent biological feedbacks (D'Odorico et al. 2013, Figure 4). Because of this, and because desertification is often difficult to reverse (Reynolds et al. 2007), many research efforts have focused on monitoring desertification processes and developing useful plant and soil indicators that could detect potential regime shifts (for reviews see Verstraete et al. 2011, Kéfi et al. 2014, Kairis et al. 2014, Wiesmeier 2015).

Vegetation cover has been frequently used as an indicator of ecosystem health and degradation status in drylands, and is a key component of dryland monitoring programs worldwide (Tongway & Hindley 2004, Herrick et al. 2005, Verstraete et al. 2011). Indeed, cover declines with degradation, because of grazing or increasing aridity (Delgado-Baquerizo et al. 2013, Eldridge et al. 2016). However, and given the possibility of threshold behavior in drylands, cover may not always be a good indicator of degradation because the cover at which the system may collapse is usually unknown (Kéfi et al. 2010b). For this reason, cover should be used in combination with additional indicators able to detect threshold-like responses when monitoring desertification processes. Among them, the spatial patterns of vegetation have been suggested as potential indicators of degradation in drylands (Rietkerk et al. 2004, Kéfi et al. 2007, Meron 2015). This is so because these patterns change in a predictable way as the ecosystem degrades (Supplemental Figure 6). Two broad types of vegetation spatial patterns have been identified in drylands: periodic (also referred to as 'regular') patterns and scale-free (also referred to as 'irregular') patterns (Rietkerk et al. 2002, Manor & Shnerb 2008, Meron 2015). Patterns observed in nature typically belong somewhere along a continuum between these two extreme types of spatial configurations as a result of the interplay between abiotic factors and the facilitative and competitive interactions among plants (Pueyo & Alados 2007). Periodic patterns are characterized by a typical scale (i.e. a typical vegetation patch size); they correspond to stripes on slopes, and gaps, labyrinths, and spots on flat terrains (Deblauwe et al. 2008). They tend to occur in competition-dominated ecosystems, and the typical patch size is then determined by the scale at which the competitive mechanism operates (Manor & Shnerb 2008). Scale-free patterns, on the other hand, are characterized by a broad range of patch sizes and seem to occur in facilitation-dominated ecosystems (Manor & Shnerb 2008). The distribution of plant patch sizes (i.e. the function that describes how the number of patches varies with the

size of the patches) typically follows heavy-tailed distributions (Kéfi et al. 2007, Scanlon et al. 2007). For periodic patterns, models and field observations have shown that the sequence of vegetation shapes shifts from gaps to labyrinth to spots along degradation gradients (Rietkerk et al. 2004). For scale-free patterns, the distribution of plant patch sizes could indicate increasing degradation, with fewer and smaller large patches as the system degrades (Kéfi et al. 2007, Lin et al. 2010). However, empirical support regarding the ability of spatial patterns as early warning indicators of land degradation remains elusive. Empirical tests conducted so far have provided contrasting results (Kéfi et al. 2007, Maestre & Escudero 2009, Lin et al. 2010, Bestelmeyer et al. 2013), and few studies have simultaneously evaluated the performance of vegetation patterns and other ecosystem features, such as total plant cover or soil properties, as indicators of land degradation (Maestre & Escudero 2009, Bestelmeyer et al. 2013). This precludes the generalization and adoption of standardized monitoring and prediction tools to detect the onset of dryland desertification.

Degraded drylands can be highly resistant to restoration attempts, particularly when the feedbacks between the biotic and abiotic factors have been altered, and when the new feedbacks in place contribute to maintaining the degraded state (Suding et al. 2004, Cortina et al. 2011). For example, when vegetation cover drops below a threshold, erosion increases, which further decreases plant growth and thereby vegetation cover (Mayor et al. 2013). Several strategies can be used to recover the initial ecosystem state. Direct abiotic amelioration aimed at improving soil conditions is a common practice in arid and semiarid ecosystems (e.g. breaking the soil physical crust, adding organic matter, or contour furrowing, Suding et al. 2004). However, our understanding of the feedbacks in place in healthy ecosystems as well as of the mechanisms behind the spatial patterns can also be used to develop innovative restoration strategies. Successful restoration can take advantage of existing plant patches within a degraded ecosystem to improve soil properties and alter microclimatic conditions (see Gómez Aparicio 2009, Padilla & Pugnaire 2006 and Cortina et al. 2011 for reviews). Yet, the success of this approach relies on the assumption that positive plant-plant interactions will promote the establishment of the introduced plant, which may not always be the case (Gómez Aparicio 2009). Available evidence suggests that the use of facilitative interactions has the potential to improve dryland restoration. However, its effectiveness depends on the level of abiotic stress experienced after planting, our knowledge of specific plant-plant interactions –not all the species have the same capacity to facilitate the establishment of other species– and our ability to develop planting techniques that maximize these interactions (Cortina et al. 2011). Another restoration option is to plant species in a spatial configuration that resembles patterns observed in drylands that are known to optimize the source-sink dynamics (Puigdefábregas et al. 1999). Although there is considerable evidence supporting the use of this approach, it has seldom been used by restoration practitioners in the field (Urgeghe & Bautista 2014, Meron 2015).

