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Dryland mechanisms could widely control ecosystem functioning in a drier and warmer world

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Abstract

Responses of terrestrial ecosystems to climate change have been explored in many regions worldwide. While continued drying and warming may alter process rates and deteriorate the state and performance of ecosystems, it could also lead to more fundamental changes in the mechanisms governing ecosystem functioning. Here, we argue that climate change will induce unprecedented shifts in these mechanisms in historically wetter climatic zones, towards mechanisms currently prevalent in dry regions, which we refer to as “dryland mechanisms”. We discuss twelve dryland mechanisms affecting multiple processes of ecosystem functioning, including vegetation development, water flow, energy budget, carbon and nutrient cycling, plant production and organic matter decomposition. We then examine mostly rare examples of the operation of these mechanisms in non-dryland regions where they have been considered insignificant at present. Current and future climate trends could force microclimatic conditions across thresholds and lead to the emergence of dryland mechanisms and their increasing control over ecosystem functioning in many biomes on Earth.

Introduction

Most regions on Earth are warmer at present than in past decades and centuries [1], and many regions are experiencing a drying trend [2,3] as a result of decreased precipitation, increased variance in precipitation (less frequent, but more intense events) and/or higher evaporative demand [4]. More climate extremes, including prolonged droughts and heatwaves, have recently occurred across the globe [1,5] (Glossary, Supplementary Table S1, Figure S1). Moreover, human activity has been shown to exacerbate a naturally-occurring drought [6]. A further increase in the spatial extent, duration and occurrence of extreme droughts is projected for many regions during the 21st century [1,7-9], with the exact outcome of the projections depending on the complexity of the modelled land, atmosphere and plant feedbacks [10-12]. Drying is expected even at high elevation and in cold regions because of warming-induced earlier snowmelt [13,14].

Drought and heatwaves have a range of negative impacts on ecosystems, including widespread tree mortality, decreased terrestrial primary production, depressed crop yields, reduced carbon sequestration, species replacement, and loss of biodiversity and ecosystem services [15-19]. However, severe climate change may not only deteriorate the state and performance of ecosystems, but could also lead to unprecedented shifts in the type of mechanisms that govern ecosystems functioning, from mechanisms traditionally studied in mesic, humid and cold systems, to a set of mechanisms so far considered absent or insignificant in most biomes on Earth. Currently, these mechanisms operate primarily in drylands (Supplementary Table S1), which cover 37-46% of the global land area (Figure 1a, Supplementary Table S1). Climate change can modify environments to a level where such ‘dryland mechanisms’ (Table 1, Supplementary Table S1) may become relevant in many regions worldwide, including regions currently not limited by water (non-dryland regions). Dryland mechanisms play a fundamental role in explaining model-field data mismatches in dry areas when predictions are based on the traditionally-studied mechanisms in non-water limited ecosystems. For example, decomposition of plant detritus (litter) and subsequent release of nitrogen in dryland ecosystems was faster than expected and could not be predicted by traditional models of decay, where microbial degradation depends on rainwater availability [20,21]. Not until the inclusion of photochemical degradation, an abiotic dryland mechanism (see below and Table 1), could decomposition and nitrogen cycling be accurately described by a prominent process-based biogeochemical model [22-24].

Here, we present evidence suggesting that dryland mechanisms may already occur to a moderate extent in historically non-water limited regions and that they will emerge to a much larger extent in many more regions in the future. We summarize the current literature, analyze published data from remote sensing and climate model ensembles, and provide outcomes of simulations of two published models to illustrate the operation of some of these mechanisms in non-water limited regions. Responses of dryland ecosystems to intensified aridity have recently been related to thresholds beyond which productivity, soil fertility and vegetation cover degrade markedly [25]. We go beyond such responses of ecosystem attributes in drylands, and focus on emergent mechanisms of ecosystem functioning in historically non-water limited biomes, many of which are increasingly exposed to rising temperatures, higher evaporative demand, and increasing frequency, duration and intensity of drought events and heatwaves. Notably, activation of most dryland mechanisms in non-dryland regions does not require their transformation into drylands (although such trajectories have been projected for several regions by some [2,26], but not all studies [27]). With this perspective we aim to provoke the scientific community to consider the unprecedented changes in ecosystem functioning that might occur as dryland mechanisms emerge elsewhere, in order to more accurately predict ecosystem responses to climate change.

Dryland mechanisms and examples in non-water limited biomes

Based on extensive literature reviews, we have selected twelve mechanisms affecting numerous ecosystem processes in dryland vegetation and soils from patch-to-landscape scales (Table 1). These mechanisms are controlled by microclimatic drivers, such as intense solar radiation, high surface temperatures, large contributions of non-rainfall water sources to moisture availability, rain pulses, and steep water potential gradients. While the mechanisms are concentrated in drylands, some occur also outside drylands (Figure 1a) where they primarily operate at xeric sites (low soil water buffering against short-term droughts) or in regions with a distinct dry season. However, for most mechanisms we have very limited knowledge on the extent of their past emergence outside drylands. We use the term emergence here in its broad sense, encompassing both, the activation of a mechanism and the shift from a marginal to a significant contribution to an ecosystem process.

We organize the dryland mechanisms into those that are fast-responding and active on relatively small patch-to-mosaic scales and those that are slow-responding and active on relatively large mosaic-to-landscape scales (see definitions in Table 1). Each of the twelve mechanisms is summarized by answering the following questions: 1) What processes define the mechanism and under which conditions is the mechanism activated? 2) For which biomes outside drylands is there evidence for the operation of the mechanism? 3) What is the potential importance of the mechanism, i.e., what would the mechanism imply for the functioning of historically non-water limited ecosystems? 4) Is the operation of the mechanism amplifying or buffering other climate change impacts on ecosystem functioning?

A more in-depth description of each mechanism, including examples of interactions among mechanisms, is found in the Supplementary information ('Synopsis of dryland mechanisms of ecosystem functioning'). A comprehensive review of the dryland mechanisms is beyond the scope of this perspective. Mechanisms other than the ones described here might also qualify as dryland mechanisms [28,29], although we sought to include as broad as possible a range of mechanisms predominantly active in drylands.

Fast-responding mechanisms at the patch-to-mosaic scales

Drying-wetting cycles

Drying of the topsoil facilitates the generation of drying-wetting cycles by discrete rainfall events (rain pulses) interspersed between dry periods, thus initiating ecological pulse responses (Supplementary Table S1). Small, medium and large rain pulses activate metabolism of soil microbial and biological soil crust organisms (see below), plants, and soil invertebrates, respectively [30-32]. Little empirical evidence of ecological pulse responses is available for temperate and boreal-transition forests, temperate grasslands (see Supplementary Figure S2), and wetlands [33-37], as non-drylands are historically less adapted to respond to rain pulses [38]. With projected increases in drought severity and duration, often combined with higher rainfall intensity, in many regions globally [1], ecological pulse responses to drying-wetting cycles are expected to become important for ecosystem functioning in non-dryland biomes. Drying-wetting cycles are expected to activate soil organisms and plants, increase resource supply to soil communities and vegetation, and enhance biotic and abiotic trace gas fluxes [30,39,40], thus partly buffering other drought effects on ecosystem functioning (Table 1).

