Article

Hotspots of biogeochemical activity linked to aridity and plant traits across global drylands

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Perennial plants create productive and biodiverse hotspots, known as fertile islands, beneath their canopies. These hotspots largely determine the structure and functioning of drylands worldwide. Despite their ubiquity, the factors controlling fertile islands under conditions of contrasting grazing by livestock, the most prevalent land use in drylands, remain virtually unknown. Here we evaluated the relative importance of grazing pressure and herbivore type, climate and plant functional traits on 24 soil physical and chemical attributes that represent proxies of key ecosystem services related to decomposition, soil fertility, and soil and water conservation. To do this, we conducted a standardized global survey of 288 plots at 88 sites in 25 countries worldwide. We show that aridity and plant traits are the major factors associated with the magnitude of plant effects on fertile islands in grazed drylands worldwide. Grazing pressure had little influence on the capacity of plants to support fertile islands. Taller and wider shrubs and grasses supported stronger island effects. Stable and functional soils tended to be linked to species-rich sites with taller plants. Together, our findings dispel the notion that grazing pressure or herbivore type are linked to the formation or intensification of fertile islands in drylands. Rather, our study suggests that changes in aridity, and processes that alter island identity and therefore plant traits, will have marked effects on how perennial plants support and maintain the functioning of drylands in a more arid and grazed world.

Drylands are characterized by a sparse plant cover, with patches of perennial plants nested within an ocean of unvegetated bare soil[1,2]. These plant patches and the enriched soil beneath their canopies act as biogeochemical hotspots, critical for the maintenance of plant and animal diversity and essential functions and services related to nutrient mineralization and storage and water regulation[1,3,4]. Dryland vegetation and the 'fertile islands' they create are predicted to be affected by livestock grazing, the most pervasive land use in drylands[5]. Overgrazing by livestock and wild (native) herbivores is known to alter surface soils, suppress the infiltration of water and increase runoff