Rehabilitating biocrusts: Replacing lost dryland function and improving resistance to climate change

Active rehabilitation of biocrusts is a timely and emerging field. Despite that biocrusts are highly sensitive to physical disturbances and that natural recovery of biocrusts from disturbance may be slow, it is becoming increasingly apparent that many biocrust organisms

can be cultured in artificial environments, with the intention of re-introducing them to degraded drylands (Zhao et al. 2016). Approaches include isolates of biocrust cyanobacteria in liquid culture (Lan et al. 2014) and soil-based mixed cultures of various biocrust biota (Antoninka et al. 2016). Some early successes suggest that it is possible to establish lab or greenhouse grown biocrust organisms in field settings, rapidly recreating a biocrust with demonstrable increases in ecosystem function (Lan et al. 2014, Zhao et al. 2014). Rehabilitation of biocrusts would offer a means to restabilize soils affected by chronic erosion, one of the most challenging expressions of desertification. It would also be expected to buffer soil microbial function from the impacts of increasing aridity expected with climate change (Delgado-Baquerizo et al. 2016b).

6 Challenges Ahead in the Study of Structure-Functioning Relationships in Drylands

Society values ecosystems that provide multiple services such as water yield, climate regulation, or food production, and the provision of such services depends fundamentally on the functioning of ecosystems (MEA 2005). Therefore, understanding the threats to dryland multifunctionality is particularly important to advance our knowledge of desertification and global change, and their consequences for human wellbeing. While dryland researchers have embraced multifunctionality as a key research topic (e.g., Maestre et al. 2012a, Bowker et al. 2013, Jin et al. 2015, Delgado-Baquerizo et al. 2016a), future research should focus more on the relative importance of biotic and abiotic variables, and on the role of multitrophic interactions, as drivers of multifunctionality (Table 1). This is of particular importance to guide conservation and restoration efforts under climate change, as biotic attributes can be actively managed at the local scale to increase the resilience of ecosystem functioning to expected changes in climate (e.g. by increasing the number of plant species or by introducing plants with particular traits or mimicking specific spatial patterns).

When forecasting the effects of global change on the functioning of drylands we must consider the different effects that multiple global change drivers, such as aridity and elevated concentrations of carbon dioxide ($[CO_2]$), exert on vegetation. Experiments and observations suggest that increases in water use efficiency (WUE) due to elevated $[CO_2]$ may enhance plant growth and water use, as well as soil C fixation, in drylands (Evans et al. 2014, Ukkola et al. 2015). Whether this WUE enhancement can compensate for the detrimental effects of increased aridity on water availability and biotic communities is, however, largely unknown. Brookshire & Weaver (2015) found that increased aridity over the last four decades in a Northern US grassland reduced plant productivity, irrespective of observed CO_2 -induced increases in WUE during this period. Additional studies of the interplay between increased aridity and elevated $[CO_2]$ are clearly needed to enable us to better understand dryland responses to ongoing climate change.

