



Introduction

It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands

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Drylands occupy large portions of the Earth, and are a key terrestrial biome from the socio-ecological point of view. In spite of their extent and importance, the impacts of global environmental change on them remain poorly understood. In this introduction, we review some of the main expected impacts of global change in drylands, quantify research efforts on the topic, and highlight how the articles included in this theme issue contribute to fill current gaps in our knowledge. Our literature analyses identify key under-studied areas that need more research (e.g. countries such as Mauritania, Mali, Burkina Faso, Chad and Somalia, and deserts such as the Thar, Kavir and Taklamakan), and indicate that most global change research carried out to date in drylands has been done on a unidisciplinary basis. The contributions included here use a wide array of organisms (from micro-organisms to humans), spatial scales (from local to global) and topics (from plant demography to poverty alleviation) to examine key issues to the socio-ecological impacts of global change in drylands. These papers highlight the complexities and difficulties associated with the prediction of such impacts. They also identify the increased use of long-term experiments and multidisciplinary approaches as priority areas for future dryland research. Major advances in our ability to predict and understand global change impacts on drylands can be achieved by explicitly considering how the responses of individuals, populations and communities will in turn affect ecosystem services. Future research should explore linkages between these responses and their effects on water and climate, as well as the provisioning of services for human development and well-being.

> Keywords: climate change; desertification; drylands; ecosystem services; human livelihood; poverty alleviation

1. DRYLAND ECOSYSTEMS: DEFINITION AND IMPORTANCE

Drylands occupy large portions of the Earth's surface characterized by low and highly variable precipitation that does not compensate for the evaporative demands imposed by the intense solar radiation and extreme temperatures [1]. Different criteria have been used over the years to define aridity and to set the climatic boundaries of drylands [2]. The classification proposed by the United Nations Environmental Programme (UNEP), based on the *aridity index* (AI, the ratio of

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Electronic supplementary material is available at http://dx.doi.org/ 10.1098/rstb.2011.0323 or via http://rstb.royalsocietypublishing.org. mean annual precipitation to mean annual potential evapotranspiration), is widely used nowadays [3]. According to this criterion, drylands are defined as regions with an AI < 0.65, and are subdivided in four categories: hyper-arid (AI < 0.05), arid (0.05 < AI < 0.20), semi-arid (0.20 < AI < 0.50) and dry–subhumid (0.50 < AI < 0.65). Overall, these areas cover 5.1×10^7 ha, totalling 41 per cent of the land surface (see [1] for a detailed account of the area occupied by each dryland subtype).

The climatic characteristics of drylands, coupled with the relatively low fertility of their soils [4], impose important limitations on their biota [5]. As a consequence of these constraints, dryland vegetation is typically sparse and forms a 'two-phase' mosaic (figure 1) where discrete vegetation patches, mostly grasses and shrubs, are separated by a matrix of bare ground and/or biological soil crusts (BSCs hereafter) dominated by lichens, mosses and cyanobacteria [6].

One contribution of 10 to a Theme Issue 'Impacts of global environmental change on drylands: from ecosystem structure and functioning to poverty alleviation'.



Figure 1. Examples of dryland vegetation. (a) Mixed shrubland dominated by *Ericameria nauseosum* in Utah, USA (photo by M. A. Bowker); (b) shrubland dominated by *Chamaecrista cytisoides* in Brazil (photo by R. Romao); (c) shrubland dominated by *Quercus coccifera* and *Rosmarinus officinalis* in Spain (photo by J. L. Quero); (d) *Stipa tenacissima* grassland in Morocco (photo by F. T. Maestre); (e) *Festuca orthophylla* grassland in Peru (photo by J. Monerris); (f) open woodland dominated by *Eucalyptus populnea* and *Acacia aneura* in Australia (photo by S. Soliveres); (g) shrubland dominated by *Eulychnia acida* in Chile (photo by C. Barraza); (h) grassland dominated by various *Stipa* and *Festuca* species in Argentina (photo by J. Gaitán); (i) Larrea cuneifolia shrubland in Argentina (photo by E. Pucheta); (j) savannah of *Acacia totalis* in Kenya (photo by V. Polo).

The extensive areas devoid of vascular vegetation characterizing dryland landscapes, their harsh climate and some environmental problems caused by the mismanagement of their natural resources (e.g. dust bowls and desertification; see [7,8]), have contributed to the general public's impression that drylands are unproductive and 'useless' ecosystems, both from the ecological and socio-economical points of view [9].