water and sediment discharge[6,7], potentially intensifying the fertile island effect by exacerbating the loss of resources from the interspaces and its supplementation in nearby islands[8]. Yet, there is little support for this notion, other than studies showing that overgrazing leads to a greater relative effect of woody island soils over interspace soils but that severe overgrazing leads to total collapse[9]. Globally, there is little empirical support for the putative importance of grazing as a causal agent of the fertile island effect[10,11], particularly when considering the wide range of plant types characterizing drylands, from grasses to shrubs and trees. This makes it difficult to disentangle grazing effects
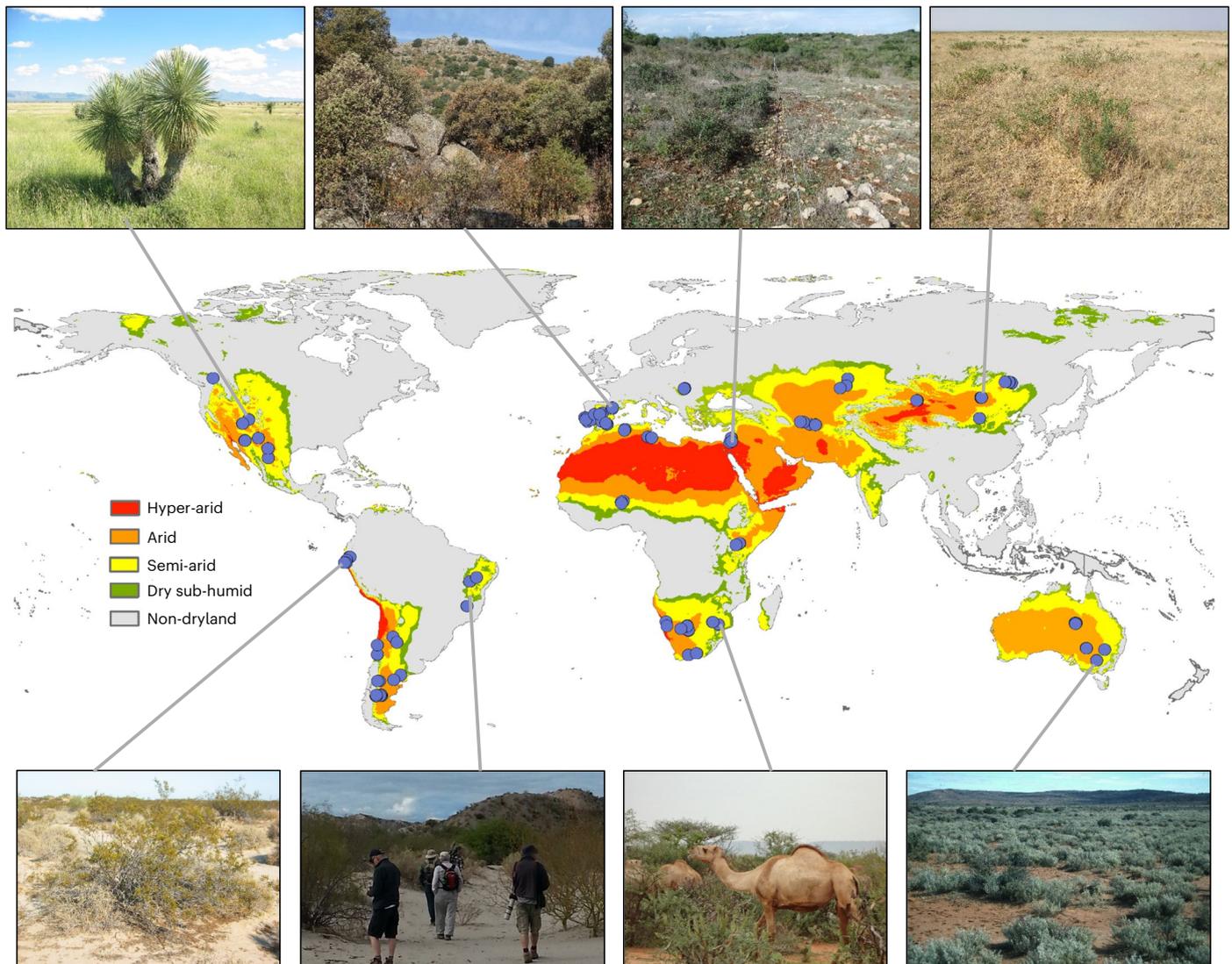
Fig. 1 | Average function for the 288 plots at 88 sites across global drylands and examples of fertile islands at selected sites. The background map shows the distribution of aridity (1 − [precipitation/potential evapotranspiration]) across global drylands. The mean RII value is calculated across 24 soil attributes (Methods).

from the inherent effects of those plants that form the islands. This is an important knowledge gap, as predicted declines in rainfall, changes in the structure of island plants and forecasted increases of grazing over the next century will likely place increasing pressure on drylands and their perennial components, compromising their ability to sustain livestock, people and their cultures[12].

Yet, despite the extensive body of knowledge dedicated to their study, the relative importance of grazing, climate and the traits of the focal island species on the distribution and magnitude of fertile islands across global drylands remains virtually unknown. To address this knowledge gap, we assess the relative association between grazing, plant traits, climate and soil properties, and fertile islands in grazed drylands worldwide. This improves our ability to predict the future of dryland biodiversity and function and can improve the management of perennial vegetation, particularly as grasslands are likely to contract and woody dominated systems increase in a drier and more heavily grazed world[8,13].

In this Article, we examined the fertile island effect by comparing 24 soil physical, chemical and functional attributes beneath the canopy of perennial vegetation compared with their adjacent unvegetated interspaces across global drylands. The 24 attributes were assembled into three synthetic functions that represent the capacity of soils to

