

## Dryland productivity under a changing climate

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### Abstract

Understanding dryland dynamics is essential to predict future climate trajectories. However, there remains large uncertainty on the extent to which drylands are expanding or greening, the drivers of dryland vegetation shifts, the relative importance of different hydrological processes regulating ecosystem functioning, and the role of land-use changes and climate variability in shaping ecosystem productivity. We review recent advances in the study of dryland productivity and ecosystem function and examine major outstanding debates on dryland responses to environmental changes. We highlight often-neglected uncertainties in the observation and prediction of dryland productivity and elucidate the complexity of dryland dynamics. We suggest prioritizing holistic approaches to dryland management, accounting for the increasing climatic and anthropogenic pressures, and the associated uncertainties.

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## Main

Drylands are commonly defined as regions where precipitation is substantially smaller than atmospheric water demand (as quantified by potential evapotranspiration, PET). They are the largest biome on Earth<sup>1</sup>, covering about 40% of the terrestrial land surface (Fig. 1a). Their climates are typically characterized by infrequent, seasonal, and highly variable precipitation, and intense solar radiation<sup>2, 3</sup>. Despite their low and often discontinuous vegetation cover (Fig. 1b), drylands contribute to about 40% of global net primary productivity (NPP) (Fig. 1c) and play an important role in the global carbon budget<sup>4, 5</sup>, particularly in determining the variability and long-term trend of the terrestrial CO<sub>2</sub> sink<sup>5, 6</sup>. Dryland productivity is mainly controlled by the amount and variability of precipitation<sup>7</sup>, though plant water stress can be mitigated by ecohydrological feedbacks between plant communities and hydrological processes, access to groundwater and non-rainfall water, and — in cultivated areas — irrigation<sup>3, 8</sup>.

Drylands host more than two billion people (Fig. 1a) and provide essential ecosystem services associated with the supply of plant biomass for food, fiber, and energy<sup>3, 9</sup>. Therefore, vegetation productivity is also of great economic importance in the agrarian societies populating dryland regions of the world, where crop and livestock production serve as the major source of employment and livelihood. Despite their usual low ecosystem productivity, drylands are often more agriculturally productive than the tropics or boreal forests which have higher ecosystem productivity. This is due to their favorable temperature and radiation conditions, and, where feasible, the use of irrigation. As such, drylands have been breadbaskets for millennia and multiple staple crops (e.g., wheat) originated from drylands. In recent decades, major land use changes occurred in global drylands and agriculture has been expanding to meet local and global demands for food, feed, and bioenergy. For example, ~220,000 km<sup>2</sup> of tree covered dryland were converted into other land cover types between 1992 and 2015; 56% of that area transitioned to shrubland, while 40% was converted into cropland (Fig. 2).

Dryland productivity trends are affected by both climate change and natural climate variability (e.g., El Niño Southern Oscillation, ENSO) through changes in plant water availability driven by trends and fluctuations both in precipitation and temperature. Climate change typically induces changes in both mean state and variability of climate variables. While projected precipitation changes are still uncertain, global warming is expected to increase climate variability including precipitation variability<sup>10, 11</sup>. How drylands respond to the ongoing and future climate change will significantly affect the trajectory and magnitude of the terrestrial carbon sink and land-atmospheric coupling. However, questions remain open on how climate change will alter the spatial extent of drylands, trends and drivers of dryland vegetation productivity, and dryland contribution to the global carbon cycle.

In this review, we provide a synthesis of the recent advances in the understanding of trends and drivers of dryland productivity and ecosystem functions. We also delve into the ongoing debates around dryland expansion, greening, and vegetation response to both hydroclimatic drivers and human action (Fig. 3). We finally highlight major knowledge gaps and suggest future research opportunities and priorities.

## Observed trends and debates on the future of drylands

Here we present the key observations of dryland vegetation dynamics and discuss the ongoing debates regarding dryland expansion/greening.

### *Observed global dryland vegetation dynamics and drivers*

Spatiotemporal vegetation productivity dynamics and their drivers are of great interest to assess changes in environmental conditions in drylands. Satellite remote sensing demonstrates global dryland greening trends in the last three decades<sup>12</sup> (Fig. 4). However, while greening was observed across the Sahel<sup>13</sup>, the Tibetan Plateau, and the Western United States<sup>14</sup>, large areas of the southwestern United States, southern Argentina, Kazakhstan, Mongolia, Afghanistan, and regions of Australia have instead seen a decrease in vegetation cover<sup>15</sup>. Some of the observed differences in vegetation trends may be caused by different time periods selected and the sensitivity of these regions to decadal climate oscillations. Harder to detect from space are ongoing trends in plant community composition such as shrub encroachment, exogenous grass invasions<sup>16</sup>, tree die-offs<sup>17</sup>, and the increasing dominance of plants with crassulacean acid metabolism<sup>18</sup>.

The main drivers of dryland vegetation dynamics could be broadly divided into factors related to global climate (e.g., precipitation and temperature) and human actions (e.g., grazing, afforestation/deforestation, agriculture, fire management, urbanization)<sup>19, 20</sup>. At the global scale, drivers of greening have been mainly related to atmospheric CO<sub>2</sub> fertilization, increased vegetation water use efficiency (WUE), and climate warming<sup>12, 21, 22</sup> (Fig. 3). While precipitation is the main driver of changes in dryland greenness globally, local controls are also important<sup>23, 24, 25</sup>. At the regional scale, other factors such as nitrogen deposition and land use change also play important roles in determining vegetation dynamics<sup>20</sup> (Fig. 3). Climate change factors such as warming, altered precipitation regimes (e.g., increased variability), and increased CO<sub>2</sub> levels can facilitate woody plant encroachment (i.e., the increasing abundance of woody plants in grasslands and savannas) at the global scale<sup>26</sup>, while human activities such as fire suppression and overgrazing act at more local scales. Other human activities including agriculture and deforestation, however, can locally offset the global trend of increasing woody plant abundance<sup>27</sup>. While changes in vegetation phenology as a result of climate trends and changes in plant community composition are expected to affect spatiotemporal patterns of plant growth in ecosystems, their impact on the productivity of the global drylands remains unclear. Modeling studies constrained by field observations<sup>28</sup> found an improvement in modeled grassland productivity when accounting for trends in semi-arid grassland phenology<sup>29</sup>. These results suggest that a future shift toward both earlier growing season onset and delayed senescence could compensate for drought-induced reductions in summer grass cover and productivity, resulting in widespread increases in grassland fractional cover over the coming century across the majority of North American grasslands.

### *Dryland expansion debates under future climates*

It has been argued that climate change will increase the aridity of existing drylands and/or lead to their expansion with negative impacts on ecosystem productivity and livelihoods<sup>30,31</sup>. These trends, however, are still debated<sup>32</sup>. According to the dryland expansion hypothesis, the expected intensification of dryland aridity will lead to vegetation loss and reduced primary productivity. At the same time, there is empirical evidence of dryland greening, suggesting an increase in productivity consistent with the known effects of increased atmospheric CO<sub>2</sub><sup>21, 33</sup>. Despite the positive CO<sub>2</sub> effect on WUE, drylands are expected to expand in a warming climate<sup>30,31</sup>, based on model estimates of the aridity index (AI = Precipitation/PET). Indeed, model projections show that warming is expected to induce a global increase in potential evapotranspiration (~5% °C<sup>-1</sup>) outpacing the global increase in precipitation on land (1-2% °C<sup>-1</sup>). Moreover, in the specific case of drylands (i.e., regions with AI < 0.65) precipitation has been observed to decrease in the last 40 years, with a few exceptions<sup>34</sup>. Thus, under climate warming scenarios AI is projected to decrease worldwide, particularly in drylands, which are also predicted to expand.

Such conclusions, however, have been recently challenged because AI does not seem to be suitable for the prediction of dryland extent and aridity under future climate scenarios. In fact, the calculation of AI using the Penman-Monteith PET equation, does not consider vegetation response to higher CO<sub>2</sub> concentration. If this response is dominated by stomatal closure, neglecting CO<sub>2</sub> effects may lead to an overestimate of PET response, aridity increase, and dryland expansion under climate warming<sup>35</sup>. Lastly, changes in soil dryness are ultimately driven by the soil water balance through differences between precipitation and actual evapotranspiration (ET) instead of PET. ET's complementary relationship (i.e., the decrease in ET with increasing values of PET) has been invoked to argue that warming is not necessarily associated with drying trends, consistent with paleoclimatic evidence<sup>36</sup>. New aridity metrics developed to address the shortcomings of AI suggest that climate warming is not expected to significantly change the spatial extent of drylands<sup>35</sup>. Interestingly, a recent study found that over the last 30 years vegetation growth in the Northern Hemisphere showed increasing water constraints<sup>37</sup>, suggesting that even without invoking dryland expansion under climate warming, vegetation growth in both drylands and nearby areas may suffer from increasing water limitations.