Hydraulic redistribution

Hydraulic redistribution is the passive movement of soil water from moist to dry soil layers via the plant root system and fungal hyphae [41,42]. This mechanism requires that plant canopies do not compete for water with the rhizosphere of dry soil layers, limiting hydraulic redistribution to periods when canopy conductance is at or near zero, e.g., at night. Hydraulic redistribution has first been described in drylands [43,44], but has since been reported across a broad range of plant taxa (from old-growth conifers to C_3 grasses) and ecosystems (e.g., tropical and temperate forests) [41,42,45], which are mostly characterized by low soil water holding capacities (e.g., well-drained sandy soils) or the presence of a dry season [46-49]; hydraulic redistribution outside drylands has also been artificially induced by experimental rainfall exclusion [50]. Hydraulic redistribution increases plant gas exchange and production by facilitating nutrient uptake in the relatively fertile topsoil, extending fine root lifespan and maintaining xylem hydraulic conductance [41,42,51]. An increased influence of hydraulic redistribution on ecosystem water balance could occur directly via increases in soil water potential gradients within the rooting profile, or indirectly over time via increased rooting depths [52] or decreased vulnerability to xylem cavitation [53]. Thus, hydraulic redistribution partly buffers deleterious effects of drought on plants and ecosystems.

Humidity-enhanced biotic activity

Humidity-enhanced biotic activity is initiated when living organisms, dead organic materials, and surface soils absorb moisture from non-rainfall atmospheric water sources, such as dew and fog (Supplementary Table S1), during intervals between rainfall events. Non-rainfall moisture can be an important water source for plants, biological soil crusts and animals in drylands [54,55]. Furthermore, dry soil and plant litter adsorb dew and water vapor during periods of high humidity [56-58], thus enabling humidity-enhanced microbial degradation of organic materials leading to their decay [59,60]. Outside drylands, foliar and/or root uptake of moisture from dew and fog during dry periods is an important water source for trees, epiphytes and understory plants in tropical montane cloud and lowland forests [61,62] [63]. Decomposition of dead plant material by humidity-enhanced microbial degradation has been reported in a temperate grassland, salt marsh and wetland [64-66]. With increasing heat and dryness, biotic activity enhanced by non-rainfall water is projected to gain importance for plant water relations and biogeochemical cycling in many ecosystems, as exemplified for the decay of the surface litter layer in a temperate forest (Box 1). Non-rainfall water may partly buffer against desiccation, thus maintaining ecosystem functions and counteracting climate drying effects.

Soil hydrophobicity

Dryness and heat directly increase soil hydrophobicity (soil water repellency), which is caused by organic substances with low surface free energy [67,68]. Soil hydrophobicity reduces infiltration rates into the topsoil and creates preferential flow paths of water in the subsoil. Soil hydrophobicity further increases with hydrophobic organic compounds derived from microorganisms, aboveground vegetation and roots [68-70]. In temperate and tropical forests, grasslands, and agricultural fields, soil hydrophobicity has been recorded primarily on dry sandy soils, in regions with a dry season, and following fires [69-75]. Increased frequency and severity of climate extremes (drought, heatwaves) and drying-wetting cycles (see above) are expected to increase the prevalence of hydrophobicity outside drylands [76,77]. As a consequence, hydrophobicity-induced changes in surface moisture will decrease litter decomposition, nitrogen mineralization and plant productivity and will increase soil erosion, leading to changes in microbial and plant community composition and dynamics [68,77,78]. Soil hydrophobicity is therefore expected to amplify the negative effects of climate change on ecosystem functioning.

Photochemical degradation

Intense solar irradiance induces photochemical degradation (photodegradation) of dead organic material, such as plant litter and surface soil organic matter [79,80]. Photodegradation leads to organic matter decomposition and release of nutrients and trace gases, either directly or indirectly by facilitating microbial degradation in subsequent wet periods [81,82]. Photodegradation of leaf litter and wood outside drylands has been reported in temperate grasslands [83], tropical and temperate forests [84-87], and a temperate bog undergoing peat mining [88]. Higher temperatures and reduced precipitation, particularly at low vegetation cover, may significantly increase the importance of photodegradation in temperate forests (Box 1, Figure 2). Highly energetic ultraviolet irradiance is projected to increase in the tropics over the 21st century, which will also enhance the importance of photochemical processes [89]. Therefore, photodegradation is expected to become a more significant global mechanism for organic matter decomposition in the future [90,91], partly buffering climate change-induced slowing down of biotically-driven decomposition of organic matter.

Thermal degradation

Soil surface temperatures are high in many drylands, reaching >70°C [92], which induces thermal degradation of organic and inorganic materials, and trace gas emissions [92-95]. Thermal degradation is promoted by reduced vegetation cover and associated decreased shading (Figure 2), and interacts with photochemical degradation (see above) [93,96]. While this mechanism has not been reported so far outside drylands, thermal degradation is likely to become important also in regions that currently undergo climate warming and increasing exposure of soil and litter to heating by solar radiation. Thermal degradation partly buffers climate change-induced reductions in biotically-driven processes.

Soil-litter mixing

In dry landscapes characterized by bare soil patches and discontinuous vegetation cover, erosion by water (runoff) and wind deposit soil particles on plant litter, inducing soil-litter mixing. In addition, aboveground transport of detached litter by runoff and wind results in heterogeneous spatial distribution of plant litter and partial or complete litter burial by soil particles [97,98]. Mixtures of soil and litter can hold moisture over longer periods of time compared to litter alone, and create favorable conditions for microbial activity and litter decomposition by forming soil films on organic materials that consist of soil particles, fungal hyphae and microbial exudates[99,100]. On the other hand, soil-litter mixing can inhibit photochemical degradation (see above) [100]. Soil-litter mixing has not been described so far outside drylands, but its contribution to decomposition is expected to increase with decreasing precipitation [101] wherever discontinuous vegetation cover leads to soil erosion and mixing with litter [97]. Soil-litter mixing partly buffers drought effects on decomposition by enhancing microbial degradation.

Slow-responding mechanisms at the mosaic to landscape scales

Biological soil crusts

Soil surfaces not covered by vascular plants due to abiotic constraints are generally colonized by biological soil crusts (biocrusts), a community of poikilohydric organisms that include cyanobacteria, lichens, algae, bryophytes, bacteria, and fungi. These organisms are desiccation tolerant and do not actively regulate their water status [102]. Biocrusts currently cover ~12% of the global land area, mainly in drylands [29,102-106], but can also be found in temperate and subtropical settings where soil moisture and/or fertility limits vascular plants, e.g., pine barrens, terminal moraines, short-grass savannas, sand ridges/dunes, dry acidic grasslands, and xeric shrublands [107-113]. Biocrust organisms stabilize soils by actively secreting polymeric substances that bind soil particles together. They can also regulate major ecosystem functions, including hydrological processes, carbon and nutrient cycling (especially through inputs of newly fixed carbon and nitrogen), and ecosystem energy balance [114-118]. Thus, biocrusts may play a critical role in the functioning of non-dryland ecosystems under increased aridity and help buffer the negative effects of climate change.

Self-organization of vegetation patchiness

Self-organization of vegetation patchiness induced by aridity is a dryland mechanism of vegetation pattern formation [119,120] (Box 2). It is generated by a positive feedback between localized vegetation growth and lateral redistribution of water [121], and modulated by divergent rates of water infiltration [122]. While most prominent in drylands [123], self-organization of vegetation patchiness has also been observed outside drylands in tropical savannas, temperate and boreal peatlands, temperate rainforests and salt and freshwater marshes, and cold temperate ribbon forests [124-130]. In those ecosystems, patch formation is caused by limitations in resources such as nutrients and light, rather than water [129,131]. Self-organization of vegetation patchiness caused by aridity can reduce ecosystem plant biomass (Box 2), and increase water fluxes and nutrient cycling in vegetation patches [132]. For shallow-rooted plant species adapted to mesic conditions, self-organization of vegetation patchiness amplifies degradative climate change effects, while transition to deep-rooted, drought-adapted species buffers against such effects (Box 2) [133].