The vision of drylands as areas of little value does not match reality. Not only are these ecosystems very diverse, but they also provide a fascinating natural laboratory to study evolution and species adaptation to extreme conditions, as well as offering ecosystem services that are essential for the maintenance of life [2,10]. Drylands include some of the most diverse biomes in terms of animal diversity, such as deserts and xeric shrublands [11], and host about 20 per cent of the major centres of plant diversity worldwide [12]. In addition to their high plant diversity, which are in some cases higher than those found in more productive biomes [13,14], dryland ecosystems also harbour highly diverse microbial and soil communities [15,16]. Many dryland species also show high levels of genetic differentiation among populations [17]. Such a biodiversity is crucial for maintaining ecosystem multifunctionality (i.e. the ability of ecosystems to maintain multiple functions and services simultaneously, such as carbon storage, productivity and the build-up of nutrient pools [18]), as suggested by recent studies

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carried out with vascular plants and BSCs worldwide [19-22]. Moreover, drylands also display a wide array of vegetation (figure 1) and soil types. As an example of the latter, a global survey of 224 dryland ecosystems in 16 countries identified 26 different soil types [19].

Drylands are also of paramount importance for humans for multiple reasons. First of all, over 38 per cent of the global human population lives in them [11]. Second, drylands possess a massive amount of key resources, including most of the world's oil reserves [23], as well as large deposits of valuable minerals such as gold, copper and silver [12]. Third, these environments are crucial for achieving global sustainability, and for the well-being of human populations worldwide [8,24]. Over 90 per cent of the dryland human settlements are located in developing countries, and a substantial part of them lag far behind the rest of the world with regards to development indicators [10]. Some features of these settlements, coupled to their biophysical features, underlie their socio-economical situation in the so-called drylands syndrome [7]. These characteristics include the sparse distribution of human populations over the territory, and their remoteness from markets and political centres. These limitations impose serious difficulties on delivering services efficiently, and on deploying effective communication, healthcare and educational systems [8]. Furthermore, severe land degradation and desertification is also

present in 10-20% of drylands, and their consequences are estimated to directly affect approximately 250 million people in the developing world [7]. These numbers are likely to expand substantially as a consequence of both climatic changes and the projected exponential human population growth [25].

2. GLOBAL ENVIRONMENTAL CHANGE EFFECTS ON DRYLANDS

Increases in temperature, nutrient availability and atmospheric carbon dioxide (CO_2) concentration, as well as changes in precipitation patterns and land use are key drivers of ongoing global environmental change (hereafter *global change*) faced by terrestrial ecosystems worldwide [25]. With the aim to set the context for this theme issue, in this section we highlight some of the most important socio-ecological consequences of global change in drylands. However, we do not intend to provide a comprehensive overview on how such changes will affect dryland ecosystems and the people living in them, as such a thorough review is beyond the scope of this introduction.

The biophysical characteristics of drylands make them highly vulnerable to global change drivers, and to climate change in particular [8,26-28]. Two components of climate change are of particular interest for drylands: the expected increase in temperature and the predicted changes in precipitation patterns. There is much ongoing discussion on the range of temperature increase, which depends on the greenhouse gases emission scenario and the geographical region considered, and this may have been overestimated in dryland regions owing to model deficiencies [29]. However, there is generalized agreement by most models that a warming of over 3°C and a 100 per cent increase in the frequency of extremely warm years is expected for drylands worldwide by the late twenty-first century [25]. Projections of the changes in precipitation amounts and patterns are subject to a greater degree of uncertainty. A multi-model analysis projects variations in annual precipitation from -30 per cent to +25 per cent in drylands, depending on the geographical region considered [30]. Specifically, most climatic models project that drylands located in China are expected to see an increase in total rainfall amounts by 10-20%, but precipitation will be reduced by 5-30% in large portions of the drylands in the Americas, Africa, Australia and the Mediterranean Basin [30]. However, regional models predict important localscale variations superimposed upon these overall trends [31-33]. Even in areas where precipitation will increase, the expected rise in temperature will increase evapotranspiration rates, which may cancel out the expected positive effects of enhanced precipitation on soil moisture and ecosystem productivity. As a consequence of expected climatic changes, soil moisture is projected to decrease by 25 per cent in a substantial portion of drylands worldwide [30]. However, these overall trends may need to be interpreted with caution when translated to concrete situations in the light of expected changes in rainfall variability. Climate models project an increase in precipitation variability in drylands, including more extreme rainfall events

and intense droughts [34]. Large rainfall pulses infiltrate deeper and last longer than smaller rain events [35], and thus even areas undergoing decreases in annual precipitation could experience increased soil moisture if precipitation becomes more variable but is characterized by larger pulses [36,37]. Nevertheless, there is evidence that climate change will exacerbate the aridity of most drylands worldwide, such as the southwestern US [38], the Mediterranean Basin [39], southern Africa [40], Australia [41], South America [42] and China [33].