### **Complexity in the water-productivity relationship in drylands**

Water availability and its timing play a pivotal role in dryland dynamics and productivity. Dryland response to climate change has typically been investigated with reference to trends in mean climate variables (e.g., rainfall and soil moisture), while the effect of their variability (e.g., seasonality, interannual variability) received much less attention<sup>24, 26, 38</sup>. Even less is known about the role of variability in non-rainfall water inputs (mainly fog and dew) and groundwater fluctuations<sup>40,41</sup> on dryland vegetation dynamics. In this section, we highlight these less studied but equally important factors affecting dryland productivity globally and at a regional scale.

### *Inter-annual rainfall variability and productivity*

Dryland climates are characterized by a strong intra- and inter-annual variability of precipitation, associated with precipitation intermittency, seasonality, and year-to-year fluctuations. In arid and semiarid regions, precipitation typically occurs clustered in one (or more) rainy season(s) interrupted by dry periods with low or no rain. Rainy seasons exhibit a few scattered events separated by rainless days. Interannual variability relative to average totals, which is often expressed by the coefficient of variation (CV) of annual precipitation, is particularly strong in drylands and tends to increase with aridity, as shown by trends in CV along precipitation gradients<sup>39</sup>. Most of the interannual variability results from changes in the number of rainy days rather than from changes in the average precipitation amount on rainy days<sup>40</sup>.

Overall, interannual precipitation variability decreases aboveground NPP and the terrestrial carbon sink in dryland ecosystems with mean annual precipitation >300 mm, while aboveground NPP increases with precipitation variability in drier climates, as vegetation benefits from the wet anomalies<sup>38, 41</sup>. Within this general pattern, an increase in interannual precipitation variance typically increases the interannual variability of vegetation cover or plant productivity.

The effects of random interannual precipitation fluctuations, however, could be less ‘trivial’ when they interact with non-linearities in ecosystem dynamics and induce newly organized states, bifurcations, and spatiotemporal patterns that would not exist in the absence of environmental variability<sup>42</sup>. For instance, an increase in precipitation variability may lead to the emergence of alternative stable states in soil moisture dynamics, indicating that a certain region may have a higher likelihood to be in a dry or in a relatively wet state while intermediate conditions have a lower probability of occurrence. The opposite can also occur. Interannual precipitation variability may remove bistability in systems that would otherwise exhibit two alternative stable configurations and stabilize vegetation dynamics in an intermediate state<sup>39, 42</sup>. Coupled vegetation-climate models have shown how in the absence of interannual climate variability the savanna belts across the Sahel and Southern Africa tend to exhibit bistable dynamics with two preferential states of ‘desert’ and ‘vegetated’ land. This bistable behavior, however, can be inhibited by interannual climate fluctuations<sup>43</sup>, which stabilize the system in a state with intermediate vegetation density (and productivity), thereby enhancing its resilience<sup>39</sup>.

In dryland ecosystems, interannual precipitation variability can also induce vegetation patterns, including the periodic spotted, banded, and labyrinthine vegetation configurations widely documented in drylands<sup>44</sup>. A major implication of pattern formation is its ability to enhance the resilience and productivity of plant ecosystems<sup>45</sup>. Past research, however, has strongly relied on model simulations with only few manipulative experiments<sup>46</sup>. Because self-organized patterns with similar geometries can result from models that account for different processes, the mechanisms underlying pattern formation and the role of interannual precipitation variability still need to be conclusively assessed<sup>44</sup>.

Precipitation variability plays an important role also in the dynamics of dryland plant communities and has been invoked to explain changes in woody plant dominance<sup>47</sup>. Interannual

precipitation fluctuations are also expected to have a stronger impact on annual than perennial species, thereby potentially reshaping the composition of grass communities<sup>48</sup>.

### *Intra-annual rainfall variability, productivity, and pulses*

The intra-annual variability of precipitation is also an important determinant of vegetation composition and productivity. Tree cover increases with increasing frequency of rainy days and decreasing precipitation intensity<sup>49</sup>, and similarly productivity increases when the precipitation events occur regularly, thus limiting the effects of water stress. In some drylands, even though average precipitation amount does not change, there are alterations in seasonal, daily or sub-daily rainfall regime characteristics (frequency, duration, intensity)<sup>50, 51</sup>. These changes could have profound impacts on vegetation functioning and species composition (e.g., C<sub>3</sub> vs. C<sub>4</sub> plants). For example, C<sub>3</sub> plant abundance increases under low rainfall and high temperatures, despite C<sub>4</sub> plants being better adapted to such conditions<sup>52</sup>. This surprising finding can be explained by higher precipitation falling during cooler months—when C<sub>3</sub> grasses are most active—during extreme drought years<sup>52</sup>. Precipitation variability may also influence ecosystems through interactions with the temperature regime. Additionally, the physiological impact of rising CO<sub>2</sub> (through higher WUE) may act by downregulating or elevating the sensitivity of dryland plants to precipitation variability<sup>53</sup>.

Intra-annual precipitation variability also triggers biogeochemical pulses. In drylands, prolonged dry periods between rain events or seasonal droughts are followed by marked increases in soil moisture at rewetting that re-establish microbial catabolic activity and plant gas exchanges (over hours to days), followed by a growth pulse in both microbial communities (hours to days) and plants (days to weeks)<sup>54, 55</sup>. As microbial activity resumes, a pulse of respiration and nutrient release ensues. These pulses are important because they are responsible for a large fraction of the annual greenhouse gas (GHG) exchanges (thus affecting soil carbon stocks) and for supplying nutrients fueling plant productivity<sup>56</sup>. While the occurrence of these pulses is well-known, there remain several open questions: What drives the pulse in microbial activity? Are the pulses of respiration, microbial growth, and nutrient release synchronous, indicating efficient resource use and nutrient retention in the ecosystem? How are pulse dynamics changing with the ongoing increasing precipitation variability and lengthening of dry periods?

Heterotrophic respiration pulses are caused by several simultaneous processes, ranging from mineralization of dissolved organic compounds accumulated during the dry period, to consumption of microbial byproducts or necromass, to physical disruption of aggregates that were protecting organic matter during the dry period<sup>57</sup>. These processes are intensified by large changes in moisture after a long dry period, leading to the hypothesis that ongoing increasing precipitation variability is increasing the contribution of respiration pulses in drylands<sup>58</sup>. Importantly, microbial growth at rewetting might be de-coupled from respiration, as microbial growth recovery often lags behind respiration after long dry periods<sup>59</sup>. This could lead to larger carbon and nutrient losses as dry periods lengthen, because carbon and nutrients are not efficiently retained in the microbial

biomass. However, microbial communities can adapt to increasing precipitation variability, thereby tightening carbon and nutrient cycles<sup>59</sup>.

As microbes are reactivated at rewetting, nitrogen and phosphorus mineralization rates increase<sup>60</sup>. The released inorganic nutrients can be leached, volatilized, or taken up by plants. If mineralization is faster than uptake, nutrients can accumulate (e.g., nitrate) and be lost<sup>61</sup>. It is therefore critical for the retention of nutrients that microbial and plant activity are synchronized, but that is often not the case, especially after a dry season or long dry period when plant recovery is much slower than microbial recovery<sup>55</sup>. Moreover, with increasing aridity, geochemical and biological processes are likely to change at different rates, promoting for example phosphorus accumulation due to continued weathering when plant phosphorus uptake is low, and nitrogen depletion as organic matter production and mineralization are both inhibited under dry conditions<sup>62</sup>. Therefore, ongoing precipitation intensification and lengthening of dry periods can decouple nutrient availability and utilization, as well as create nutrient imbalances, thereby promoting nutrient losses and negatively affecting dryland productivity.

#### *Fog and dew impacts on vegetation and ecosystem functions*

With water being the predominant limiting resource in drylands, the form, rate, and timing of water input are crucial to how ecosystems can utilize and respond to water availability<sup>63</sup>. While the role of rainfall is undisputed, in many dryland regions, small but critical amounts of fog and dew are also essential for ecosystem productivity and function<sup>64, 65</sup>. Fog and dew are the least studied components of the hydrological cycle in drylands<sup>8</sup>. Overlooking these non-rainfall components could lead to inaccurate results. For example, climate warming experiments commonly use infrared heater warming systems to simulate warming conditions, which can greatly reduce dew formation<sup>66</sup>.