Wind- and water-driven horizontal resource redistribution

Drylands are typically composed of mosaics of densely vegetated patches interspersed with interpatch areas with sparse vegetation, biological soil crusts (see above) or bare soil. The spatial connectivity of interpatch areas promotes wind- and water-driven horizontal resource redistribution whereby water (both a driver and a resource), soil particles, organic materials, nutrients, and plant propagules are transported towards sinks of densely vegetated patches (often termed 'islands of fertility') [134-137]. Outside drylands, horizontal transport of plant litter by wind and snow drift has been observed in the Arctic tundra where it caused nutrient translocation and changed the carbon-neutral system to a carbon source [138]. Wind- and water-driven horizontal redistribution of resources is of potentially high importance under climate change because it increases the spatial heterogeneity of multiple ecosystem functions, including vegetation development, hydrological processes, carbon and nutrient cycling, and animal habitat suitability. Increased spatial heterogeneity and connectivity are expected to amplify adverse climate change impacts through losses of water, organic matter and nutrients, ultimately resulting in reduced productivity and altered species composition [139,140].

Decoupling of soil biogeochemical cycles

The composition of the elements and their quantitative (stoichiometric) relationships are well conserved in organisms. Thus, biogeochemical cycles regulated by plants, microbes and animals are tightly coupled in terrestrial ecosystems [141]. However, concentrations of soil elements and their stoichiometric relations may change in different directions and magnitudes with increasing aridity, thus causing an imbalance of elemental relationships [142-146]. Such decoupling of soil biogeochemical cycles implies that the use of some element(s) in a system becomes independent from the level of other element(s). Decoupling under more arid conditions in drylands results from a more pronounced reduction in soil carbon and nitrogen contents relative to soil phosphorus contents [143-145]. A global analysis of datasets from drylands and non-drylands showed a decrease of the nitrogen:phosphorus ratio in plants under experimental warming and drying, indicating decoupling of these nutrients in plants across a broad climatic range [147]. Soil carbon and/or nitrogen responded differently from soil phosphorus to experimental drying or warming in several non-dryland biomes, such as wetlands, and temperate forests and grasslands [142]. We expect this mechanism to have large future implications for ecosystem functioning, including decreased primary production, decomposition, and carbon sequestration, and larger restrictions for biological activity and diversity [141,144,145], thus amplifying adverse climate change effects on ecosystems.

Canopy convector effect

Low water availability in dry forests and woodlands results in reduced tree density and modified canopy structure, commonly increasing surface roughness and decreasing the aerodynamic resistance to heat transfer relative to wetter systems. The combination of low tree density and low aerodynamic resistance provides the physical basis for the canopy convector effect, which increases the efficiency of air-cooling through convective heat flux in dry forests and woodlands, in contrast to water-cooling through evapotranspiration in more moist environments [148]. The convector effect exists to some extent in all forest canopies, and its relevance increases markedly with decreasing canopy density, particularly during heatwaves [149]. Doubling of convective heat loss was observed in temperate European forests during the heatwave in summer 2003, leading to a significantly cooler land surface (a reduction in temperature up to 3.5°C) than measured in adjacent grasslands that relied on evaporative cooling despite dwindling soil water reserves [150]. Because water scarcity poses a challenge for canopy temperature control, further exacerbated by the low albedo and the high radiation load in many regions [151], the canopy convector effect is of potentially high importance for forest and woodland survival worldwide, thus buffering to some extent the adverse effects of a warmer and drier climate.

Reduced plant cover and the emergence of dryland mechanisms

Dryland mechanisms are activated directly by climate change-induced drying and warming, and indirectly through reduced vegetation density and opening of canopy gaps. The latter are caused by decreased productivity and increased plant mortality, disturbance and land use change (Figure 2). Reduced vegetation cover exposes soil and litter surfaces to increased solar irradiance, higher temperatures and soil drying [152], which are main preconditions and drivers of dryland mechanisms (Table 1). For example, intense solar irradiance can reach organic materials on the ground through gaps in vegetation, thus triggering photochemical degradation. This and other mechanisms are further enhanced by local conditions, particularly xeric microsites and dry seasons (Figure 2).

At the global scale, analyses of satellite time series data revealed the trend of a net increase in vegetation density and leaf area during the past decades ('vegetation greening') [153,154] (Figure 1b). However, in many regions, a ‘browning’ trend has been observed, and this trend has grown in importance over time [155,156]. Browning trends in mesic, humid and cold regions, including North American boreal forests and South American tropical forests, have been linked to increasing deforestation and fire frequency, and to higher atmospheric evaporative demand [157,158] that lead to plant biomass loss and decreased productivity [159]. In a drying climate, evergreen species may be replaced by deciduous species, thus seasonally creating vegetation gaps and sparse canopies [160]. More extreme drought events and heatwaves may override the greening effects of CO_2 and nitrogen fertilization [161], and lead to additional browning, as predicted by models which consider soil moisture deficits [162] (see also Supplementary Figure S3).

Threshold-based concepts of emerging dryland mechanisms

Current and future climate change could prompt microclimatic drying and heating to an extent that would lead to the emergence of dryland mechanisms of ecosystem functioning in many mesic, humid and cold climatic zones (non-dryland regions). Significant droughts have already been observed in many historically non-water limited regions in the last 70 years, and more drought events are expected to occur with continued warming [1]. Our climate model projections indicate that topsoil water potential, the drought metric relevant for the operation of most dryland mechanisms, will decrease in non-dryland regions by the end of this century. The greatest decreases by 0.15-0.20 MPa on average are projected for South America, Africa and Oceania, with considerable regional drying also in North America and Europe (Figure 3a-d). Altogether, 74% of the global land area currently not classified as drylands are expected to experience reduced topsoil water potential. A global study projected that soil surface water content will decline on 70% of the total terrestrial area by the end of the century [163]. Additionally, our modeling results suggest that topsoil and surface air will warm globally. The total non-dryland area with mean topsoil temperature of >40°C is estimated to increase by about 17 million km^2 (approximately equivalent to the sum of the total land area of the USA and Brazil) by the end of the century (Figure 3e-h, Supplementary Figure S4).

Extreme drought events and heatwaves leading to short-term soil drying and heating could induce the emergence of fast-responding dryland mechanisms operating on small spatial scales (patch-to-mosaic; Figures 2 and 3). Mechanisms regulated by one dominant microclimatic driver could emerge once this driver is forced across a threshold. Hydraulic redistribution, and specifically hydraulic lift, is activated below a topsoil water potential threshold, provided that an adequate water potential gradient is created between surface and deeper soil layers (see examples of thresholds in Supplementary Table S2). Soil hydrophobicity is likewise activated below a soil water potential threshold, the exact value of which is modulated by the nature and amount of hydrophobic soil organic compounds. Notably, some of these critical thresholds of soil water potential are projected to be reached in many non-dryland regions by the end of the century (Figure 3a-c). In addition, extreme heatwaves may induce thermal degradation, resulting in the emission of various trace gases from soils and litter once soil surface temperatures exceed critical values. Such temperature thresholds are expected to be reached in multiple locations in the future (Figure 3e-g).