We must also better understand how biological feedbacks operate in drylands, i.e., how abiotic factors can alter biotic attributes, which in turn can affect abiotic factors and ultimately ecosystem multifunctionality (Figure 1). These feedbacks determine ecosystem responses to climate change, and are key to understand dryland desertification (Schlesinger

et al. 1990, D'Odorico et al. 2013). Despite substantial integration of existing databases (Verstraete et al. 2011), the establishment of large-scale monitoring networks (Herrick et al. 2010, Gaitán et al. 2014a) and advances in the development of conceptual models (Reynolds et al. 2007, D'Odorico et al. 2013, Bestelmeyer et al. 2015), considerable uncertainties exist in our ability to predict the ecological consequences of desertification (Table 1). Current analytical tools have substantially increased our ability to predict abrupt transitions (Kéfi et al. 2014, Schefer et al. 2015), but they do not fully incorporate the mechanisms driving them. Adaptations to prevent undesired transitions must be based on a solid understanding of the ecological mechanisms underpinning these phenomena, and this requires considering ecosystem structure-functioning relationships (Table 1). Although there are some field studies dealing with the resilience of drylands to desertification (e.g., Washington-Allen et al. 2008, Bestelmeyer et al. 2013, Mora & Lázaro 2013), most research on this topic has used mathematical models to explore the theoretical relationships between changing biotic attributes, system resilience and potential thresholds (reviewed by D'Odorico et al. 2013). Consequently, there are large uncertainties regarding the *in situ* detection and quantification of critical thresholds in ecosystem variables beyond which drylands become desertified (MEA 2005, Reynolds et al. 2007). These knowledge gaps limit our ability to understand the relative importance of climate change and human activities as drivers of desertification. They also restrict our ability to develop standardized early warning systems to detect the onset of desertification (Verstraete et al. 2011).

Another major source of uncertainty in the study of ecosystem structure-functioning relationships stems from issues of spatial scale. Most studies to date are conducted at spatial scales either too large to accurately capture the effects of biotic attributes on ecosystem processes or too small to provide a basis for extrapolation to regional or global scales (MEA 2005, Xu et al. 2011). This situation, is, however beginning to change with the development of regional and global coordinated surveys focusing on drylands, which are collecting local-scale information over large regions within continents and globally (e.g., Herrick et al. 2010, Maestre et al. 2012a, Gaitán et al. 2014a). The integration of the data provided by these field surveys with those obtained from widely available remote sensing tools, such as Google Earth (Xu et al. 2015) or the Moderate Resolution Imaging Spectroradiometer (Delgado-Baquerizo et al. 2016b), have an enormous potential to advance our ability to monitor changes in ecosystem structure and functioning in global drylands. Information on how climate and overgrazing jointly affect above- and belowground biotic attributes and, ultimately, multifunctionality in global drylands are virtually lacking. Future global coordinated surveys and experiments should target this information gap.

The last two decades have seen an increased research effort devoted to understanding structure-functioning relationships at multiple spatial scales, which has substantially increased our knowledge of how terrestrial ecosystems function and are responding to ongoing global change. This is of major importance in drylands, where the livelihood of a large part of human populations directly depends on ecosystem services. Advances in this research topic over the next few years will undoubtedly yield crucial insights that will improve our ability to predict changes in life-supporting services in drylands, and to detect the onset of desertification before it becomes irreversible.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Summary points

1. Climate and its interactions with other abiotic features, such as geomorphology and soil texture, shape ecosystem structure and functioning in global drylands.
2. There is a growing recognition of the important role that biotic attributes (e.g., species richness, abundance and spatial patterns), and their interactions with abiotic factors, play as drivers of ecosystem functioning in drylands.
3. Species richness has consistently positive effects on ecosystem functioning regardless of the spatial scale (from local to global) and trophic level (vascular plants, biocrusts and microbial communities) considered.
4. Grazing exerts major negative impacts on ecosystem structure (e.g. plant cover, species composition) and functioning (e.g. soil C and N contents and primary productivity), particularly at local and regional scales. Grazing effects depend on climatic conditions, shared evolutionary history and the type of livestock.
5. Expected increases in aridity and drought frequency will negatively impact ecosystem structure and functioning directly, by enhancing water stress, and indirectly, by reducing the abundance and diversity of vascular plants, moss- and lichen-dominated biocrusts and soil microbes.
6. The effects of woody encroachment on ecosystem structure and functioning are largely dependent on the attributes of encroachers, the functions considered and climate; more negative impacts are generally observed in the driest areas.
7. Understanding the links between abiotic factors, biotic attributes and multifunctionality is of particular importance to guide conservation and restoration efforts in drylands, and to improve our abilities to forecast and monitor desertification processes.