Although the input of dew and fog is rarely a limiting factor for species or biome distributions, it can have a measurable impact on carbon and water fluxes by increasing the leaf water potential and impacting the temperature, albedo, and local vapor pressure deficit (VPD) of the canopy, and providing a latent heat ‘sink’<sup>67</sup>. Fog and dew allow plants to retain more moisture in cells and soil moisture remains higher, increasing plant resilience during hot and dry conditions<sup>65</sup>. There is also a long history of human utilization of fog and dew to meet societal needs<sup>68</sup>. Fog harvesting systems in the Atacama desert of Chile and Peru have been used for water supply and crop irrigation<sup>69</sup> and there are reports of natural dew collection in other desert ecosystems such as the Negev of Israel<sup>70</sup>.

Despite the importance of fog and dew to the functioning of different dryland ecosystems (Supplementary Fig. 1), there are important gaps in knowledge regarding the magnitude of fog and dew formation under different climatic conditions and the extent that fog and dew impact the water, carbon, and energy fluxes at the canopy scale. Research has largely focused on a limited number of field measurements at the leaf or plant levels. Lack of knowledge of the canopy-scale effects of fog and dew makes it difficult to constrain the degree of fog and dew contribution to ecosystem functioning and evaluate the effects of climate change on water limitations. In fact, rising nighttime

and daytime VPD with climate warming<sup>71</sup> is expected to generate a global-scale decline in fog and dew occurrence and duration<sup>66, 72</sup>, possibly contributing to the increasing water constraints on vegetation growth across diverse biomes observed over the past 30 years<sup>37</sup>.

### *Dryland bistability and desertification*

The response of dryland ecosystems to changes in climate and land use may be non-linear and undergo relatively abrupt and often irreversible transitions to a different configuration, suggesting that the underlying dynamics might have two (alternative) stable states. Such a bistable behavior is typically attributed to positive feedbacks between vegetation and the physical environment<sup>73</sup>. For instance, plants can modify the surrounding environment, creating their own habitat. This phenomenon is widespread in drylands where plants can reduce soil erosion, enhance infiltration, enhance fog and nutrient deposition, or prevent soil salinization, thereby favoring their own survival and growth<sup>73, 74</sup>. As a result of these feedbacks, dryland ecosystems have a limited resilience: if disturbed beyond a critical threshold, they can shift to an undesirable state characterized by land degradation, and loss of ecosystem services or productivity<sup>39</sup>.

The term desertification is often used to denote the critical transition of dryland ecosystems to undesirable ‘desert-like’ conditions<sup>75, 76</sup>. This notion suffers from inherent ambiguity, resulting from the fact that desert landscapes can be very different and the shift to desert-like conditions can result from a variety of drivers and processes. Desertification may consist of a loss of soil productivity due to erosion, salinization, or soil toxicity. It may also result from aridification trends sustained by vegetation loss, or from shifts in plant community composition associated with woody plant encroachment or biological invasions<sup>75</sup>. However, some of these undesired shrubland states may have higher productivity and biodiversity than their grassland counterpart<sup>77</sup>. Thus, ‘desertification’ and ‘land degradation’ often refer to a loss of ecosystem services and economic productivity and not necessarily a shift to ecologically unproductive states<sup>75</sup>. Overall there is some ambiguity in what desertification actually entails, which is partly contributed by the inconsistent definitions of this phenomenon<sup>75, 78</sup>.

### *Regional differences in dryland productivity changes*

Depending on the major geographic and hydroclimatic factors determining dryland occurrence, drylands may respond differently to climate change. Regions with divergent air masses and subsiding air such as the subtropics (e.g., the Sahel, the Arabian Peninsula, the Kalahari, Central Australia, and the Chihuahuan and Sonoran Deserts) are expected to become drier under climate warming, a phenomenon that has been ascribed to (a) the enhancement of existing subtropical aridity zones and/or (b) the poleward expansion of the subtropics, a phenomenon that is stronger in the Southern Hemisphere<sup>79</sup>. Other drylands such as those in central Asia are located far from ocean sources of atmospheric moisture (the so-called “continentality effect”). Because local transpiration can be an important contributor to atmospheric moisture in these drylands, their precipitation regime can be altered by local vegetation cover and land use changes. Coastal deserts



(e.g., the Namib and the Atacama) exhibit frequent water inputs through fog and dew. In such systems changes in fog and dew regimes are expected to drive changes in ecosystem productivity. Specifically, the amount of fog and dew water input is expected to decrease as a result of climate warming and its effects on condensation. The productivity of some drylands is co-limited by water and temperature (e.g., the Qinghai-Tibetan plateau, the Gobi Desert, and the Chihuahuan Desert). As such, productivity in these regions could benefit from warming (at least in the short term). For other dryland regions where snowmelt from high mountain chains is the primary source of recharge (e.g., western South America and western North America), warming leads to an increase in the fraction of precipitation falling as rain compared with snow, resulting in a decline in spring and summer streamflow, groundwater recharge, and seasonal water storage in these regions<sup>80</sup>. Dryland soil and land management may also play a role in determining regional differences and divergent responses of drylands to climate trends (more details are in Supplementary Notes 1).

### **Dryland agriculture, grazing and land cover changes**

Some drylands are considered ‘marginal lands’ because they exhibit relatively low ecosystem productivity or biodiversity<sup>81</sup>. However, agricultural and natural ecosystems differ in productivity. Agriculture in drylands can be productive due to irrigation and fertilization. Indeed, drylands sustain livelihoods and wildlife, and also provide a sense of place to rural communities, including indigenous peoples that have stewarded these lands under communal or traditional uses for generations. Dryland agriculture supplies much of the world’s food and fibers, providing about 44% of the global agricultural land and 60% of global food production<sup>82</sup>. Nevertheless, the dependence of primary productivity on water resources may limit crop production in drylands, where reliable and sufficient water availability is necessary to stave off the effects of water and heat stress and achieve high and stable crop yields. Thus, yield gaps are often high in drylands, particularly in rainfed agriculture<sup>83</sup>.

Cropland area in drylands has increased by about 10% from 2003 to 2019 (Fig. 5), as a result of both local needs and global markets through international trade<sup>84</sup>. This global telecoupling between crop demand and production regions is associated with a global displacement of land use<sup>85</sup>. In the aftermath of the 2008 food and financial crisis, large tracts of land worldwide have been targeted by large-scale land acquisitions (LSLAs), allegedly with the aim of increasing food and energy production or curbing GHG emissions, though oftentimes for mere financial speculation<sup>86</sup>. In the last few decades, cropland and rangeland in North and sub-Saharan Africa, South America and central and southeast Asia have expanded at the expenses of natural ecosystems (Fig. 5), to some extent as a result of LSLAs<sup>87, 88</sup>. In the mid-latitude drylands of Russia, Ukraine, and Kazakhstan, land investors have restored abandoned croplands to their previous agricultural use. LSLAs are also contributing to a transition from small scale/subsistence farming to large-scale commercial agriculture in dryland regions of the developing world. These transitions may have negative socio-environmental impacts on rural livelihoods, land stewardship, common property regimes, natural capital, water resources, and land degradation<sup>89</sup>.

Dryland agriculture is expected to be negatively affected by climate change, with a decline in both crop and livestock productivity as a result of temperature extremes (hot and cold), decreasing precipitation, lowering groundwater tables, and increasing land degradation<sup>78</sup>. By 2050, under the ‘middle of the road’ socioeconomical pathway (SSP2) at 1.5°C warming, 178 million people are projected to be vulnerable to water stress, drought intensification, and habitat degradation in dryland regions<sup>78</sup>. Climate change will also reshape the global distribution of regions suitable for sustainable expansion of irrigation, while requiring increased annual water storage capacity<sup>90</sup>. Despite these challenges, drylands are expected to remain crucial for global food and bioenergy production, with further expansion of agriculture and intensification of existing crop production, mostly in the tropics<sup>78</sup>. Agricultural intensification in drylands will require investments in precipitation conservation and irrigation<sup>91</sup> to improve crop productivity in regions with big yield gaps. Nevertheless, a sustainable expansion of irrigation can be achieved only in semiarid to sub-humid dryland regions, while in drier areas water resources will be sufficient to irrigate only part of the land or meet part of the crop water demand (i.e., deficit irrigation will be needed). Major increases in cropland productivity via irrigation expansion are thus expected in Sub-Saharan Africa and Southern Eurasia<sup>90</sup>, unless inadequate land and water governance prevents investments in irrigation.

In addition to climate change, evolving dietary habits are placing further pressure on cropland and rangeland. Meat consumption in developing countries is expected to increase by 125% from 2005-2007 to 2050<sup>92</sup>. The growth in livestock production observed in the last few decades is projected to continue in the near future and expand to dryland regions of the developing world, e.g., as now occurring in the Asian Dryland Belt<sup>93</sup>. Grazing systems are already threatened by combinations of land degradation, declining grassland productivity, and overgrazing<sup>94</sup>, possibly leading to regime shifts to low productivity states particularly in drylands. Nevertheless, smallholders operating mixed crop-livestock systems in developing countries are projected to remain the main producers of ruminant livestock by 2050<sup>95</sup>.