Emergence of some mechanisms depends on the combination of at least two factors (e.g., a driver and a precondition; Table 1). Drying-wetting cycles induce ecological pulse responses, which are driven by rain pulses, provided that antecedent soil moisture is below a water potential threshold (Supplementary Table S2). The thresholds for the rain pulses themselves differ substantially among ecological processes and functions, including primary production, microbial respiration, and soil invertebrate activity. During drought periods, humidity-enhanced microbial degradation of organic materials, which constitute one aspect of humidity-enhanced biotic activity, is enabled above critical levels of litter moisture as determined by relative air humidity and litter characteristics. Some mechanisms might not have an activation threshold. Soil-litter mixing driven by runoff and wind can be enabled by dryness and/or heat to create preconditions, such as vegetation gaps and bare soil surfaces. Photochemical degradation is assumed to operate continuously during day-time, even at low light levels and particularly in vegetation gaps (Box 1).

Long-term gradual trends of increasing aridity and warming will lead to continuing declines in soil moisture and increases in soil surface and air temperatures. In addition to the dryland mechanisms operating on the small scales, these trends may promote slow-responding mechanisms on large spatial scales (mosaic-to-landscape; Figure 2). Self-organization of vegetation patchiness and decoupling of soil biogeochemical cycles increase in importance below critical P/PET values for their preconditions (Supplementary Table S2). These thresholds were assessed in drylands, but could be considerably higher in currently wetter regions due, for example, to vegetation not adapted to drought (see simulations of shallow-rooted vs. deep-rooted vegetation in Box 2).

Some mechanisms, such as wind- and water-driven horizontal resource redistribution and the canopy convector effect operate under various conditions, but their importance is considerably enhanced by increased aridity. For horizontal resource redistribution, water flow length above a critical threshold was linked to low vegetation cover level and led to possibly irreversible degradation of the system because of soil erosion (Supplementary Table S2). However, this example is not applicable to other regions because threshold values change with climate, geomorphology and soil properties [164]. Suitability for biological soil crust formation is favoured by low precipitation amounts during the warmest quarter of the year, low temperature during the driest quarter, and high day-night temperature fluctuations, and is moderated by soil properties and land use, with no clear threshold values [106].

For most dryland mechanisms, activation thresholds are not well constrained because they are highly scale-, context- and process-specific [165,166]. Furthermore, dryland mechanisms operate along mostly unknown response curves relative to drivers, modulators and preconditions. For example, in our simulations, the contributions of humidity-enhanced microbial degradation and photochemical degradation to total litter decomposition increases linearly or exponentially with decreasing precipitation, with response trajectories depending on the temperature increase (Box 1). Thus, projecting the emergence of a mechanism requires additional information about activation thresholds and response trajectories in relation to the operation of other mechanisms acting on the same process.

Research needs and experimental approaches

We have presented existing empirical and experimental evidence as well as new model projections to illustrate conditions under which dryland mechanisms become relevant in environments historically not limited by water. However, to enhance our understanding of these mechanisms and their operation, we need fundamental knowledge regarding the likelihood of their emergence, the exact context-specific conditions at which they operate, their contribution and importance to ecosystem functioning in historically non-water limited areas experiencing extreme climatic conditions, and their direction of action in combination with other mechanisms subjected to climate change.

One way to gain insight into the operation of these mechanisms is through long-term research and monitoring networks [167], which could expand their focus to the mechanisms and metrics listed in Table 1. Coordinated distributed experiments that include a set of common measurements relevant to dryland mechanisms [168] could be used to identify overarching patterns and context-specific variation in mechanisms. Similar findings across regions would suggest a common mechanism driving the response, while differences would imply that local conditions (e.g., soil type, species composition, land use history, etc.) modify the underlying response [169]. These approaches enable establishing baseline contributions of dryland mechanisms to ecosystem processes under current climate conditions (see, e.g., simulations in Boxes 1 and 2 under present climate), gaining knowledge on fundamental changes in ecosystem functioning during and following extreme drought and heat events.

Research could focus on areas where recent vegetation browning and soil drying has been observed (Figure 1b, Supplementary Figure S3), in addition to regions where a drier and hotter climate is expected (Figure 3, Supplementary Figure S4). Xeric sites and regions with a dry season, including temperate dry grasslands, steppes and forests, and tropical dry forests, likely feature dryland mechanisms already today. They can therefore serve as experimental grounds for studies on the future operation of such mechanisms outside drylands. Drought and heat experiments, including those imposing long-term recurrent drought, climatic gradients and environmental conditions beyond the current observational range [166,170-172], can be applied to improve our understanding of the biological processes underlying dryland mechanisms and to identify thresholds beyond which they emerge in various biomes.

Research in this context would greatly profit from synergies between scientists studying non-water limited ecosystems and those investigating drylands. In addition, research projects involving both experimentalists and modelers enable an iterative process of hypothesis testing by experiments and models on the influence of dryland mechanisms, which in turn may lead to new hypotheses [173]. Specifically, there is a need for a modeling framework combining dryland and other mechanisms to simulate ecosystem functions under a future climate. Such approaches could create flexible modes that shift between different dominant mechanisms, including dryland mechanisms, depending on current and projected environmental conditions.

Conclusions and broader implications

Climate change may alter not only process rates, but also the mechanisms underlying ecosystem functioning. It is expected that mechanisms observed in drylands will come into play in historically non-water limited mesic, humid and cold regions. Some fast-responding mechanisms are activated once microclimatic thresholds are crossed, while the emergence of some of the slow-responding mechanisms depends on a combined set of climatic and local conditions. Dryland mechanisms affect fundamental ecosystem processes, including vegetation organization, water and energy flows, carbon and nutrient cycling, primary production and organic matter decomposition. The operation of dryland mechanisms can buffer or amplify other impacts of climate change on ecosystems (Table 1). Moreover, dryland mechanisms could act synergistically, thus increasing their importance and impacts, and may ultimately lead to regime shifts and alternative ecosystem states [174]. Traditional models based on continuous responses would miss such outcomes, unless dryland mechanisms and their interactions are incorporated.

Alterations of the mechanisms underlying ecosystem functioning have immediate consequences for ecosystem services, i.e., nature’s contributions to people [175]. Some of the projected changes will occur in regions with large human populations, especially in subtropical and mid-latitudes, and, thus, will significantly affect the well-being of society in these regions. Research on ecosystem functioning under increasing frequency and severity of droughts and heatwaves will improve our understanding of the underlying emergent processes. The new insights can contribute to advancing the adaptive capacity of social-ecological systems to withstand such climate extremes and their impacts on nature and people [176]. This knowledge can be conveyed to stakeholders to inform and direct environmental policy in its efforts to adapt to consequences of climate change for humans and nature.

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Author contributions

JMG conceptualized this perspective, informed by discussions with HJDB, AR, MJS, MB, and HLT. MJS produced the NDVI and soil moisture maps. OA downloaded and analyzed the climate model data. DH and YM produced and analyzed the soil water potential data. OA, DH, and YM generated the temperature and soil water potential panels. GD and OF (Box 1) and EM and OT (Box 2) performed model analyses of the dryland mechanisms and produced the Box figures. JMG drafted the manuscript, and HJDB, AR, MJS, OA, MB, JB, GD, SCD, DG, DH, KRH, LL, EM, ES, HLT and DY contributed discussions to different draft versions. All authors gave their final approval for submission.

Competing interests

The authors declare no competing interests.