mineralize organic matter (Decomposition), enhance fertility (Fertility) and conserve water and maintain stability (Conservation; Methods). We gathered data from 288 dryland sites across 25 countries on six continents (Fig. 1) to test the following two contrasting hypotheses. First, we expected that the magnitude of the fertile island effect would increase with increasing levels of both recent (standardized dung mass) and long-term or historic (heuristic assessment; ungrazed to high) grazing pressure (Hypothesis 1a). This prediction is based on the understanding that greater grazing pressure will destabilize surface soils, mobilizing sediment, seed, nutrients and organic matter from unvegetated interspaces to plant patches, strengthening fertile islands[14,15]. In addition, livestock might be expected to have a greater effect than wild herbivores because they have not co-evolved with indigenous vegetation and therefore have more deleterious effects on both island plants and their soils[6] (Hypothesis 1b). Alternatively, changes in climate and plant traits, factors that operate at much larger (regional and global) scales, could overwhelm the impacts of grazing, a factor that operates at the local scale, on fertile islands (Hypothesis 2a). More specifically, irrespective of grazing pressure, we would expect that plants would make a greater contribution to fertile islands in arid and hyper-arid ecosystems where soils are extremely bare and infertile compared with less arid ecosystems where the influence of
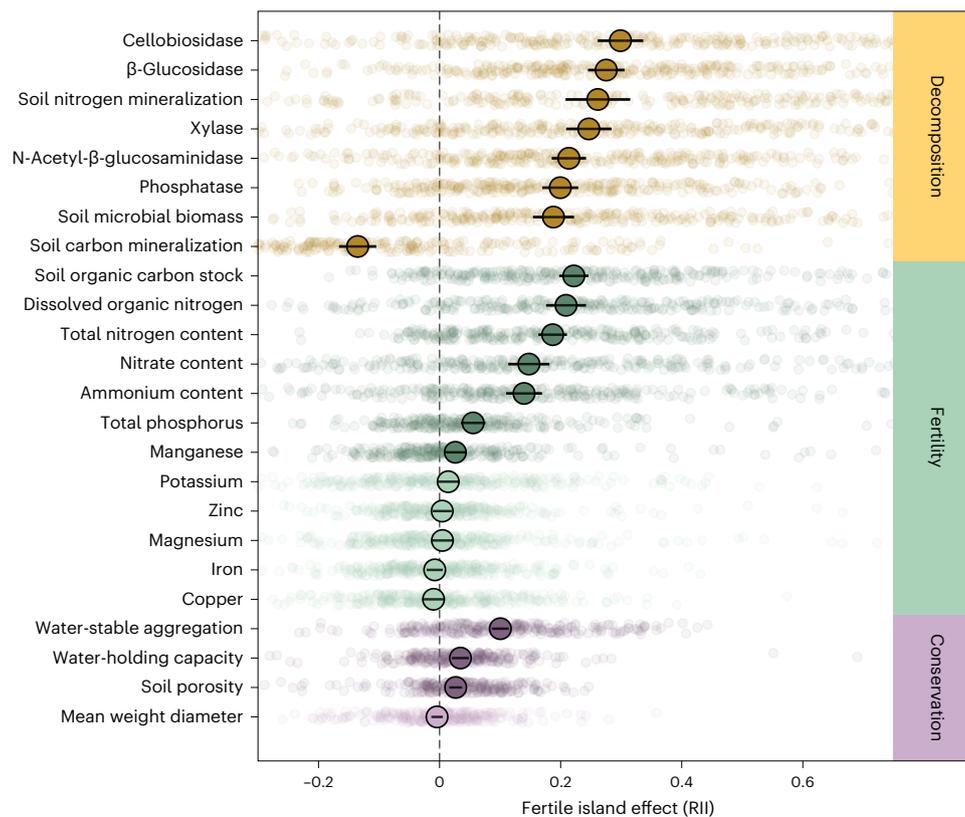
Fig. 2 | The fertile island effect, as measured with the RII, beneath perennial dryland plants for the 24 soil attributes measured across three functions. $N = 288$ for all the attributes; data are presented as mean ± 95% CI, and darker colours indicate significant positive effects.

plants would be relatively lower. For example, reduced rainfall and/or increased temperature would increase the harshness of the interspaces compared with the vegetated and more protected islands, thereby strengthening the fertile island effect. Plant effects might also be expected to vary among broad functional groups (tree versus shrub versus grass; Hypothesis 2b). These broad groups could have varying effects on soil biogeochemistry because of marked differences in shape, size and structural complexity. Quantifying the contribution of grazing by different herbivores at different pressures, plant traits, climate and soil properties on fertile islands allowed us to assess current and future impacts of grazing on ecosystem structure and functioning across global drylands, where woody vegetation is a predominant plant form[12].