## **Uncertainties and opportunities**

Here we present the key uncertainties in dryland productivity observation, modeling, and driver attribution. We also highlight the future opportunities.

### *Uncertainties in observing dryland productivity*

Despite recent advances in the study of dryland vegetation, some large uncertainties remain in assessing its productivity. One of the major sources of uncertainty comes from the choice of dryland productivity indicator. For example, while vegetation indices (e.g., Normalized Difference Vegetation Index, NDVI) are sensitive to chlorophyll concentrations and canopy cover fraction, their effectiveness is limited in areas with low vegetation cover and large soil background<sup>96</sup>. Analyses of global vegetation products showed both greening of dryland vegetation and a hidden global browning trend, depending on underlining canopy density<sup>97</sup>. There are also uncertainties

arising from climate variability and the sensitivity of temporal trend analysis to starting and ending periods<sup>25, 98</sup>. Finally, uncertainties in satellite imagery interpretations and lack of high-quality ground observations cause misclassification of land cover types that sustains ongoing debates on changes in dryland vegetation cover<sup>99, 100</sup>.

### *Uncertainties in predicting dryland productivity*

The role drylands play in the global carbon cycle is often evaluated using process-based global terrestrial biosphere models (TBMs), but uncertainties in TBM predictions remain large<sup>101, 102, 103</sup>. For example, the recent model inter-comparison TRENDY v7, based on a suite of 14 TBMs, showed that all models underestimated both mean annual net ecosystem exchange (NEE) and its inter-annual variability when compared with *in situ* CO<sub>2</sub> flux measurements in the Southwestern USA<sup>102</sup>. This NEE underestimate was caused by the models showing a too weak response of vegetation growth and gross primary productivity (GPP) to changes in plant water availability. Moreover, both in Australia and the Southwestern USA, models dramatically underestimated inter-annual variability in GPP (Fig. 6). The uncertainties in the magnitude of the inter-annual variability of net biome production simulated by the TRENDY models for 1900-2018 led to a ~14 PgC spread across models, and no agreement on whether the ecosystem is a net carbon sink or source.

Missing or misrepresented processes in TBMs cause inaccurate long-term carbon uptake and accumulation estimates. Incorrect vegetation sensitivity to changes in water availability undermine predictions of productivity inter-annual variability<sup>101, 102, 103, 104</sup>. Uncertain satellite-derived estimates of plant functional type fractional cover lead to large inter-model spread in dryland productivity and water fluxes<sup>105</sup>. Discrepancies exist also between observed and modelled fractional cover. TBMs generally do capture well the daily to inter-annual variability of dryland *in situ* soil moisture and ET (as a proxy of plant water availability)<sup>103, 106</sup>, but model-data discrepancies remain when considering the partitioning of ET at dryland sites into its constituent transpiration and bare soil evaporation components<sup>106</sup>. Future TBM evaluation studies should test processes related to dryland vegetation composition, structure, and functioning, particularly in relation to plant water uptake and use, and fire dynamics. More elaborated discussion on this topic can be found in Supplementary Notes 2.

### *Uncertainties in understanding dryland productivity drivers*

Despite consistency in broad trends in dryland vegetation changes, large uncertainties remain in explicitly attributing the drivers of observed dryland vegetation dynamics<sup>107</sup>, in part due to the uncertainties in the TBMs used in attribution studies. A number of open questions and source of uncertainties in model estimates remain. How is dryland productivity affected by climate oscillations such as ENSO<sup>107</sup>? To what extent can rising CO<sub>2</sub> ameliorate plant water stress in water-scarce conditions<sup>108</sup>, considering that CO<sub>2</sub> fertilization enhances plant photosynthesis and leaf area (LAI)<sup>109</sup> and transpiring biomass<sup>110</sup>, while also reducing stomatal conductance and thus transpiration per unit leaf area<sup>21, 111</sup>? Does land-atmosphere feedbacks increase the concurrence of

high VPD and low soil moisture, consequently increasing plant water stress and limiting plant growth<sup>112, 113</sup>? In addition, model-based dryland productivity driver analyses do not always agree with remote sensing-based studies<sup>15, 107, 109</sup>, likely because of the lack of integration of high-resolution data with field observations<sup>107</sup>. Understanding the key drivers of dryland vegetation dynamics is urgently needed in the light of the projected increasing drought frequency and severity<sup>114</sup>.

There are also significant biases of prediction models in simulating extreme precipitation<sup>115</sup> and drizzle<sup>116</sup>, with only small improvements of CMIP6 over CMIP5<sup>117</sup> in precipitation modeling. The uncertainty of predicted precipitation also enhances the uncertainty of dryland productivity estimates and predictions into the future. Also, groundwater trends and fluctuations due to climate change and human actions are not well constrained in many drylands<sup>118</sup>. This has large implications on the understanding and projection of dryland functioning, because access to subsurface water, especially groundwater, contributes to dryland productivity<sup>119</sup>.

#### *Future opportunities and research priorities*

While uncertainties remain, there have been significant recent advances in observation technologies, modeling approaches, and statistical tools to quantify vegetation productivity and attribute it more accurately to different drivers. The development of ground observation networks and remote sensing technology focusing on both land cover/land use and vegetation productivity provide unprecedented opportunities for reconciling the differences in trends of dryland vegetation dynamics across spatial scales. The increasingly available ground observations through meteorological and flux tower networks reduce uncertainties from satellite remote sensing retrievals. At the same time, novel satellite-based data allow mapping vegetation structure—not only vegetation greenness (Supplementary Notes 3). TBMs testing, optimization, and developments are under way. Specific processes that require TBM advances include vegetation sensitivity to changes in water availability, a more dryland-specific phenology scheme, disturbance representation, and the relative control of VPD and soil moisture on dryland vegetation productivity. Developments in remote sensing approaches and deployment of networks of *in situ* dryland observations will be crucial in this regard. These steps will increase the reliability of TBMs to predict dryland productivity and the role of drylands in the global carbon cycle, under changing climates.

Beside scientific research, a more holistic dryland management and planning is required to avoid potential degradation. It is imperative that we address these research and management challenges urgently because drylands are an important player in the Earth system, provide essential ecosystem services to human society, and are undergoing dramatic, and potentially irreversible, changes due to climate trends and land use. New observational platforms and rapidly improving process-based models that offer novel insights on the complexity of dryland dynamics can help reduce uncertainties and suggest ways to overcome these challenges.

## Data Availability

The Advanced Very High Resolution Radiometer GIMMS-NDVI3g is available at <https://ecocast.arc.nasa.gov/data/pub/gimms/3g.v0>. Global Land Surface Satellite (GLASS) LAI could be obtained from <http://www.glass.umd.edu/Download.html>. Aridity index dataset is available at <https://cgiarcsi.community/data/global-aridity-and-pet-database/>. Moderate Resolution Imaging Spectroradiometer (MODIS) based EVI and GPP datasets are available at are available from the NASA Land Processes Distributed Active Archive Center at <https://lpdaac.usgs.gov>. MODIS NPP dataset is available from <https://lpdaac.usgs.gov/products/mod17a3hgv006>. Ku-band VOD datasets are available from <https://zenodo.org/record/2575599#.XyLqfLdME0M>. European Space Agency (ESA) based land use/land cover product is available from <https://www.esa-landcover-cci.org/>. light response function (LRF) based GPP data is available from <https://doi.org/10.17894/ucph.b2d7ebfb-c69c-4c97-bee7-562edde5ce66>. light use efficiency model (EC-LUE) based GPP data could be obtained from <https://doi.org/10.6084/m9.figshare.8942336.v3>. Eddy covariance flux tower data are available for SW US sites from the AmeriFlux database (<http://ameriflux.lbl.gov>) and for Australian sites from the FLUXNET 2015 database (<https://fluxnet.org/data/fluxnet2015-dataset/>). More information on the TRENDY MIP and related simulations is available at <https://sites.exeter.ac.uk/trendy/>.

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## Competing Interests

The authors declare no competing interests.