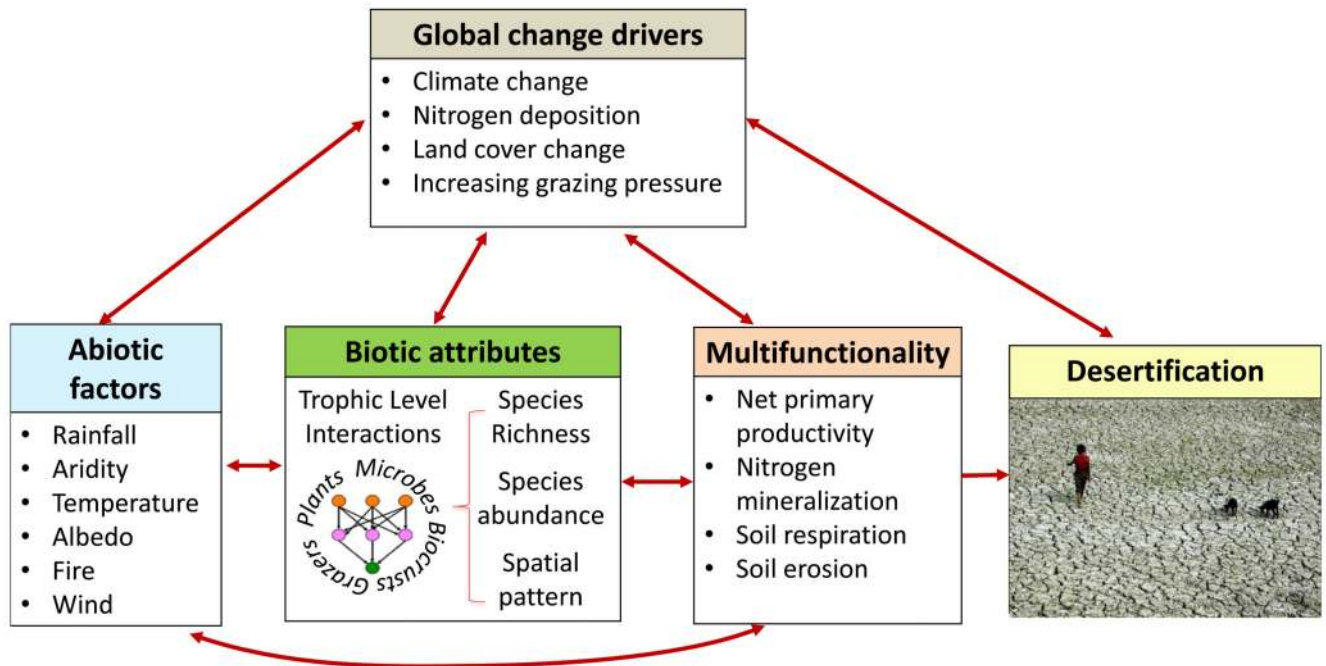


Figure 1.

Conceptual framework showing the relationships and feedbacks between global environmental change drivers, biotic attributes, multifunctionality and desertification. Photograph by Lighttruth (<https://www.flickr.com/photos/58648496@N02/5379922369/>), available under a Creative Commons Attribution-NonCommercial 2.0 Generic license (<https://creativecommons.org/licenses/by-nc/2.0/>).