Predicting effects of global change on dryland ecosystems is not straightforward. This is because of the complex interactions and contrasting effects of predicted changes in different global change drivers. For instance, while the expected reductions in water availability will likely exacerbate water stress and reduce productivity of dryland vegetation [43-45], increases in $[CO_2]$ may improve the water use efficiency (WUE) of plants, and thus ameliorate and potentially counterbalance negative effects of reduced soil moisture [46-48]. However, improvements in WUE may not suffice to compensate negative effects on soil moisture of increased evapotranspiration and reduced rainfall scenarios, particularly when feedbacks between elevated CO₂, water availability and vegetation are taken into account [49]. Indeed, reductions in above-ground biomass with increased warming and drought in drylands have been widely documented [50-53]. The size and frequency of rainfall events modulate processes such as soil and ecosystem respiration [54,55], microbial activity [56] and plant physiology and primary productivity [57]. Thus, modifications in precipitation patterns with climate change will largely affect ecosystem functioning in drylands [58], although some of these changes may not be necessarily negative (see [59] for a review). For example, increases in above-ground net primary productivity (ANPP) with increases in rainfall variability (less but more intense rainfall events) have been observed in semi-arid steppes from North America [36].

Global change will have important effects on dryland organisms other than vascular plants. The dryland biota in general is known to be well-adapted to infrequent, intense and unpredictable pulses of precipitation [4]. However, increasing temperatures and prolonged drought events associated with global change will pose physiological water balance challenges to a wide suite of organisms, including birds [60], reptiles [61] and insects [62], as transpiration increases. Expected changes in temperature and rainfall frequency may even promote extreme mortality events, as recently recorded in organisms as disparate as small birds [63] and mosses [64]. Recent experimental studies have also shown that warming by 2-3°C will reduce the cover and diversity of BSCforming lichens [65], and will promote declines in both bacterial and fungal activity and biomass, overall bacterial diversity and the bacteria:fungi ratio [64,66,67] in drylands.

Experiments and syntheses conducted in recent years have projected modifications and disruptions in species and multi-trophic interactions in drylands [61,68]. The complexities in the responses of organisms to global change challenge the establishment of general predictions. However, the expected overall decrease in water availability under global change is likely to promote higher competition among vascular plants, stronger herbivory effects on plants and more intense predator-prey interactions (see [61] for a review). Such responses may cascade throughout the whole ecosystem, ultimately promoting shifts in the structure and composition of dryland communities [69].

Dryland biogeochemistry is largely driven by rainfall and the associated effects on net primary productivity [35,70,71]. Thus, changes in precipitation frequency and amount, as well as in evapotranspiration rates projected by climatic models, are expected to result in important changes in processes such as soil C and nutrient cycles. These alterations may be mediated by changes in land use (see Thomas [72] for a discussion), and by modifications in the richness and composition of biotic components, such as plants and BSCs, induced by global change [65,73-75]. Experimental reductions in overall precipitation have been found to lower litter decomposition rates in the Argentinean Patagonia [76] and the Chihuahuan Desert [77]. However, similar results have not been found in observational studies [78]. Contradictory responses of nitrogen (N) mineralization and availability to changes in water availability have also been reported [76,79,80]. Maestre et al. [20] found that a 2.5°C experimental warming enhanced soil CO₂ efflux, particularly in areas dominated by BSCs, in a semi-arid environment from Spain. However, Lellei-Kovàcs et al. [81] did not find a significant effect of warming on this variable in a semi-arid forest-steppe ecosystem from Hungary. Studies conducted in the Sonoran Desert suggest that soil respiration may be less related to soil moisture and more to available carbon [82]. These results contrast with many other studies conducted in drylands worldwide suggesting that C fluxes are either tied to photosynthesis, and therefore fluxes will change as plants respond to variation in soil moisture availability [54], or that variations in seasonal rainfall, coupled to associated changes in temperature, largely regulate C fluxes [73,83]. In this direction, reductions in approximately 30 per cent in annual precipitation have been reported to lower daily soil CO₂ efflux by 50 per cent in Mediterranean semiarid shrublands [51]. Moreover, less frequent, more intense rainfall pulses have been found to increase this variable up to 30 per cent in the Chihuahuan Desert [37]. Modelling studies suggest that expected changes in precipitation and temperature, coupled with increases in [CO₂], will increase soil respiration in a nonlinear fashion in this desert [84]. Other studies have found that soil organic matter can be negatively affected by expected changes in climate and [CO₂] in drylands [74]. However, this response does not seem to be universal, as global change may promote C storage in soil through increased biomass production and reduced C turnover [85]. These results emphasize the nonlinear dependency between biogeochemical cycles in drylands and global change, and the difficulties faced by dryland researchers when projecting the ecological effects of such change.