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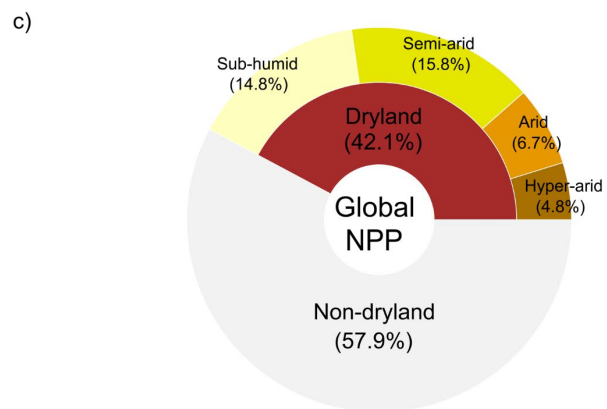
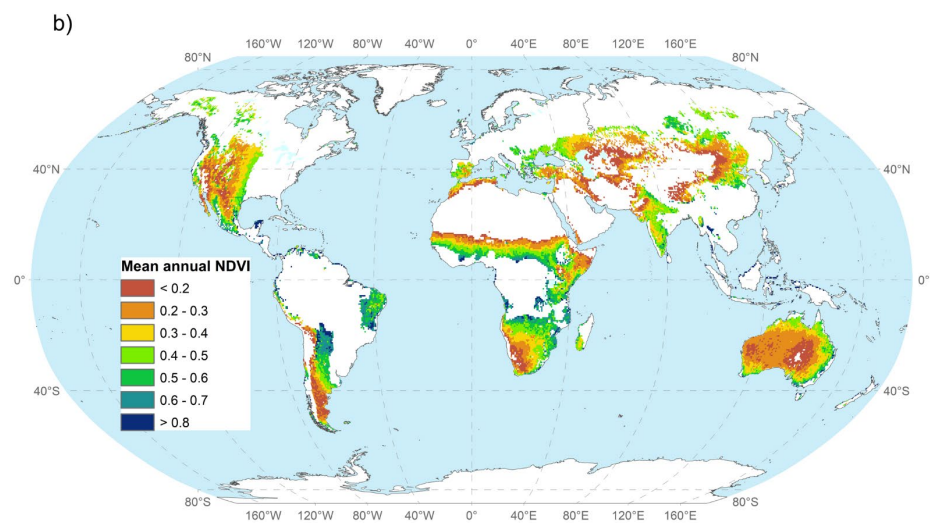
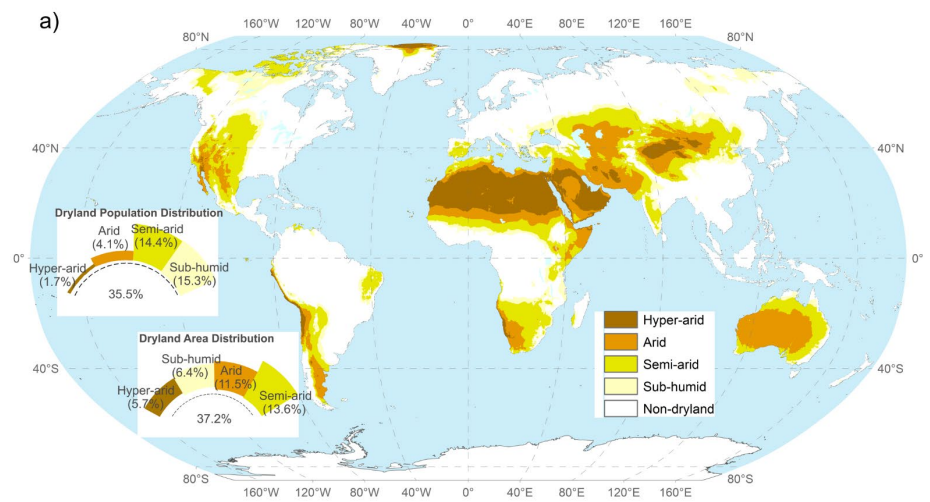
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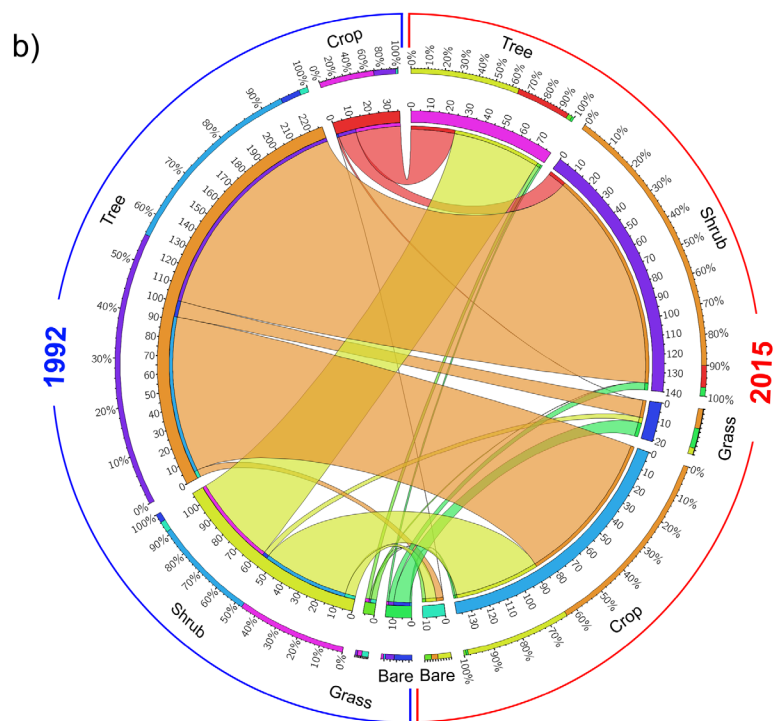
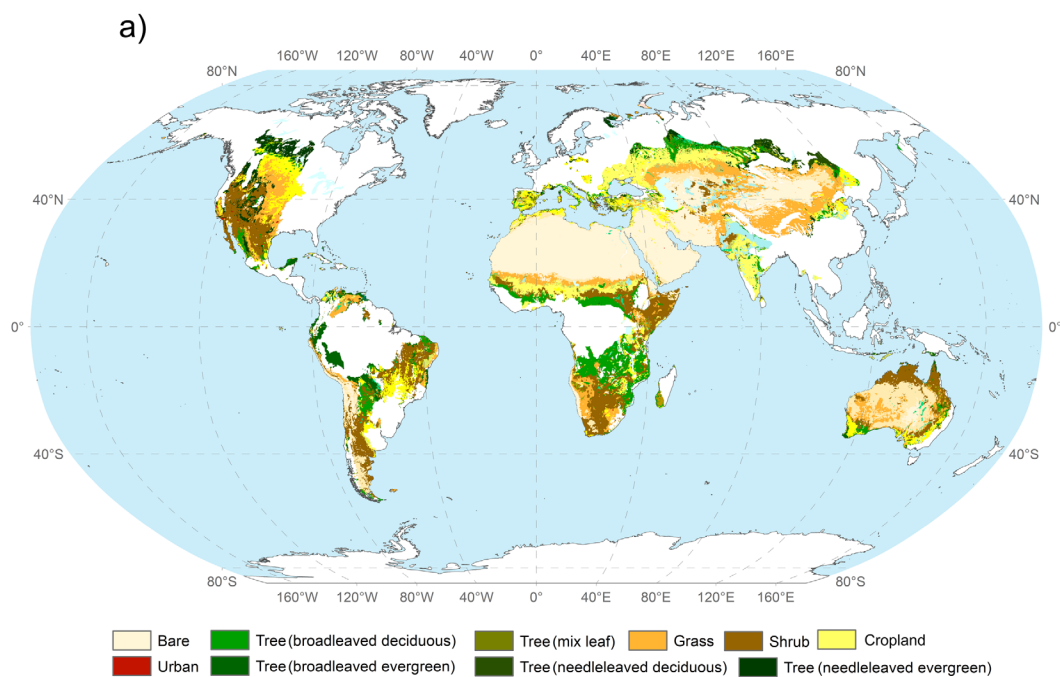
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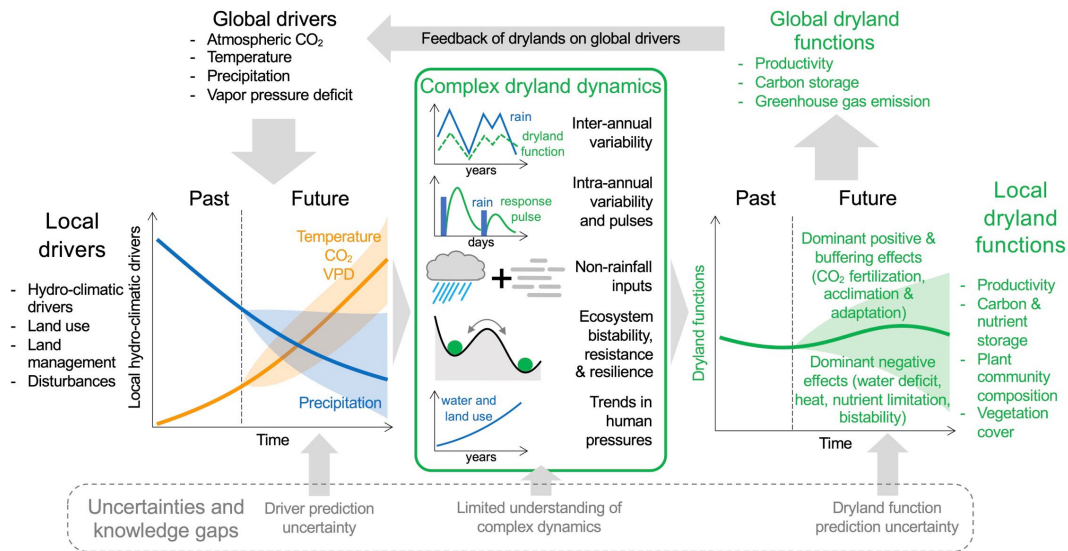
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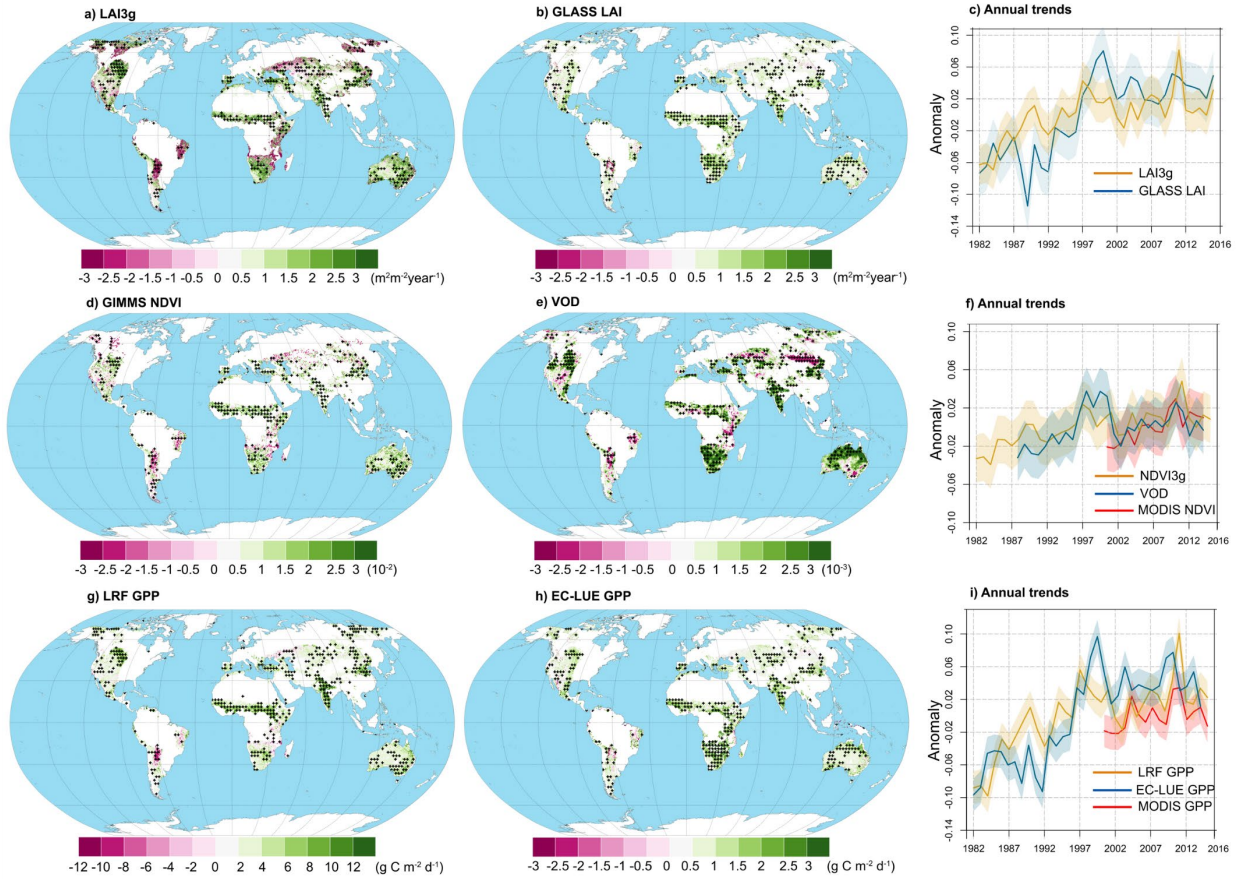
**Fig. 1. Global dryland distributions, dryland vegetation greenness and dryland productivity.** The global distribution of drylands of different aridity classes and the percentages of the global population they support (a). Mean dryland vegetation greenness as indicated by the Normalized Difference Vegetation Index (NDVI) from Moderate Resolution Imaging Spectroradiometer (MODIS, MOD13C2 product, 2000-2020) (b). The percentage of net primary productivity (NPP) of different aridity classes in comparison to the global NPP (MODIS, MOD17A3 product, 2000-2020) (c).