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Table

Table 1. Selected mechanisms of ecosystem functioning currently operating primarily in drylands (dryland mechanisms), but projected to emerge in various other regions. Likelihood of mechanisms emerging in non-dryland regions was estimated based on the breadth of reports in these regions, the number of preconditions (P), drivers (D) and modulators (M), and known activation thresholds (Supplementary Table S2). Importance signifies the potential influence of dryland mechanisms on ecosystem functioning outside drylands, based on the scope of affected functions, the outcome of model simulations (Boxes 1 and 2), and reports in non-dryland regions. Direction means amplification (↑) or buffering (↓) of other impacts of climate change by the mechanisms. Metrics to monitor dryland mechanisms refer to direct and feasible measures of the operation of the mechanism. Spatial scales: patch (relatively homogenous area of <1−10 m^2 covered by vegetation/rock/soil, experiencing distinct microclimatic conditions), mosaic (area of <0.01-1 km^2 containing several patches) and landscape (area of >1 km^2 containing several mosaics) [28]; temporal scales: fast (weeks-years), slow (decades). 'Moisture' is used as a general term for available water. ● low, ●● intermediate, ●●● high. OM, organic matter (soil, plant litter); RH, relative air humidity; ROS, reactive oxygen species; T_a, air temperature; T_s, soil temperature.

Dryland mechanism	Precondition, driver, modulator	Immediate consequences	Affected functions	Reports outside drylands	Likelihood	Importance	Direction	Metrics for monitoring
Patch-to-mosaic scales, fast- responding								
Drying-wetting cycles	P: soil drought D: rain pulse M: soil texture, vegetation density	Ecological pulse responses to sudden soil and plant rehydration	Plant production, plant/microbe/animal activity, OM decay, nutrient cycling, trace gas emission	Temperate, boreal-transition; forest, grassland, wetland	●●●	●●●	↓	Organism activity, soil trace gas emissions (e.g. CO_2, N_2O, CH_4)
Hydraulic redistribution	D: soil water potential gradient M: rooting depth (vegetation type and density)	Transient soil rehydration	Plant production, nutrient uptake, OM decay, carbon cycle, water use, species composition	Temperate, tropical; natural, agriculture; regions with dry periods	●●●	●●●	↓	Reverse sap flow in roots, nocturnal increases in soil moisture
Humidity-enhanced biotic activity	P: drought D: fog, dew, water vapor (non-rainfall water)	Increased soil, litter and plant moisture	Plant activity, microbial degradation of OM, water use	Temperate; salt marsh, wetland, grassland	●●●	●●●	↓	CO_2 emission (litter/topsoil OM; dark), RH, T_a
Soil hydrophobicity	D: drought, heat M: hydrophobic soil organic compounds	Low soil moisture	Plant production, root water access, OM decay, soil erosion, plant mortality	Temperate, tropical; agriculture; burnt areas	●●●	●●●	↑	Depth profile of soil moisture, rainfall
Photochemical degradation	D: solar radiation M: vegetation cover	Increased energy uptake by OM	OM decay, trace gas emission, ROS production	Temperate, tropical; grassland, forest, bog	●●●	●●	↓	OM mass loss, trace gas emission at sun exposure
Thermal degradation	D: heat M: vegetation cover	Increased energy uptake by OM	OM decay, trace gas emission	No known reports	●●	●●	↓	Trace gas emission (litter/topsoil OM; dark); T_s
Soil-litter mixing	P: vegetation gap D: runoff, wind M: dry or disturbed soil, lowered soil stability	Buffering of litter moisture depletion, decreased light exposure	Microbial OM degradation, photochemical degradation	No known reports	●●	●●	↓	Litter mass loss, litter ash content
Mosaic-to-landscape scale, slow-responding								
Biological soil crust formation	P: increased aridity, vegetation gaps D: non-rainfall water availability M: soil properties, land use	Soil surface colonization by microbes/ microphytes	Plant production, water flow, carbon and nutrient cycling, energy budget, soil stabilization	Temperate, subtropical; dry sites	●●	●●●	↓	Presence of groups of soil crust organisms
Self-organization of vegetation patchiness	P: increased aridity D: lateral water redistribution M: plant growth, water infiltration	Vegetation patchiness, bare-soil gaps	Plant production, water and nutrient budgets	No cases caused by drought	●	●●●	↑↓	Vegetation cover and continuity
Wind- & water-driven horizontal resource redistribution	P: increased aridity, vegetation gaps D: water, wind	Concentration of resources	Water, carbon and nutrient budgets, vegetation development	Tundra	●●	●●●	↑	Aboveground water flow, wind speed
Decoupling of soil biogeochemical cycles	P: increased aridity D: element input and loss, element cycling	Reduction in soil OM and/or nitrogen, increase in phosphorus	Plant production, respiration, OM decay	Global	●	●●	↑	Total soil nitrogen and phosphorus, soil organic carbon
Canopy convector effect	D: increased aridity, sparse vegetation cover, low aerodynamic resistance to heat transfer	Decrease in surface temperature	Energy budget, plant production, boundary layer dynamics, secondary circulations	Temperate	●	●●●	↓	Sensible heat flux

Figures captions and Boxes

Figure 1. Global representation of dryland and non-dryland regions, and of recent trends in vegetation cover. (**a**) Dryland and non-dryland regions (Glossary in Supplementary Table S1; the map is based on data from https://datadownload.unep-wcmc.org/datasets). Icons of dryland mechanisms were added to approximate geographical locations of selected reports on dryland mechanisms operating in non-dryland regions. (**b**) linear trends in greening and browning (change in NDVI per year based on AVHRR GIMMS data between 1982 and 2008; reproduced from [155]). Panel (**b**) is also available in grey scale (Supplementary Figure S5).

Figure 2. Conceptual model for the potential enhancement of dryland mechanisms of ecosystem functioning by climate change in non-dryland regions. 'Surface' (moisture and temperature) is used here as a generic term for the conditions in the soil and near ground surface. Potential coupling of and interactions among mechanisms were omitted for the sake of clarity. Full arrows: direct impacts; dashed arrows: indirectly enhancing effects.

Figure 3. Current and projected changes in soil water potential (SWP) and topsoil temperature in non-dryland (mesic, temperate and cold) regions by the end of the 21st century. Shown are projections of annual mean SWP in the top 0.1 m of the soil profile and annual mean temperature at a depth of 0.01-0.05 m (depending on the model). (**a**,**e**) Current conditions, (**b**,**f**) future conditions, and (**c**,**g**) change from current to future conditions; (**d**) mean continental change (with the standard deviation marked as an error bar) in SWP for non-dryland regions; (**h**) added area by the end of the century with a mean soil temperature of >0-50°C. The more negative the SWP values, the drier the soil [darker colors in panels (**a**) and (**b**)]; negative values illustrated by red colors in panel (**c**) indicate soil drying. Non-dryland areas do not include Greenland and Antarctica. For methods, see Supplementary information, Climate model projections.

Box 1. Illustration of dryland biotic and abiotic decomposition mechanisms in a temperate forest
Simulations of a published, process-based soil model indicate that under the current climate, humidity-enhanced microbial degradation induced by dew contributes 5.5% and photodegradation contributes 7% to annual surface-litter decomposition in a temperate forest with 75% canopy cover (Box figure, panels c,e). Without canopy cover, the relative effect of photodegradation increases to 25% (Box figure, panel f). The contribution of humidity-enhanced microbial degradation under the canopy rises significantly ($P \leq 0.05$, Mann-Whitney-Wilcoxon test) to 11.5% at a 10% decrease in precipitation and a temperature increase of 4°C. When we simulated extreme drought and warming we found a sharp decline in litter decomposition (Box figure, panels a,b), but remaining decay was largely due to microbial degradation under the canopy and to photodegradation in open areas (Box Figure, panels c,f).

[ADD BOX 1 FIGURE]

Changes in plant litter decomposition and the relative importance of dryland decay mechanisms under simulated precipitation and temperature changes. Simulations were conducted for a humid forest at 75% canopy cover (left panels) and 0% cover (right panels) by applying the model to data from a pine forest in Belgium (for detailed methods, see Supplementary information, Soil model). (**a, b**) Annual litter decomposition in the top-litter layer; (**c, d**) contribution of humidity-enhanced microbial degradation induced by dew to total annual litter decomposition in the top-litter layer (dew is defined as non-rainfall water source, Supplementary Table S1); (**e, f**) contribution of photochemical degradation induced by solar radiation to total annual litter decomposition in the top-litter layer. Climate simulations include the change in mean annual precipitation amounts and the change in mean annual litter temperature.