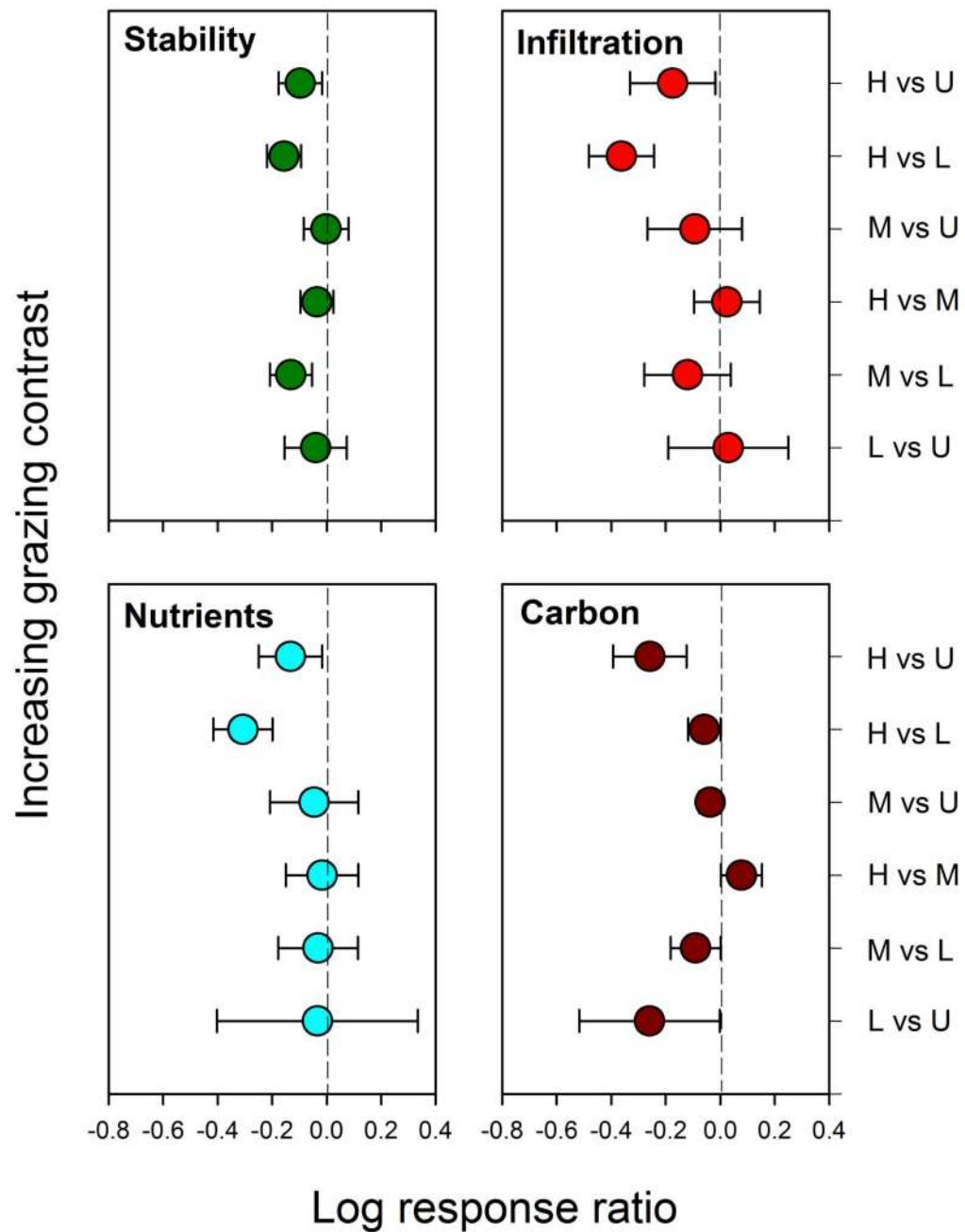
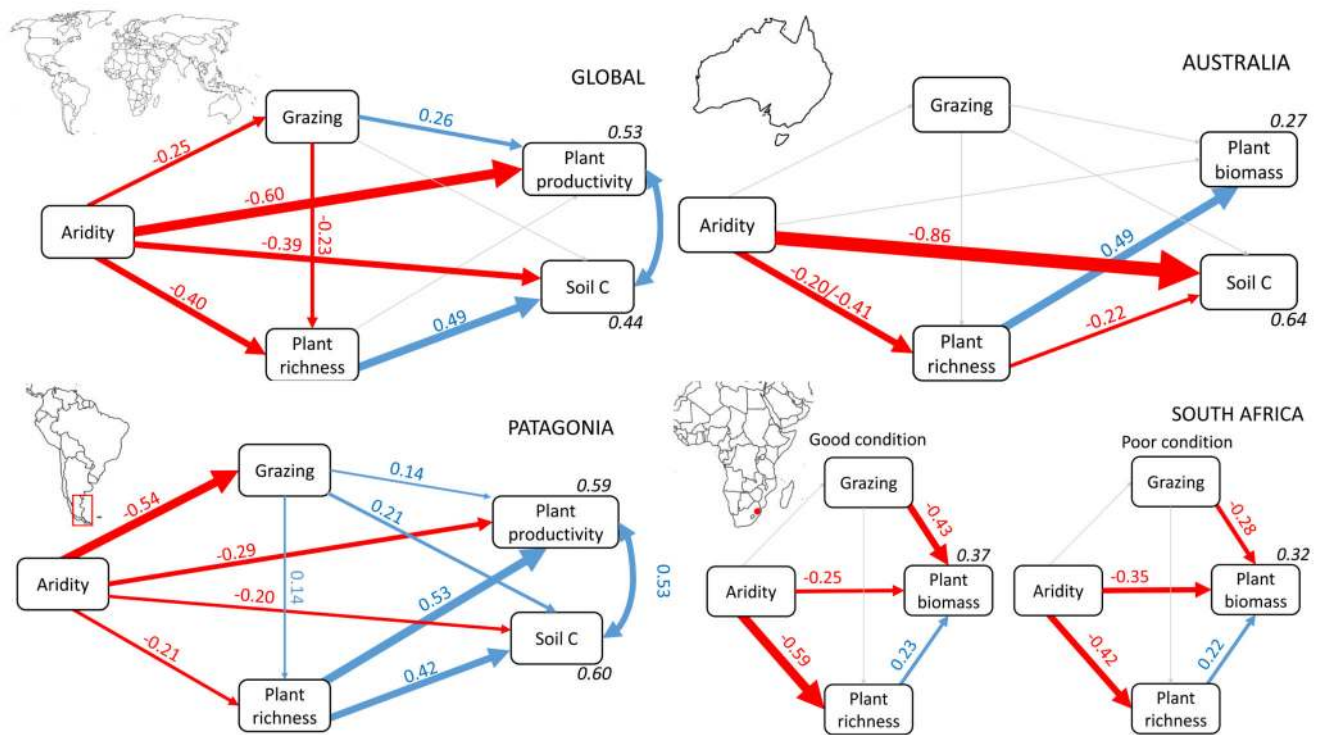