**Fig. 2. Global dryland land-use and land-use changes.** a) indicates the spatial distribution of the major land-use/land-cover types in 2015. Land-use/land-cover data is from European Space Agency (ESA) Climate Change Initiative (CCI). The circos plot of b) shows the land-use/land-cover change from 1992 to 2015. The color of the outside circle indicates the percentage of land cover change, the first-layer inner circle color represents the land use type in the corresponding year, the second-layer inner circle indicates the changed land cover area in the unit of 1,000 km<sup>2</sup>. Colored flows show pathways of land-use transitions from 1992 to 2015. For example, ~220,000 km<sup>2</sup> of the tree covered regions are converted into other land cover types between 1992 and 2015 (orange color in the interior circle). Among all the converted tree cover regions, 56% of the decreased tree cover regions (purple color for the outside circle for the “Tree cover” region in 1992) are changed into shrubland in 2015. Of all the added shrubland in 2015, 90% is from regions that were tree covered in 1992 (orange-colored outside circle for “Shrub” region in 2015) and 10% are from regions that were cropland in 1992 (red-colored outside circle for “Shrub” region in 2015).

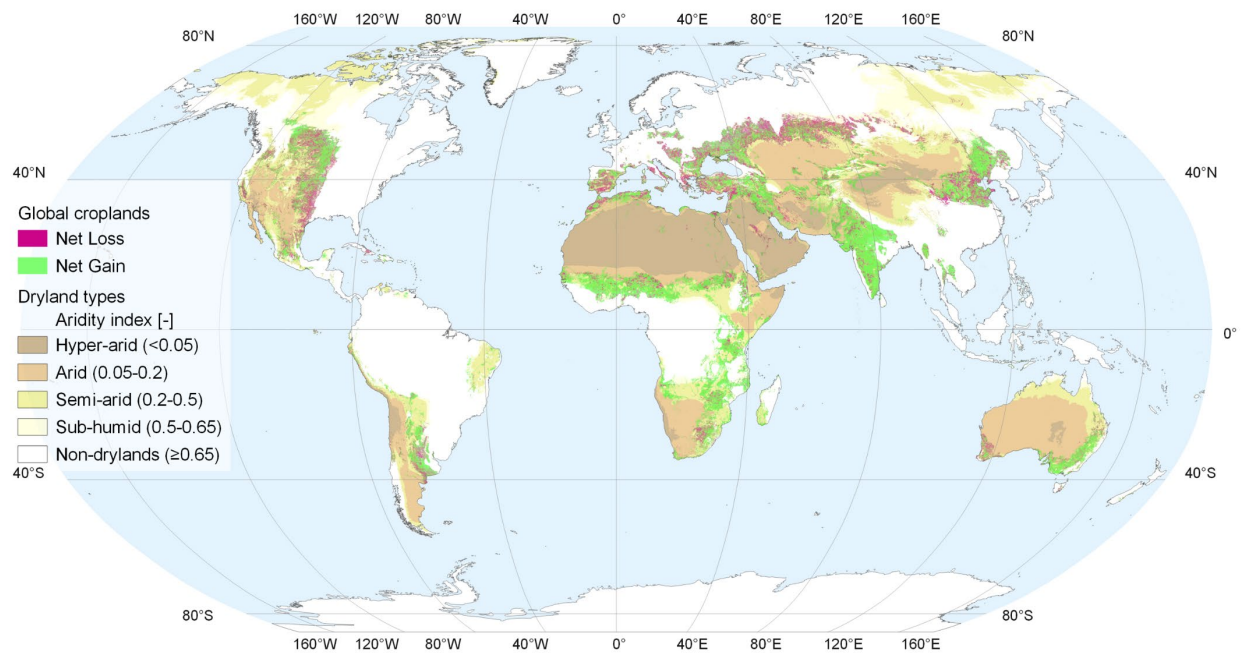


**Fig. 3. The key drivers and major uncertainties of dryland dynamics.** The complexity of dryland dynamics is elucidated in the central panel. These complexities interact with local and global climatic, ecological, and land management drivers (schemes on the left), and ultimately determine dryland productivity and functions in current and future climates (schemes on the right). The often-neglected major uncertainties in observations and predictions of dryland productivity are highlighted at the bottom.