Results and discussion

We found stronger associations among factors such as aridity and plant traits (Hypothesis 2) than factors such as grazing pressure (Hypothesis 1a) and herbivore identity (Hypothesis 1b) and the fertile island effect in drylands worldwide. This knowledge is key to contextualize the ecosystem consequences of increased livestock grazing pressure on the capacity of plants to create and maintain hotspots of biogeochemical activity.

Global fertile island effects

Before exploring potential effects of grazing, plant traits or environmental conditions, we examined the relative interaction effect relationships of the 24 attributes distributed among the three synthetic functions. This exploration gives us a better understanding of how individual biogeochemical attributes and their three synthetic ecosystem functions might differ between islands and their interspaces (the fertile island effect). We found strong empirical evidence of a pervasive fertile island effect across all sites and continents and for

16 (67%) of the 24 attributes (Fig. 2). Our results are consistent with findings from empirical local studies revealing greater resource accumulation beneath perennial plant canopies for attributes as diverse as soil geochemistry[11,13,16,17], soil physical properties[9], hydrology[18,19] and microbial community structure[4]. Of all possible effects, the Decomposition function (which comprised C, N and P mineralization), was the most strongly developed function within the islands (Fig. 2), likely due to greater litter inputs[4,20], microbial activity and plant biomass[21] beneath perennial plant canopies[22,23]. The fertile island effect for the other functions was mixed, with strong positive effects for C and to a lesser extent for P, but not for micronutrients (Fig. 2). The fertile island effect for C and N was also greater in more arid drylands. These findings reinforce the view that perennial plant patches are hotspots of biological activity in drylands[4], and this likely accounts for their potential role as facilitators of protégé plant species through resource supplementation[24].

The influence of grazing, island type and plant traits

We then sought to quantify the importance of potential associations among measures of grazing and fertile islands. Using hierarchical linear mixed modelling (Methods), we found no consistent influence of grazing, either recent (standardized grazing pressure) or long-term (ungrazed, low, medium, high) grazing pressure on the mean (overall) fertile island effect (the average standardized value of all 24 attributes shown in Supplementary Table 1). We also found a consistent but extremely weak negative effect of recent grazing pressure on Decomposition, contrary to the results of global meta-analyses[25]. There were no significant effects of increasing recent grazing pressure on either the Fertility or Conservation function (Fig. 3a and Supplementary Table 2). There were no significant effects of long-term (historic) grazing pressure (ungrazed, low, medium, high) on any measures (Supplementary Fig. 1 and Supplementary Table 2).
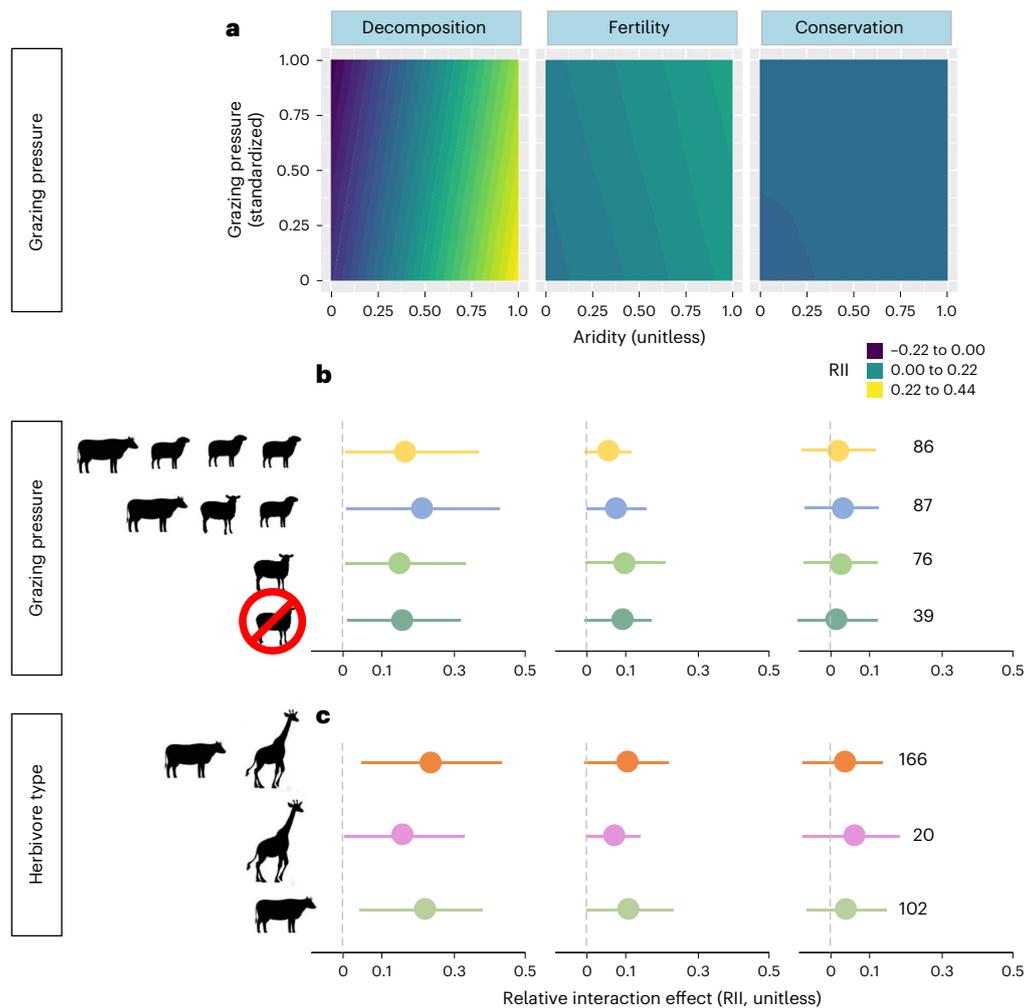
Fig. 3 | Impacts of recent grazing and climate on the fertile island effect.
a–**c**, RII value surfaces for the three measures of ecosystem function (Decomposition, Fertility, Conservation) in relation to recent grazing pressure (standardized dung mass) and aridity, and mean (±95% CI) predicted RII value for the three functions (**a**) in relation to long-term (historic) measure of herbivore grazing pressure (ungrazed, low, medium, high) (**b**), and herbivore type (livestock, native, mixed) (**c**). Numbers in **b** and **c** are replicates for each category.