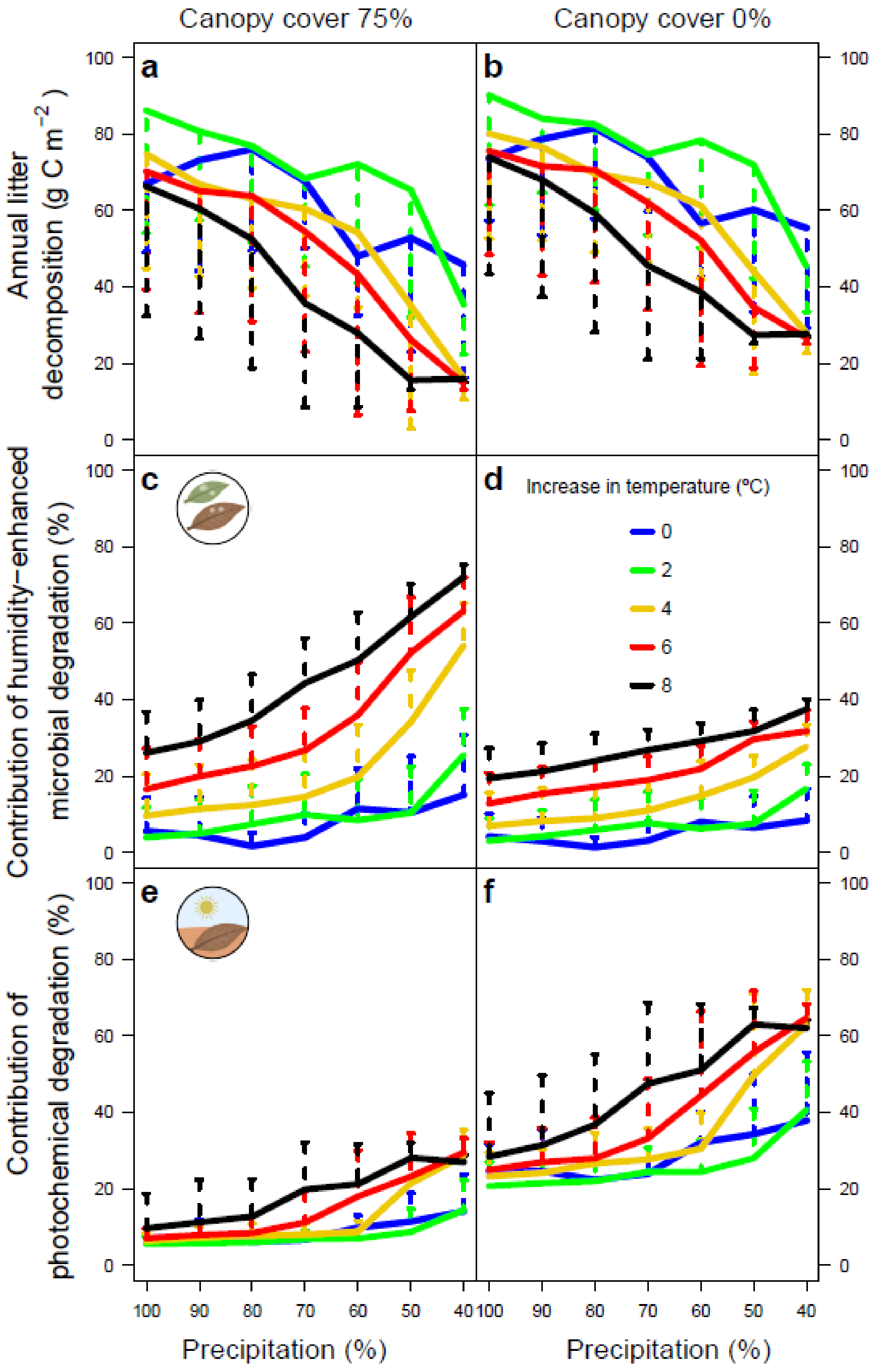
Box 2. Illustration of self-organization of vegetation patchiness in a drying climate

Simulations using a published model of reductions in long-term annual precipitation (*P*) showed that spatially uniform cover of vegetation was broken into patches of vegetation interspersed by bare soil, ranging from gaps, to labyrinths and spots (Box figure). The threshold level of *P* beyond which self-organization of vegetation patchiness occurred was much higher for shallow-rooted plants than for deep-rooted, drought-resistant plants capable of extracting water from deep soil layers. The shallow-rooted plants represent species from mesic ecosystems that are not adapted to drought. Consequently, the threshold of *P/potential evapotranspiration* for the emergence of this mechanism in regions with drought-adapted plant types (Supplementary Table S2) will likely be higher for regions with unadapted plants. The simulations also showed that following further reduction in *P*, vegetation patterns ultimately collapsed to bare soil, which again occurred at much higher *P* for shallow- than for deep-rooted plant species. The implications of this mechanism for ecosystem functioning are significant, considering the influence of a small decline in *P* (e.g. from 650 to 600 mm) on total biomass per area, which is much more pronounced in shallow-rooted species (35%) than in deep-rooted species (11%; Supplementary Table S3).

[ADD BOX 2 FIGURE]

Responses to a gradual precipitation decrease (aridity increase) in shallow-rooted vs. deep-rooted plant community types as simulated by a vegetation model (for detailed methods, see Supplementary information, Vegetation model). The shallow-rooted type is typical of non-dryland species that compete for light and grow fast, while the drought-resistant, deep-rooted type is typical of dryland plants that compete for water at depth. Shown are spatial distributions of biomass density (*B*) of each vegetation type at decreasing long-term annual precipitation rates (values varying from 650 to 330 mm yr^{-1} in the top row apply also to the bottom row) on square domains of 47 m × 47 m, with a spatial extent indicated by Y and X dimensions.

Box 1 Figure


Canopy cover 75%
Canopy cover 0%
a
b
c
d
e
f
Annual litter decomposition (g C m^{-2})
Contribution of humidity–enhanced microbial degradation (%)
Contribution of photochemical degradation (%)
Increase in temperature (ºC)
0
2
4
6
8
0
20
40
60
80
100
100
90
80
70
60
50
40
Precipitation (%)
Precipitation (%)