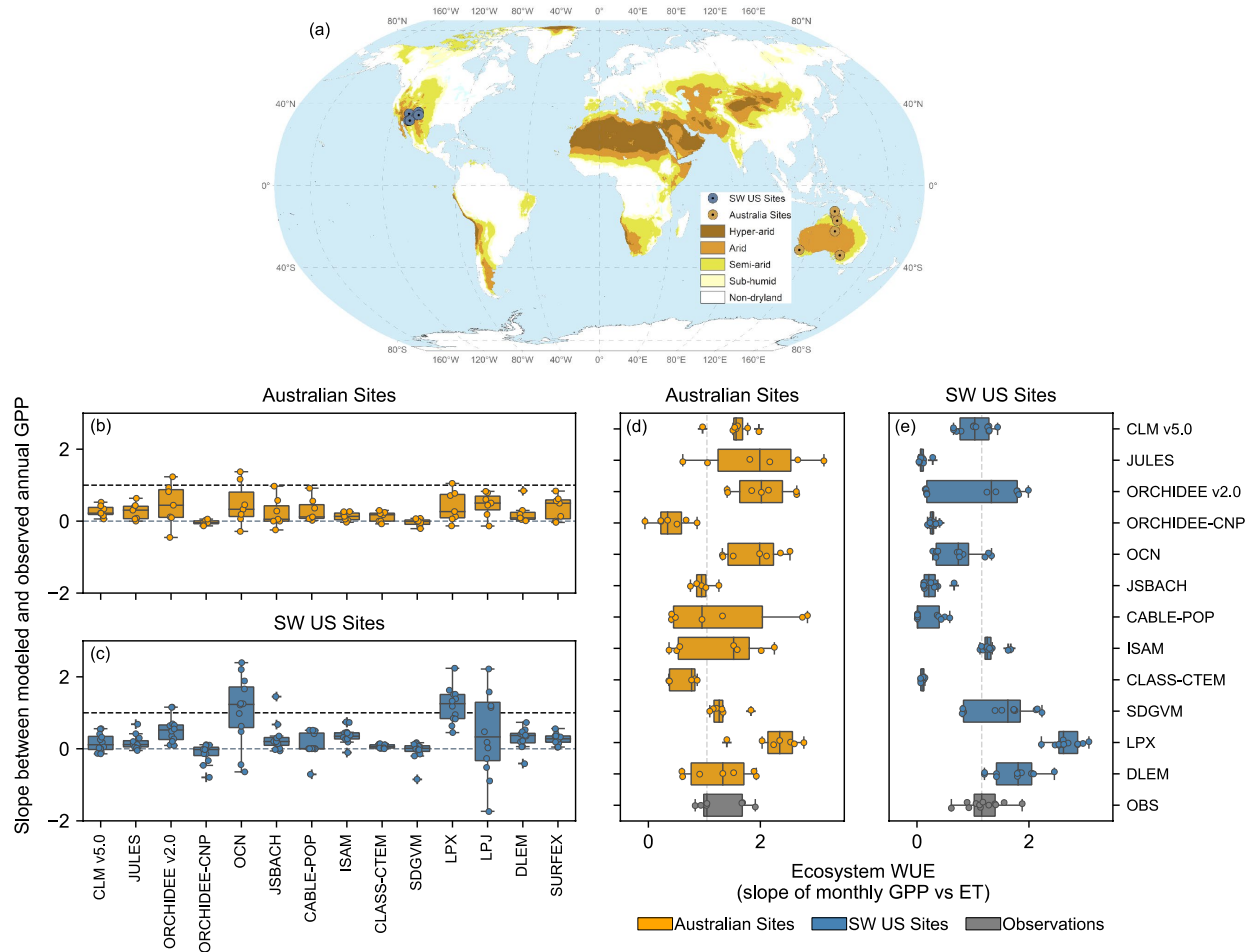
**Fig. 4. Global dryland vegetation trends.** a), b), d), e), g), h) represent the spatial distribution of vegetation productivity trends (i.e., slopes of productivity-time relationships) indicated by Global Inventory Modeling and Mapping Studies (GIMMS) Leaf Area Index (LAI3g), Global Land Surface Satellite (GLASS) LAI, GIMMS Normalized Difference Vegetation Index (NDVI3g), Vegetation Optical Depth Climate Archive (VOD), Moderate-resolution Imaging Spectroradiometer (MODIS) NDVI, Light Response Function (LRF) based gross primary production (GPP), Eddy Covariance and Light Use Efficiency based GPP (EC-LUE GPP), respectively; c), f), and i) show the trends of annual mean global dryland productivity anomaly (z-score) based on different products. Dots in the spatial maps indicate significance at  $\alpha = 0.05$ .





**Fig. 5. Cropland gain and loss between 2003 and 2019 in global drylands.** The cropland gain and loss data are taken from<sup>120</sup> and the aridity data are taken from<sup>121</sup>. Cropland area in drylands has increased by about 10% from 2003 to 2019.





**Fig. 6. Dryland productivity modeling uncertainties.** A comparison of annual gross primary productivity (GPP) and water use efficiency (WUE) from a suite of global terrestrial biosphere models (TBMs) from the TRENDY v7 model intercomparison project against eddy covariance data from 19 flux tower sites in Australia (orange symbols and bars) and the southwestern US (SW US, blue symbols and bars). Site locations are shown in map (a). (b) Slope of the linear regression between annual GPP simulated by all 14 TRENDY v7 models and observed annual GPP across all Australian sites. (c) Same as (b) but for Southwest (SW) US sites. The slopes are close to zero, indicating the inter-annual variability was not well captured by the models. (d) Slope of the relationship between monthly GPP ( $\text{gC m}^{-2} \text{month}^{-1}$ ) and monthly ET ( $\text{mm month}^{-1}$ ) (i.e., a measure of ecosystem water use efficiency, WUE) across all months and all Australian sites for 12 of the TRENDY v7 models (orange bars) compared to the observed ecosystem WUE in grey bars. (e) Same as (d) but for SW US sites. Australian sites included AU-ASM, AU-Cpr, AU-DaS, AU-Dry, AU-Gin, AU-How and AU-Stp and the GPP and ET data were taken from FLUXNET 2015 database<sup>122</sup>. Southwest US sites include US-Fuf, US-Mpj, US-Wjs, US-Vcm, US-Vcp, US-Ses, US-Seg, US-Aud, US-SRM, US-SRG, US-Wkg, and US-Whs and the GPP and ET data were

obtained from the site PIs (see ref. <sup>102</sup> for further details on data processing and for the full list of site names, see Supplementary Table 1). TRENDY TBMs include CLM v5.0, JULES, ORCHIDEE v2.0, ORCHIDEE-CNP, OCN, JSBACH, CABLE-POP, ISAM, CLASS-CTEM, SDGVM, LPX, LPJ, DLEM and SURFEX. TRENDY v7 S3 simulations were used, which include changing climate forcing, rising atmospheric CO<sub>2</sub> concentrations, and land use change (see ref. <sup>102</sup> for further details).

## **TITLE**

Dryland productivity under a changing climate

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## SUPPLEMENTARY INFORMATION

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## I. SUPPLEMENTARY NOTES

### Supplementary Note 1 | Regional differences in dryland productivity changes

Dryland soil may also play a role in determining regional differences and divergent responses of drylands to climate trends and land use change. Some dryland soils (e.g., Loess Plateau in China, the Great Plains in the USA, the Southern Kalahari in Southern Africa, or the Mallee in Australia) are prone to erosion. In these regions, the exposure of the soil surface to the erosive action of wind and water because of drought, cultivation or overgrazing are expected to exacerbate topsoil losses, thereby leading to a decline in plant productivity.