The effects of other global change drivers, such as enhanced N availability, on drylands are also difficult to predict. Studies have reported both positive and negative effects of increased N fertilization on these

ecosystems (see [86] for a review). These effects depend both on the amount of N considered and on factors such as overall water availability and the relative concentrations of other nutrients, such as phosphorus [87]. In addition, there is evidence that the frequencies of wildland fires in many dryland regions (e.g. the Mediterranean Basin) have increased during the last century [88]. Expected increases in temperature and decreases in ambient moisture are likely to further increase fire recurrence intervals [89]. More fires may act synergistically with N deposition and the invasion by exotics to alter vegetation structure [86]. For example, many drylands are being invaded by exotic species, a process that reduces ecosystem functioning [90] and is expected to be further worsened with global change [91]. Moreover, the productivity and cover of these exotics has also been reported to be enhanced with N deposition [92]. This process may favour the accumulation of flammable biomass and enhance the connectivity of otherwise isolated plant patches, further altering fire regime and severity [93].

Ongoing global change is also promoting important shifts in species composition, and reductions in species richness in drylands worldwide [94-96]. These processes will likely have cascading effects on other biota and on ecosystem functioning [93,97,98]. As an example, a recent survey of global drylands has shown that plant species richness is positively linked to ecosystem multifunctionality, which is also negatively related to annual mean temperature [19]. These results suggest that changes in climate and biodiversity expected under global change will negatively impact the provision of ecosystem functions and services in drylands. The phenomenon of shrub encroachment (i.e. the expansion of woody vegetation into former grasslands [99]), a key land-cover change affecting drylands worldwide, has multiple effects on ecosystem structure and functioning [100]. Although this phenomenon has not been found to significantly affect ecosystem attributes such as biodiversity at the global scale [100], it may either enhance or reduce plant species richness at local and regional scales [97,101]. Some studies have suggested that different global change drivers, such as increases in [CO₂] and in the frequency of large precipitation events, may favour shrubs at the expenses of grasses in drylands [49,102,103]. Thus, it is likely that shrub encroachment will be augmented in the future [35], even if other factors known to promote this land-cover change (e.g. grazing [99]) are reduced. Many dryland regions are experiencing other land-use changes, including: (i) large-scale growth of urban and industrial areas (e.g. the case of Phoenix in the USA [104]), (ii) the afforestation of former grassland areas (e.g. large-scale plantations of fast-growing tree species in Australia, Argentina, Paraguay and Uruguay [105]), (iii) the replacement of traditional agricultural uses by modern, irrigation-based, agriculture (e.g. Almería province in southeast Spain [106]), and (iv) the extensive deforestation of dry forests (e.g. Cerrado, Caatinga, Chaco of Brazil, Bolivia, Paraguay and Argentina) to expand the area devoted to the production of intensive crops such as soy [107-109].

These processes are substantially affecting the hydrology [110-112] and biogeochemistry [113] of dryland ecosystems worldwide. Land-use change is also a major threat to their biodiversity [28], and the effects on ecosystem processes and services may act synergistically with those of other global change drivers [114].

Global change will also have dramatic impacts on the human populations in drylands. Such impacts are mostly linked to water availability, food security and socio-political conflicts in developing regions, as well to reductions and/or alterations in other ecosystem services important for human development and well-being. The intrinsic variability in precipitation characterizing drylands, which is inversely proportional to the total amount received [115], together with recurrent droughts promoted by phenomena such as El Niño, have a direct impact on millions of people who practise subsistence farming in drylands and whose crop yields are largely dependent on precipitation [116,117]. Most climatic projections agree with the fact that many drylands, such as the Mediterranean Basin, western USA, southern Africa and northeastern Brazil, will suffer a decrease of water resources with ongoing climate change because of increases in the variability of rainfall and in the frequency and duration of droughts [10,30]. These climatic changes will exacerbate food production and security issues. Moreover, they are likely to worsen already existing socio-political conflicts and limit the development of agricultural programmes, particularly in regions where water conflicts are already arising (e.g. Egypt, Sudan and Israel [118,119]).