Box 2 Figure

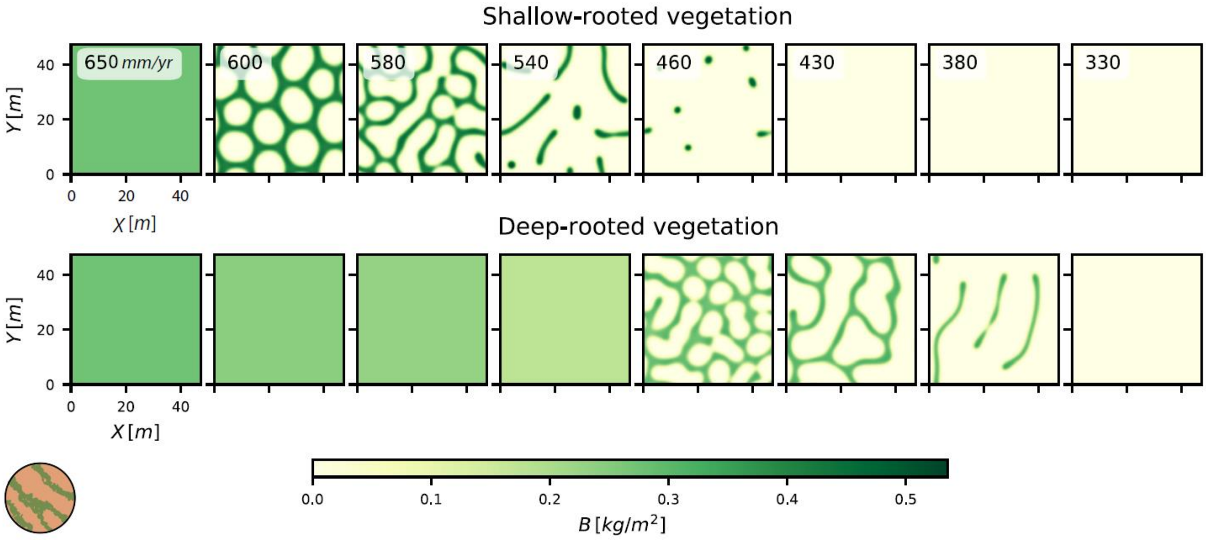

Shallow-rooted vegetation
650 mm/yr
600
580
540
460
430
380
330
Y [m]
X [m]
0
20
40
Deep-rooted vegetation
0.0
0.1
0.2
0.3
0.4
0.5
B [kg/m²]

Fig. 1

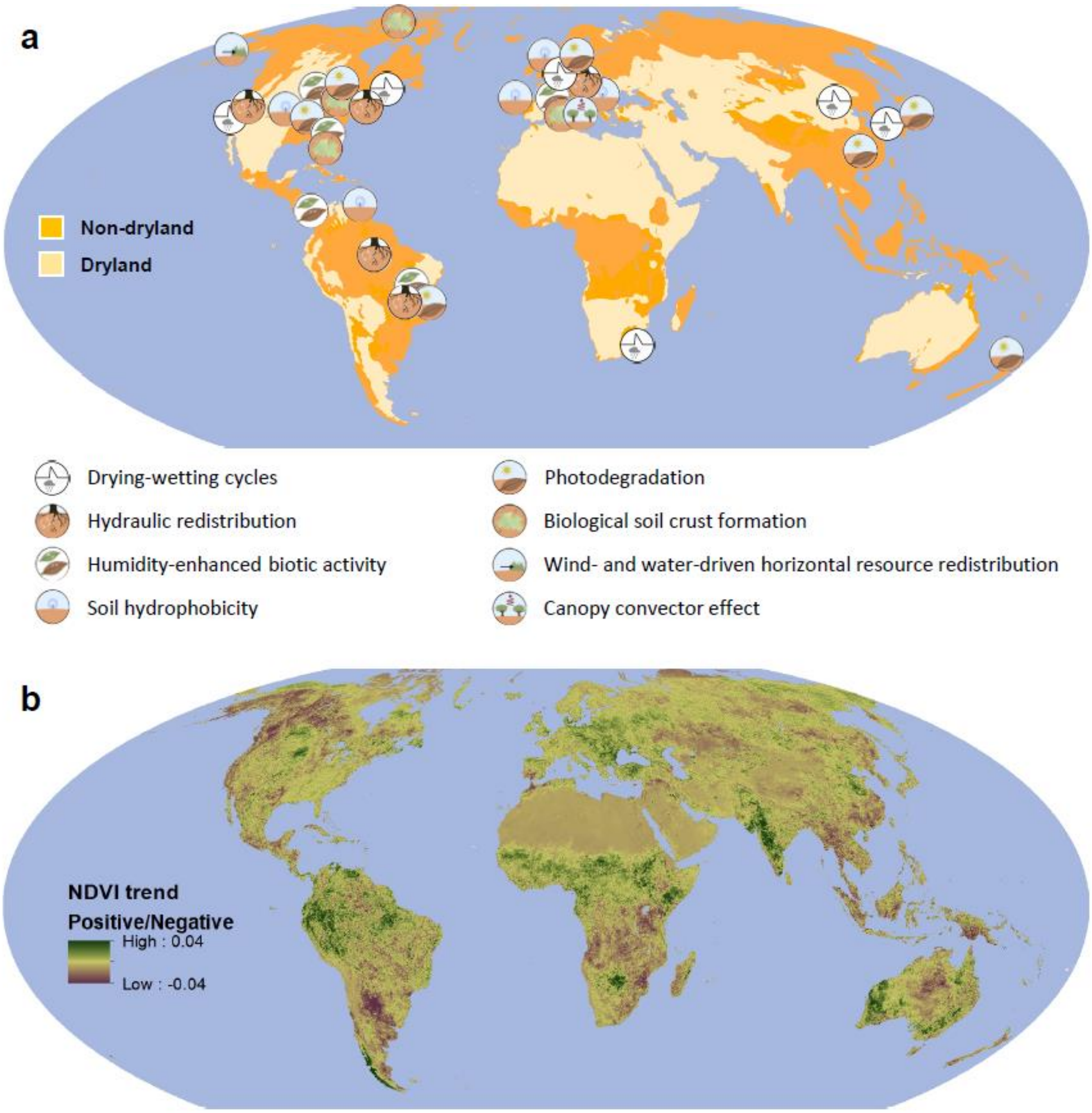

a
Non-dryland
Dryland
Drying-wetting cycles
Hydraulic redistribution
Humidity-enhanced biotic activity
Soil hydrophobicity
Photodegradation
Biological soil crust formation
Wind- and water-driven horizontal resource redistribution
Canopy convector effect
b
NDVI trend
Positive/Negative
High : 0.04
Low : -0.04