Figure 2.

Estimates (\pm 95% CI) of the log response ratio for percentage soil carbon (dark red circle, $n = 184$) and indices of soil functioning ($n = 37$ for each index) in relation to increasing intensity of grazing by European livestock across Australian drylands. U = ungrazed, L = low grazing, M = moderate grazing, H = high grazing.

**Figure 3.**

Structural equation models synthesizing the four datasets available to test the relative importance of aridity, grazing and plant species richness on dryland functioning (soil carbon [C] and plant biomass or productivity). Standardized path coefficients are provided (non significant, but tested, paths are shown with grey lines), with red and blue lines indicating negative and positive effects, respectively. Further details of the models can be found in Supplemental Figure 4.

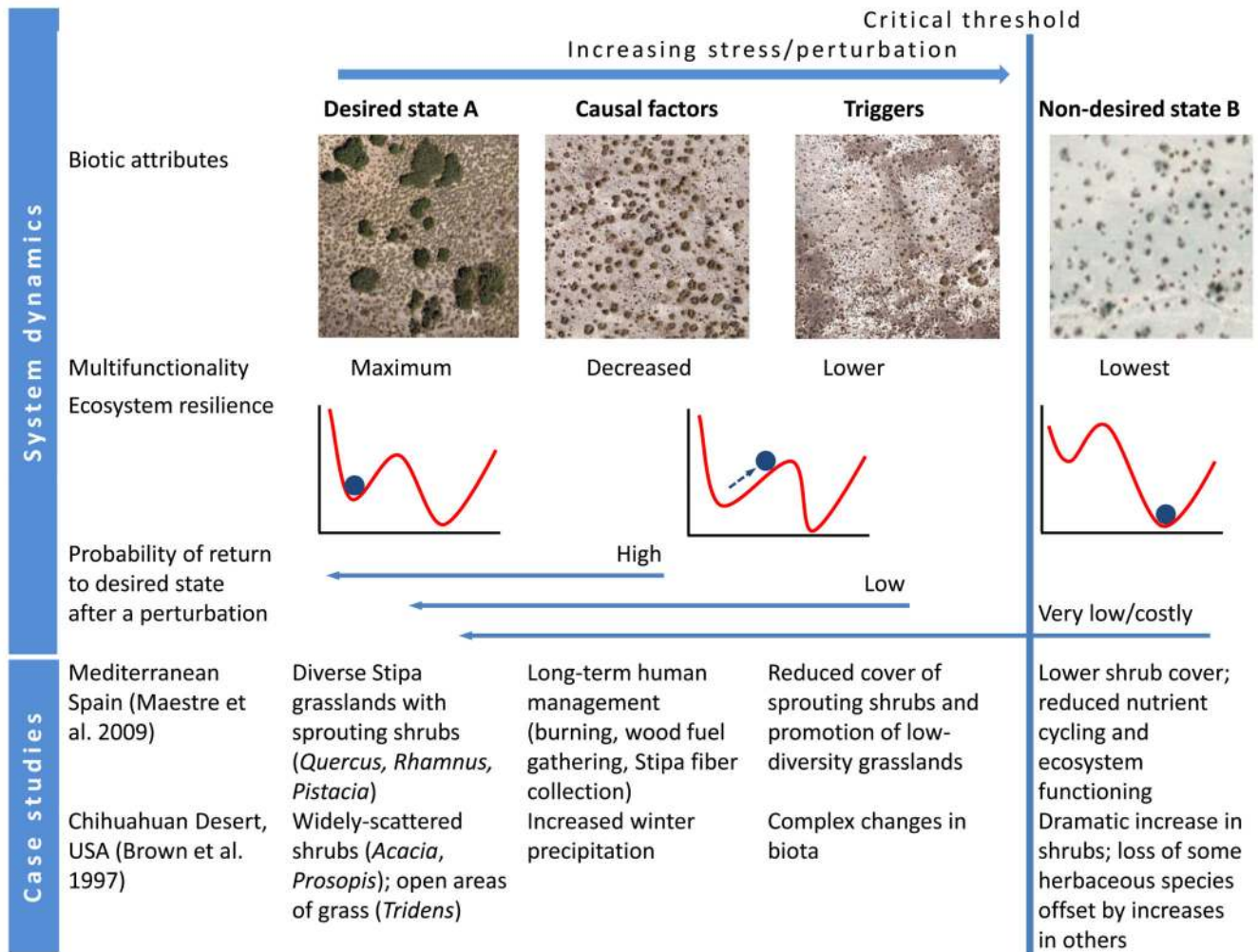


Figure 4.

Hypothesized changes in the structure and multifunctionality of dryland ecosystems as increasing stress and/or perturbation trigger a regime shift (from state A to B) once a threshold is surpassed. Resilience is visualized using the metaphor of a landscape of hills, valleys and balls. The location of the ball in the landscape represents the ecosystem's current state; valleys represent "attractor states" and the degree of its ecosystem resilience is represented as the size of the valley or basin of attraction, i.e. the maximum perturbation that a system can absorb without shifting to an alternative state.

Table 1

Some major gaps in our knowledge of the main topics addressed in this review, and recommended approaches to address them.

Gaps in our knowledge	Approach recommended
Relative importance of abiotic factors and biotic attributes as drivers of multifunctionality	<ul style="list-style-type: none"> - Explicitly consider the interactions among biotic and abiotic variables when studying multifunctionality at multiple spatial and temporal scales - Conduct coordinated experiments and surveys at continental and global scales that collect local-scale information using collaborative networks of researchers