Of all effects, aridity was by far the strongest (Supplementary Table 2), with a strong positive effect on the Decomposition function, weak effects on the Fertility function, but no effect on the Conservation function (Supplementary Fig. 3a and Supplementary Table 2). Although the effects of island type (tree, shrub, grass) were minor compared with the large aridity effect, we did identify some trends. For example, there were consistent positive, although weak, fertile island effects beneath shrubs and to a lesser extent trees, irrespective of grazing pressure. The only other noteworthy grazing-related effect was the negative interaction between shrubs, and to a lesser extent trees, and mixed herbivores (Supplementary Table 2).

Our results provide fresh insights into the links between grazing and fertile islands, demonstrating that, across global drylands, grazing cannot be considered a causal agent of the fertile island effect. Thus, placed in a global context, the local influence of grazing on fertile islands is overshadowed by global environmental variability. This result challenges the view of fertile islands and their formation, which posits that islands are a biproduct of grazing[11]. This view has largely been shaped by studies from the Chihuahuan Desert in the western United States where increases in woody plant (generally shrub) density are linked to a dominance of woody plant islands and ensuing desertification[26]. Undoubtedly, grazing-induced disturbance can aggravate differences between perennial plants and their interspaces in some

situations by disturbing interspaces and intensifying the movement of resources from interspace to island patches[27]. However, neither short- nor long-term grazing pressure nor herbivore type were associated with the fertile island effect under the conditions experienced across our extensive global dryland survey.