Expected changes in water availability will likely increase the frequency and magnitude of humanitarian crisis in many dryland areas around the world [120]. Health conditions and diseases are likely to be magnified under climate change because of the expansion of illness vectors (e.g. malaria and dengue [121,122]), and the reductions in the availability and reliability of freshwater supply. Both factors will increase the incidence of gastrointestinal diseases [123]. Human populations living in drylands have a great variety of mechanisms to adapt to slow climatic changes and extreme climatic events, which strengthen their ability to cope with projected water shortages [124,125]. However, there is increasing agreement that global change will increase human migration in drylands [126]. Not surprisingly, the term climatic refugees, persons who migrate because of direct and indirect effects of global change, is being increasingly used [127]. Recent studies have also highlighted the tight connections between drought and warming and the rise of armed conflicts in drylands worldwide [66,128,129]. Thus, accumulated evidence suggests that the expected changes in precipitation and temperature will further worsen the disastrous humanitarian consequences resulting from armed conflicts and food shortages, as well as migrations, in many developing dryland regions.

Human populations living in drylands will also be affected by the alterations induced by global change in ecosystem services other than food production and freshwater supply. For example, primary production is a key supporting service that in drylands is negatively correlated with temperature and positively with precipitation [130]. Expected changes in these climatic attributes in most dryland regions will likely reduce the productivity of both crops and natural vegetation. This will not only affect food production and security, but also will have key implications for soil conservation and climate regulation, given the strong impacts of vegetation and its development on processes such as soil erosion, nutrient cycling, carbon sequestration and water run-off and infiltration [5,95,111,112]. Such impacts may act synergistically with global change-induced biodiversity losses, as biodiversity is crucial for maintaining ecosystem services in drylands [19,131]. Climate-induced migrations and land-use changes are also expected to negatively impact on important cultural services, such as social identity and diversity, tourism and recreation [120,132,133].

To summarize, the contrasting effects of various global change drivers, and the complexity of the responses to such drivers, challenge the elaboration of accurate projections on their consequences for dryland ecosystems. However, the evidence accumulated so far clearly indicates that global change will increase the degree of abiotic stress experience by multiple organisms living in drylands, will promote important changes in ecosystem structure and functioning and will negatively affect the food security, health and welfare of dryland human populations. While some of these changes may not necessarily be perceived as negative from the ecological point of view (e.g. increase in WUE of dryland vegetation and positive effects of shrub encroachment on carbon storage), the plethora of effects expected on both biotic and abiotic components, and the synergies that can be established between multiple global change drivers (e.g. land use and global change), will make drylands more vulnerable to disturbances, reducing their ability to provide goods and services to humans [7,19,35].

3. RESEARCH GAPS AND FUTURE DIRECTIONS

Understanding how global change will affect the composition, structure and functioning of dryland ecosystems, and how these changes might affect the livelihoods of the millions of people depending on their goods and services has been declared a top priority by the scientific community [25]. As such, it is not surprising that hundreds of studies on the topic have been published in the international, peer-reviewed literature (figure 2 and electronic supplementary material, appendix S2). Despite increasing research efforts, dryland regions such as the Guajira (Colombia), deserts such as the Thar (Pakistan, India), Sahara (Morocco, Argelia, Mauritania, Egypt, Mali, Chad, Libya, Niger, Sudan and Tunisia), Kavir (Iran) and Taklamakan (NW China, Kazakhstan, Uzbekistan and Turkmenistan) and countries such as Burkina Faso and Somalia remain poorly studied (figure 2), and deserve further attention in order to attain a better knowledge of drylands worldwide. Gaining this basic knowledge will further increase our ability to predict global change impacts. Naturally, we acknowledge that political and economic instability in certain regions does not warrant the feasibility of broader scale dryland research. Nonetheless, we suggest that logistic constrains can be solved in many places by involving local researchers.



Figure 2. Research efforts on global change conducted in drylands (indicated by dashed borders), according to the country where the work was carried out. To obtain data for this map, we searched for peer-reviewed field studies on this topic in the ISI web of knowledge database (http://www.isiwebofknowledge.com) published between 1899 and 2011 (see electronic supplementary material, appendix S2 for details). Dashed areas represent drylands, as defined by UNEP [3]. The studies from countries such as the UK mostly reflect research based on paleo-scales, when these regions were drylands.