Fig. 2

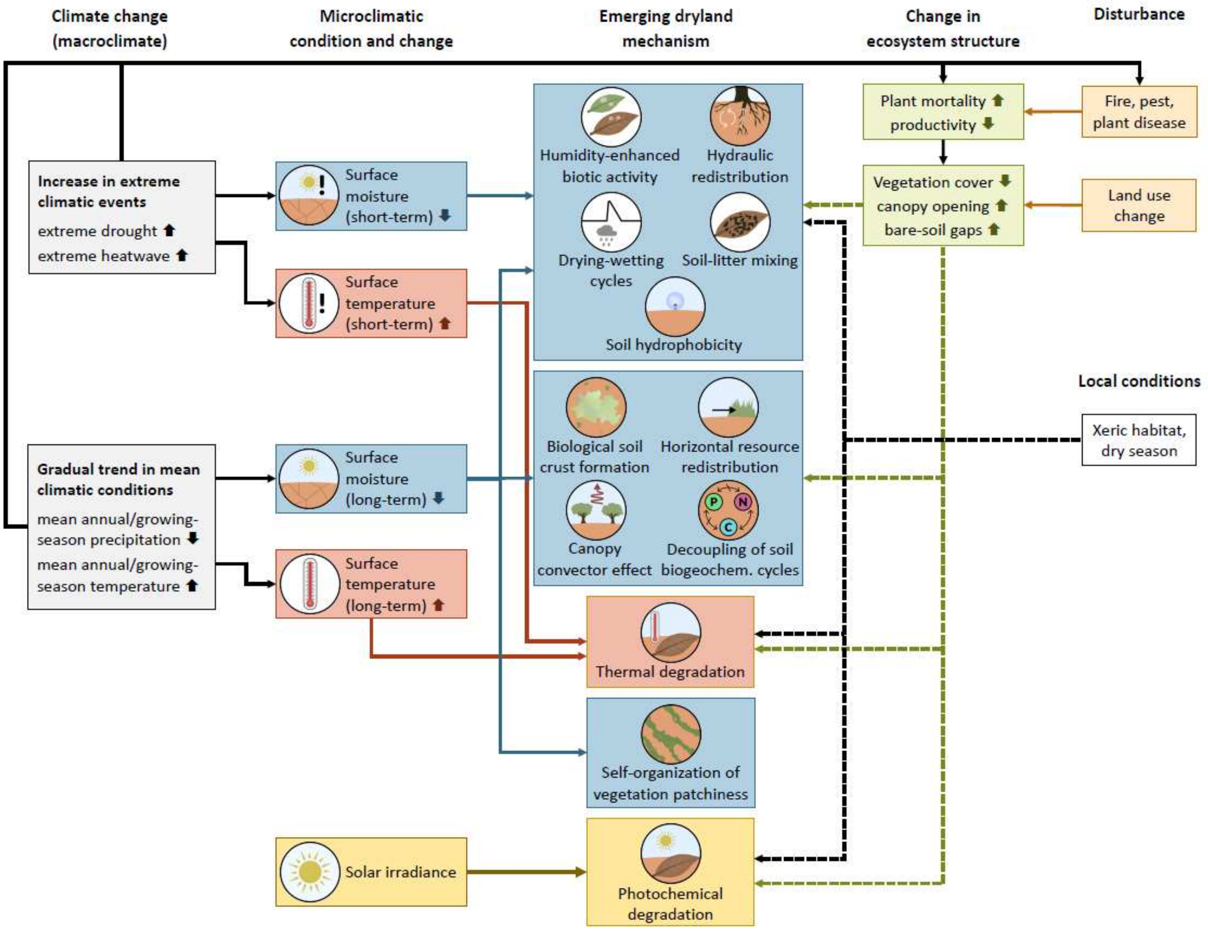
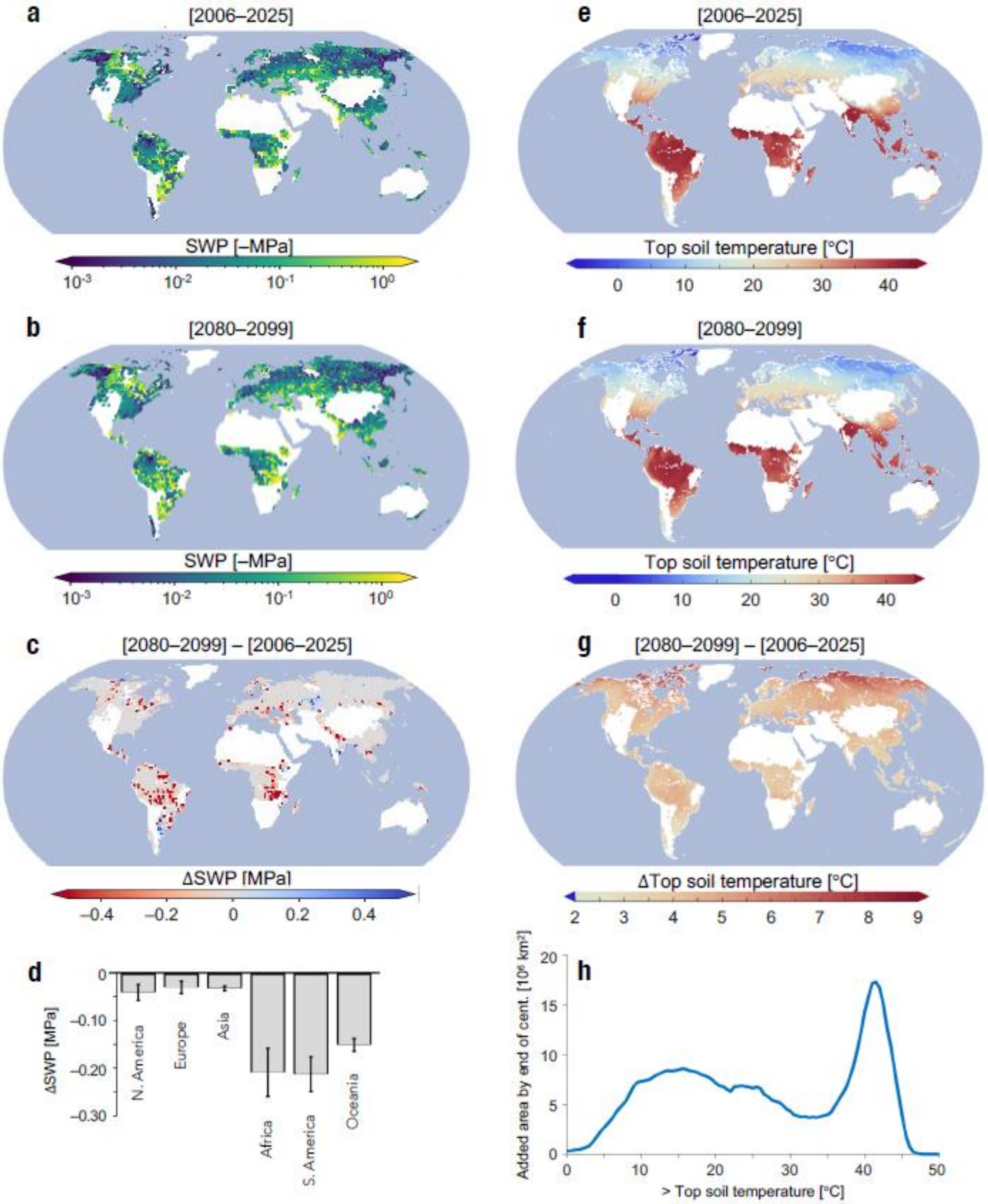

Climate change (macroclimate)
Microclimatic condition and change
Emerging dryland mechanism
Change in ecosystem structure
Disturbance
Increase in extreme climatic events
extreme drought ↑
extreme heatwave ↑
Gradual trend in mean climatic conditions
mean annual/growing-season precipitation ↓
mean annual/growing-season temperature ↑
Surface moisture (short-term) ↓
Surface temperature (short-term) ↑
Surface moisture (long-term) ↓
Surface temperature (long-term) ↑
Solar irradiance
Humidity-enhanced biotic activity
Hydraulic redistribution
Drying-wetting cycles
Soil-litter mixing
Soil hydrophobicity
Biological soil crust formation
Horizontal resource redistribution
Canopy convector effect
Decoupling of soil biogeochem. cycles
P
N
C
Thermal degradation
Self-organization of vegetation patchiness
Photochemical degradation
Plant mortality ↑
productivity ↓
Vegetation cover ↓
canopy opening ↑
bare-soil gaps ↑
Fire, pest, plant disease
Land use change
Local conditions
Xeric habitat, dry season

Fig. 3


a
[2006–2025]
SWP [–MPa]
10⁻³
10⁻²
10⁻¹
10⁰
b
[2080–2099]
SWP [–MPa]
10⁻³
10⁻²
10⁻¹
10⁰
c
[2080–2099] – [2006–2025]
ΔSWP [MPa]
−0.4
−0.2
0
0.2
0.4
d
ΔSWP [MPa]
0
−0.10
−0.20
−0.30
N. America
Europe
Asia
Africa
S. America
Oceania
e
[2006–2025]
Top soil temperature [°C]
0
10
20
30
40
f
[2080–2099]
Top soil temperature [°C]
0
10
20
30
40
g
[2080–2099] – [2006–2025]
ΔTop soil temperature [°C]
2
3
4
5
6
7
8
9
h
Added area by end of cent. [10⁶ km²]
0
5
10
15
20
> Top soil temperature [°C]
0
10
20
30
40
50