Given the importance of plant traits, a random forest algorithm was then used to examine the degree to which a comprehensive suite of 15 functional traits of island woody plant species explained differences in the fertile island effect for the three synthetic functions studied. These traits, which are related to plant size and structure, leaf characteristics and the ability to respond to environmental stimuli (palatability, resprouting, deciduousness, allelopathy; Methods) potentially influence the way nutrients are stored, mineralized and made available to plants and how soil and water are conserved beneath plant canopies[28]. Our trait data, which are a comprehensive dataset gathered across global drylands, were used to evaluate the relative importance of island plant structure. We used site-specific trait values rather than global averages, allowing us to account for potential differences in the morphology of island plants under different grazing pressure, herbivore type and environmental conditions. The extent to which different plant traits affected the three synthetic functions varied depending on the function considered (Supplementary Fig. 4). We found that the relative fertile effect for our three synthetic functions
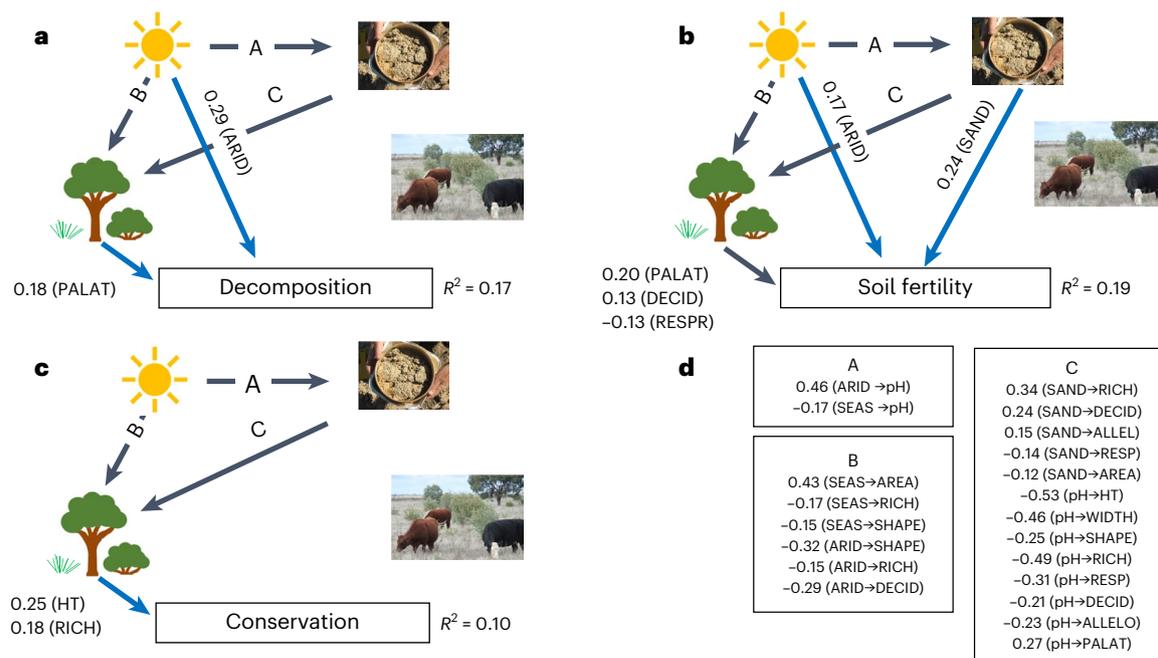
Fig. 4 | SEM assessing direct and indirect effects on the fertile island effect. **a**–**c**, The effects of climate (aridity (ARID), rainfall seasonality (SEAS)), soil (pH and sand (SAND) content), plants (perennial cover (COV), perennial plant richness (RICH)), plant height (HT), plant shape (SHAPE), leaf area (AREA), leaf length (LNGTH), canopy width (WIDTH), palatability (PALAT), deciduousness (DECID), resprouting ability (RESP) and allelopathy (ALLEL)) and grazing (standardized grazing pressure) are considered for soil decomposition (**a**), soil fertility (**b**) and soil and water conservation (**c**) after accounting for the effects of location (latitude, cosine longitude, sine longitude). Standardized path coefficients, adjacent to the arrows, are analogous to partial correlation

coefficients and indicative of the effect size of the relationship. Pathways are significantly negative (red unbroken line), significantly positive (blue unbroken line) or mixed significantly negative and significantly positive (black unbroken lines). Non-significant pathways are not shown in the models. Model fit details are as follows: **a**, organic matter decomposition: $\chi^2 = 31.9$, d.f. = 26, $P = 0.20$, $R^2 = 0.17$, r.m.s.e.a. < 0.001, Bollen–Stine = 0.40 (2,000 bootstraps); **b**, fertility: $\chi^2 = 31.9$, d.f. = 26, $P = 0.20$, $R^2 = 0.19$, r.m.s.e.a. < 0.001, Bollen–Stine = 0.40 (2,000 bootstraps); **c**, conservation: $\chi^2 = 31.9$, d.f. = 26, $P = 0.20$, $R^2 = 0.10$, r.m.s.e.a. < 0.001, Bollen–Stine = 0.40 (2,000 bootstraps). $N = 288$ for all analyses.

was generally greater when the islands were dominated by taller and wider plants and, to a lesser extent, by plants with larger leaves. Plant height was important for all functions, while the Decomposition function responded mostly to plant and leaf size, and the Fertility function was driven mostly by changes in plant size and leaf characteristics (Supplementary Fig. 4).