Beyond an overall call to action to increase future research efforts in those areas underexplored so far (figure 2), there are important issues that deserve special attention from dryland scientists. We list below some of important topics that require particular attention to achieve a better understanding of the impacts of global change in drylands, and illustrate the novel contributions of the articles included in this theme issue to fill in current gaps in our knowledge.

First, there is a need for more information on how global change drivers will affect key soil processes and stocks related to organic matter in drylands. This urgency arises from the implications of these processes for their role in soil fertility and the development of desertification. Such data are also needed to forecast possible feedback effects on the climate system promoted by expected increases in soil respiration, a component of the biosphere's C cycle representing more than 60 per cent of total ecosystem CO_2 efflux [134]. This key process has been poorly studied in drylands in comparison to other biomes. For example, less than 8 per cent of case studies of a global soil respiration database accounting for more than 800 studies come from drylands [135], and many dryland regions are completely missing from this database (e.g. northern Africa, southern Spain, South Africa, Chile, Argentina, Kenya, Mali, Niger and the Arabian Peninsula, to name a few). Recent research efforts, such as the CARBOAFRICA network (http://www.carboafrica.net), are contributing to fill this gap by gathering information on the C cycle and other greenhouse gases in multiple sites across sub-Saharan Africa. In addition to these efforts, future research must evaluate how different global change drivers affect soil C stocks and fluxes in drylands, particularly in under-studied regions of Africa and Asia. Thomas [72] explores how grazing, a major land use in drylands worldwide, affects soil CO₂ efflux and organic C in two sites in the Kalahari desert (southern Botswana; see electronic supplementary material, appendix S1 for geographical location of the study

sites of this theme issue) with well-developed BSCs dominated by cyanobacteria. He found that in areas devoid of vascular plants, which dominate these savannah-like landscapes [136], organic C is not evenly distributed through the soil profile, as it concentrates under BSCs. Soil CO₂ efflux was also significantly higher on sandy soils where the BSC was removed, and on calcrete soils where the BSC was buried under sand. These results confirm the importance of BSCs for C cycling in drylands, and show how intensive grazing negatively affects C sequestration and storage. This study also illustrates how land use affects key soil properties linked to the C cycle, and can be used to provide sound recommendations to manage grazing areas to maintain a positive C balance in African drylands.

In a survey of the published literature on global change and drylands (see the electronic supplementary material, appendix S2), we found only 84 studies with fieldwork in more than one continent (approx. 3.8% of the total of studies reviewed). A disproportionate number of these studies correspond to French-Algerian collaborations [137,138], which likely reflect colonial history. It is interesting to note, however, that the number of multi-continent studies has been increasing over recent years (number of multi-continent studies versus year of publication, Spearman correlation coefficient = 0.77, p < 0.001), suggesting that international collaborations are gaining importance [19, 139,140]. Future avenues of dryland research should also take advantage of naturally occurring latitudinal gradients of temperature and precipitation, leaving aside geopolitical barriers whenever feasible, to better encompass the biology of deserts in a variety of regions. After all, species and ecological/socio-economical issues do not understand political frontiers [141], and scientists researching them should strive to act accordingly. In addition, large-scale studies can provide important insights to understand how dryland ecosystems function, and how global change may affect them. A good example of the benefits of multi-continent research is provided in this issue by Sala et al. [142], who analyse 16 datasets from multiple continents to analyse how precipitation controls ANPP in drylands. These authors found that the relative importance of current- versus previous-year precipitation as a driver of ANPP changes along precipitation gradients, suggesting that the ANPP of dryland ecosystems will respond to global change-driven alterations in water availability. Another multi-continental study included in this theme issue is that by Salguero-Gómez et al. [143], who introduce a novel approach—coupling robust climatic projections with stochastic, stage-structured models constructed from long-term demographic datasets-to examine the effects of precipitation shifts on populations of two desert plant species from the Colorado Plateau Desert (USA) and the Negev Desert (Israel). By using simulations based on long-term field data, they found that projected precipitation changes (wetter and drier growing seasons in the USA and Israel, respectively) will increase the population growth rates of both species. Their findings suggest that native desert plants, and thus the resources they provide, might be more resilient to global change than previously thought. These studies also illustrate the importance of carrying out research on multiple sites along wide environmental gradients to fully unravel basic principles underlying the functioning of dryland ecosystems, and thus provide insight into how global change will affect them.