Empirical evidence of the existence of alternative states and catastrophic shifts in drylands	Surveys evaluating ecosystem structure and functioning along a wide range of degradation and environmental conditions
Role of plant-biocrust-soil microorganism interactions on multifunctionality	Manipulative experiments assessing how changes in plant community attributes and biocrusts affect soil microbial communities and associated ecosystem processes Surveys assessing the joint variation of plants, biocrusts, soil microorganisms and multifunctionality along environmental gradients
How global environmental change (GEC) drivers affect biotic attributes and multifunctionality	Surveys and experiments evaluating the impacts of multiple grazing levels, nitrogen deposition and land use changes on multifunctionality along a wide range of aridity conditions
Role of biological feedbacks on ecosystem responses to GEC	Long-term experiments testing how GEC-induced changes in biotic attributes affect ecosystem responses to GEC drivers
Understanding counterbalancing effects among aridity and elevated [CO ₂]	Field/controlled environment experiments and analyses of long-term field and remote sensing data to explore the joint effects of changes in aridity and elevated [CO ₂] on vegetation attributes and ecosystem functions
In situ detection and quantification of critical thresholds in key ecosystem variables that can provide insights into underlying dynamics	Surveys and analyses of long-term field and remote sensing data to test whether there are thresholds in ecosystem structural attributes and key functions along wide spatial and temporal gradients
Identification of widely applicable “early warning” desertification indicators	Surveys simultaneously assessing how changes in soil properties, plant cover/spatial patterns and multifunctionality change along degradation gradients
Understanding feedbacks among desertification and GEC drivers	Modelling approaches to assess the impacts of climate, grazing and land-cover changes on multifunctionality, and the feedbacks arising among them