Land management is another major factor dictating regional differences in dryland response to climate change. For instance, China's drylands are likely undergoing some of the most extensive desertification reversal efforts in the world. From 1978 to 2015, 13 national dryland conservation and restoration programs have been implemented, covering almost 60% of the total dryland area in China<sup>1</sup>. Such programs include the Great Green Wall and the Grain for Green Program, with a cumulative investment of US\$67.92 billions (in 2015 US\$) from 1978 to 2015<sup>1</sup>. These programs have contributed to dryland greening across China. Similar afforestation efforts have been planned and are ongoing across the Sahel. Separating the CO<sub>2</sub> fertilization effect from the effect of human management (e.g., afforestation) on dryland greening in these heavily managed systems is challenging but a necessary step to better understand and predict shifts in dryland productivity in a changing world. Dryland management approaches have also been proposed to increase carbon sequestration, via nature-based solutions such as tree restoration<sup>2</sup>. Vast regions worldwide have been reported to have good tree restoration potential with drylands accounting for up to 36%-42% of potential restoration area<sup>3</sup>. However, dryland biomes have been recognized as inappropriate regions for expanding tree cover because of issues related to biodiversity loss and water overconsumption<sup>4</sup>. Additionally, there is evidence that tree cover is often underestimated in dryland regions<sup>3, 5</sup>, suggesting that drylands' potential for tree recovery is largely overestimated.

## Supplementary Note 2 | Uncertainties in predicting dryland productivity

Uncertainties in terrestrial biosphere models (TBMs) are likely caused by missing or misrepresented processes, which in turn result in incorrect description of vegetation sensitivity to changes in soil water availability<sup>6, 7, 8, 9</sup>. Model discrepancies in dryland productivity estimates may be induced by inaccurate timing of modeled seasonal leaf phenology<sup>7, 9, 10</sup>, errors in the prescribed or predicted vegetation composition<sup>7, 9</sup>, or potential limitations in the modeling of plant water uptake and use with changing soil moisture profiles. TBM phenology schemes are typically not well adapted to dryland plant functional types and should be updated<sup>11</sup>. Models that prescribe exponential rooting profiles for all vegetation types cannot represent water uptake from deep tap roots, which is a common strategy utilized by some plants in water-limited ecosystems; thus, for some dryland species, models likely underestimate dry season plant water uptake.

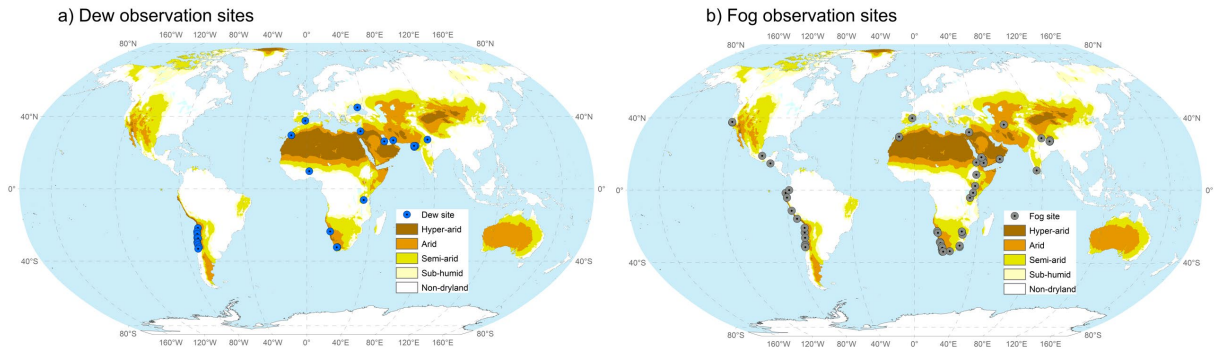
Model predictions of plant functional type fractional cover in drylands are also uncertain, causing large inter-model spread in both carbon and water cycling metrics<sup>12</sup>, and discrepancies between satellite-derived fractional cover estimates and outputs from TBMs. Both *in situ* and satellite fractional cover estimates are typically a spatiotemporal average of often highly-variable dryland vegetation and bare soil cover; however, the models require the maximum possible vegetation cover and rely on climate variability and resource limitation to limit plant growth. One possibility is that the prescribed observed vegetation fractions are underestimated, and that dryland model discrepancies arise in part because of a lack of seasonal dynamic changes in vegetation cover.

Besides uncertainties in modelling of the water cycle in drylands, other processes introduce additional uncertainties. Misrepresentations of fire dynamics have been highlighted as a key issue impacting modeled carbon fluxes<sup>9</sup>. The lack or incomplete development and testing of modeled nutrient limitations on photosynthesis is also likely a key source of biases in modeled dryland productivity<sup>13</sup>. To improve predictions, model advances in describing water availability and flows in vegetation, and fire dynamics are required. These model developments and subsequent testing will be facilitated by novel plant moisture related datasets (e.g., sap flow<sup>14</sup>, leaf and soil water potential measurements) and higher resolution remote sensing data.

### **Supplementary Note 3 | Future opportunities and research priorities**

In addition to ground-based observations and traditionally widely-used optical-based satellite datasets, new datasets such as thermal, microwave, hyperspectral, and Light Detection and Ranging (LiDAR) provide new insights into dryland structural and functional dynamics<sup>15</sup>. The application of recent ultra-high resolution remote sensing images from different platforms with high-performance computing and cloud-based data processing strategies, provide a promising path to dramatically increase the vegetation monitoring resolution on drylands<sup>16</sup>.

## II. SUPPLEMENTARY FIGURES



**Supplementary Fig. 1| The global distribution of dew (A) and fog (B) studies in drylands.** The data is from<sup>17</sup>. Fog and dew have been studied widely at a global scale but large knowledge gaps exist. Please refer to the main text for detailed description.



### III. SUPPLEMENTARY TABLES

**Supplementary Table 1 | The complete site information of the Australian and US flux tower sites used in comparison between observations and modeling.**

Site	Site full name	Reference link
AU-ASM	Alice Springs Mulga	<a href="https://fluxnet.org/doi/FLUXNET2015/AU-ASM">https://fluxnet.org/doi/FLUXNET2015/AU-ASM</a>
AU-Cpr	Calperum	<a href="https://fluxnet.org/doi/FLUXNET2015/AU-Cpr">https://fluxnet.org/doi/FLUXNET2015/AU-Cpr</a>
AU-DaS	Daly River Cleared	<a href="https://fluxnet.org/doi/FLUXNET2015/AU-DaS">https://fluxnet.org/doi/FLUXNET2015/AU-DaS</a>
AU-Dry	Dry River	<a href="https://fluxnet.org/doi/FLUXNET2015/AU-Dry">https://fluxnet.org/doi/FLUXNET2015/AU-Dry</a>
AU-Gin	Gingin	<a href="https://fluxnet.org/doi/FLUXNET2015/AU-Gin">https://fluxnet.org/doi/FLUXNET2015/AU-Gin</a>
AU-How	Howard Springs	<a href="https://fluxnet.org/doi/FLUXNET2015/AU-How">https://fluxnet.org/doi/FLUXNET2015/AU-How</a>
AU-Stp	Sturt Plains	<a href="https://fluxnet.org/doi/FLUXNET2015/AU-Stp">https://fluxnet.org/doi/FLUXNET2015/AU-Stp</a>
US-Fuf	Flagstaff	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Fuf">https://ameriflux.lbl.gov/sites/siteinfo/US-Fuf</a>
	Mountainair Pinyon-Juniper	
US-Mpj	Woodland	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Mpj">https://ameriflux.lbl.gov/sites/siteinfo/US-Mpj</a>
US-Wjs	Willard Juniper Savannah	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Wjs">https://ameriflux.lbl.gov/sites/siteinfo/US-Wjs</a>
US-Vcm	Valles Caldera Mixed Conifer	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Vcm">https://ameriflux.lbl.gov/sites/siteinfo/US-Vcm</a>
US-Vcp	Valles Caldera Ponderosa Pine	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Vcp">https://ameriflux.lbl.gov/sites/siteinfo/US-Vcp</a>
US-Ses	Sevilleta shrubland	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Ses">https://ameriflux.lbl.gov/sites/siteinfo/US-Ses</a>
US-Seg	Sevilleta grassland	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Seg">https://ameriflux.lbl.gov/sites/siteinfo/US-Seg</a>
US-Aud	Audubon Research Ranch	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Aud">https://ameriflux.lbl.gov/sites/siteinfo/US-Aud</a>
US-SRM	Santa Rita Mesquite	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-SRM">https://ameriflux.lbl.gov/sites/siteinfo/US-SRM</a>
US-SRG	Santa Rita Grassland	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-SRG">https://ameriflux.lbl.gov/sites/siteinfo/US-SRG</a>
US-Wkg	Walnut Gulch Kendall	
	Grasslands	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Wkg">https://ameriflux.lbl.gov/sites/siteinfo/US-Wkg</a>
US-Whs	Walnut Gulch Lucky Hills	
	Shrub	<a href="https://ameriflux.lbl.gov/sites/siteinfo/US-Whs">https://ameriflux.lbl.gov/sites/siteinfo/US-Whs</a>

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