A key feature of dryland ecosystems is the high interannual variability in their precipitation regime [115]. While the importance of precipitation as a key driver of ecosystem dynamics and socio-economical development in drylands is largely acknowledged [144,145], previous climate change research has mostly evaluated the impacts of changes in the mean climate variables (but see [61,146]). Therefore, it remains largely unknown how dryland ecosystems may respond to variation in the precipitation regime. This topic is of utmost importance in the dryland research agenda, given the evidence of an ongoing global increase in the interannual variability of precipitation, and the predicted intensification of extreme events by climate change models [25,147,148]. D'Odorico & Bhattachan [149] investigate current patterns of hydrologic variability in global drylands and review the implications of such fluctuations. These analyses highlight the complexities of the impacts of climate variability on drylands. While precipitation variability is often perceived as a disturbance for ecosystems and societies that makes difficult the provisioning of ecosystem services such as food production, the authors suggest that such variability may also enhance ecosystem resilience and promote the maintenance of biodiversity. This property, in turn, may allow dryland ecosystems to recover faster after severe disturbances, including those induced by extreme climatic events.

Research should also focus on understanding the responses to global change of important yet traditionally under-studied organisms. Among them, special attention must be directed to BSCs, an integral biotic component of drylands [5]. These organisms strongly influence key functional processes, including C and N cycling, soil stabilization and infiltration [6,73,150]. Despite the multiple ecosystem processes and organisms affected by them, relatively few experimental

studies have evaluated the response of BSC constituents to global change drivers, and most of them have been carried out in drylands from North America and Australia [64,151-154]. Escolar et al. [65] evaluated how the composition, structure and performance of lichen-dominated BSCs respond to predicted climatic changes in semi-arid, central Spain. Warming according to the Intergovernmental Panel for Climate Change projections [25] promoted a significant decrease in the richness and diversity of the whole BSC community, a result that was accompanied by important shifts in species composition. These results suggest that global change will strongly affect BSCs, with expected changes in richness and composition that could reduce or even reverse the positive effects of these organisms on multiple ecosystem functions.

In addition to expanding our efforts to under-studied organisms, future studies should also focus on biotic interactions across trophic levels. Their importance to predict future species distribution under climate change has already been highlighted [155]. Here, we emphasize the important research gaps in our knowledge on how dryland trophic interactions might be affected by global change. González-Megías & Menéndez [68] evaluated the effect of future changes in rainfall patterns on detritivore-plant-herbivore interactions in a semi-arid region from Spain. The authors found that changes in rainfall intensity modified the effect of below-ground detritivores on both plant traits and above-ground herbivore abundance. These results illustrate how global change will affect trophic levels and their interactions differentially. The authors also discuss the difficulties in predicting the responses of whole communities to global change when examining isolated organisms.

The importance of taking into account multiple drivers when evaluating global change impacts on ecosystems and the use of long-term experiments have been advocated many times [114]. Nonetheless, there are very few long-term experiments carried out in drylands that can inform us about how multiple simultaneous global change drivers can affect ecosystem structure and functioning (e.g. the Mojave Global Change Facility, where the impacts of changes in precipitation, nitrogen deposition and soil surface disturbance on the Mojave Desert are being explored; http://web. unlv.edu/Climate_Change_Research/MGCF/). Synthesizing data from one of these experiments, Ban & Lai [156] evaluated how N deposition affected plant community structure in a 10-year field experiment located in Inner Mongolia. The authors found significant reductions in species richness (up to 50-70%) after N addition. The responses of species richness and aboveground biomass to N inputs were greater in wet years than in dry years. Interestingly, N addition reduced the resistance of the semi-arid grassland studied to drought, diminishing ecosystem stability. Given the strong effects that N deposition has on the functioning of grasslands [157], these results have important implications for understanding the impacts of N deposition and climate change on the biodiversity and ecosystem services provided by these important ecosystems.

Owing to the multiple goods and services provided by drylands, and their importance to sustain life on the



Figure 3. (*a*) Historically, there has been a lack of integration among biogeochemistry (BGC), sociology (SOC) and ecology (ECO) in global change research carried out in drylands, as shown in the Venn diagram for the number of publications on this topic. To obtain this diagram, we classified the dryland publication list obtained from our literature search (see the electronic supplementary material, appendix S2) into three disciplines—biogeochemistry, ecology and sociology—by adding those keywords and their possible seven combinations to this search. Areas are proportional to the number of publications, and the overlap between them indicates integrative efforts. (*b*) The present theme issue undertakes an integrative approach of biogeochemistry, ecology and sociology to offer a better understanding of how global environmental change will affect dryland ecosystems and their biota, including humans. Roman number position represents areas of expertise included in each manuscript of the theme issue: (I) Maestre *et al.* (this study), (II) Thomas [72], (III) Escolar *et al.* [65], (IV) Salguero-Gómez *et al.* [143], (V) González-Megías & Menéndez [68], (VI) Ban & Lai [156], (VII) Sala *et al.* [142], (VIII) D'Odorico *et al.* [149], (IX) Huber-Sannwald *et al.* [133] and (X) Dougill *et al.* [163].

Earth [10], it is not surprising to find the large number of studies devoted to this topic in recent years [158–160]. Among them, those exploring how ecosystem services can be used to improve the livelihood of the poorest have been prioritized by scientists working in the natural and the social sciences alike. Community-based projects incorporating payments for ecosystem services (CBPES) allow individuals, governments, NGOs and private companies to pay for ecosystem services such as C storage and water conservation by supporting local-level projects promoting both community development and poverty alleviation [161]. These projects are being encouraged by international climate policies and investments [162]. In this issue, Dougill et al. [163] review multiple CBPES that deliver C and poverty reduction benefits in African forests. The authors discuss how CBPES can be successfully established in African rangelands, which have received little attention to date, despite their importance for the global C cycle and the maintenance of the livelihood of millions of persons in some of the poorest regions of the planet [164]. Through a literature review, Dougill and collaborators provide important insights and guidelines to design effective CBPES that can substantially contribute to poverty alleviation in drylands.

Most global change research carried out in drylands until now has been done on a unidisciplinary basis. When reviewing the literature on this topic (see the electronic supplementary material, appendix S2), we found very few studies that would fall in more than one of major research categories (ecology, biogeochemistry and sociology), and there is no overlapping among the three categories (figure 3a). Things are, however, starting to change, and some exemplary initiatives in this regard are GLOWA (http://www.glowa.org), a multidisciplinary team addressing water usage issues in Israel, or the International Network of Research on Coupled Human and Natural Systems (http://chansnet.org/), which facilitates communication and collaboration among scholars from around the world who are interested in coupled human and natural systems. The Central Arizona-Phoenix LTER (http://caplter.asu. edu/), where scientists from different disciplines and community partners work together to study the structure and function of an urban desert ecosystem, and how urban development in Phoenix (USA) affect ecosystem services in the Sonoran Desert, is also a noteworthy research programme. Calls for such multidisciplinary approaches have been made countless times in the past, regardless of biome. Because of the tight and intricate relationships between ecosystem services, biodiversity and human livelihoods in drylands [10], as well as the convergence of human conflicts and resource limitation, we cannot but further emphasize the need for the integration of multidisciplinary teams when conducting research on topics such as land degradation and desertification, global change and water management. Ultimately, we believe that a major breakthrough in our understanding of global change in drylands will come by the use of multidisciplinary approaches. Huber-Sannwald et al. [133] do so by combining the use of different conceptual frameworks with a thorough analysis of biophysical, socio-economical and historical data to assess the challenges and opportunities for livelihood development in drylands. Their results provide important insights to understand the complexities built into land degradation and desertification processes in socio-ecological dryland systems, and illustrate the potential of multidisciplinary studies to advance our knowledge of the links between human development, desertification and global change.

4. CONCLUDING REMARKS

There are important gaps in our knowledge of the ecological, biogeochemical and socio-economical impacts of global change in drylands, but also exciting challenges for future research on this topic. This theme issue aims to fill some of these gaps by including reviews and primary research articles illustrating the impacts of key global change drivers on fundamental ecosystem components and processes, and by examining the links between these impacts and the livelihood of human settlements in drylands from a multidisciplinary perspective (figure 3b).

Owing to the large number of matters involved in evaluating and determining global change impacts in drylands, we do not provide a complete, definitive overview of this topic in the present theme issue. Each of the topics treated would certainly require a theme issue by itself, and some important topics, such as global change effects on animals, are underrepresented in this issue simply due to lack of space (but see González-Megías & Menéndez [68]), and because they have recently been the subject of a theme issue of the journal [165]. The diverse contributions included in this theme issue are, however, highly timely in our opinion, as they deal with crucial, yet poorly understood issues on ecological impacts of global change. We believe that the topics treated here are in urgent need of conceptual advances in order to improve the livelihood of people living in drylands (e.g. desertification and management of natural resources to improve human well-being in developing areas [133,163]). We expect that the multidisciplinary, multi-organismal approach followed in this theme issue will advance our understanding of the projected effects of global change in drylands, and will stimulate further research on this important topic.

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