Direct and indirect drivers of the fertile island effect

We then used structural equation modelling (SEM)[29] to explore potential associations among biotic and abiotic factors and the fertile island effect. Our a priori model (Supplementary Fig. 5) included environmental drivers (aridity, temperature, rainfall seasonality), soil (sand content, pH) and vegetation (perennial plant richness, relative cover of woody plants) properties, plant traits (the nine most important plant traits related to size, leaf characteristics and inherent properties of woody plants such as the type of roots or whether they are allelopathic; identified using the random forest analyses; Methods) and grazing (recent grazing, long-term grazing and herbivore type). Grazing was included to test its potential indirect effects on the relative fertile island effect for the three soil functions evaluated. Our models revealed that decomposition was enhanced in areas of greater aridity (consistent with the hierarchical linear modelling, although not for carbon mineralization; Supplementary Fig. 2) and more sandy soils and where focal island species were more palatable (Fig. 4 and Supplementary Fig. 6). Fertility tended to be greater in sandy soils and with taller palatable species. Soils with larger values of the Conservation function (more stable, with greater water holding capacity) tended to be associated with taller island plants, potentially through mechanisms involving hydraulic lift[30], and at plots supporting more perennial plant species (Supplementary Fig. 6). A potential explanation for the link between the

Conservation function and both plant height and richness could relate to a greater leaf area[31] of larger island plants and therefore reduced surface evaporation[32]. After accounting for all direct and indirect pathways from both abiotic and biotic factors, our SEMs confirm that grazing had no effects on the three functions evaluated.

Among plant traits, plant size (height and canopy) was particularly important, with larger canopies associated with greater relative interaction index (RII) values of all three functions (but only for grasses) and taller grasses with greater RII values of the Decomposition function (Supplementary Fig. 7). Larger grasses are functionally more efficient at capturing resources[33] and enhancing hydrological functions[34,35] and may be a response to declining landscape productivity[36]. Larger plants may be avoided more by herbivores due to higher concentrations of tannins and secondary compounds[37]. Similarly, taller shrubs were associated with larger values of the Conservation and Fertility, but not Decomposition, functions (Supplementary Fig. 7). Taller shrubs would return more litter to the soil surface[38], provide more varied habitat[39] and concentrate more resources excreted by canopy-resident invertebrates[40], potentially accounting for greater fertility[20]. Finally, larger shrubs would support a greater density of understorey protégé species[41] and have a larger legacy effect on soils after death[42]. Interestingly, trees with larger canopies were associated with lower values of the Decomposition and Conservation functions (Supplementary Fig. 7). Large tree canopies are often preferred camping sites for herbivores[39], leading to declines in soil structure[43] and reductions in soil water holding capacity due to the proliferation of surface roots. Our results could suggest a waning of the fertile island effect under large trees.

Overall, our work provides solid evidence that factors such as climate and plant traits can overshadow the influence of factors such as grazing pressure on the capacity of plants to create fertile islands

across global drylands. Our findings indicate that fertile islands will prevail in more arid environments regardless of grazing pressure and the composition of herbivores. In these environments, fertile islands sustain healthy and functional soils and moderate adverse environmental conditions and provide refugia for plants and animals. Our results dispel the long-term assumption that increasing grazing pressure, either recent or longer term, or differences in herbivore type can explain the magnitude of fertile island effects in drylands. Plant size, with taller and wider shrubs and grasses, supported stronger island effects. Stable and functional soils were also linked to species-rich sites with taller plants. The overwhelming importance of aridity and plant traits suggests that fertile islands may represent an autogenic response to drying and warming climates. These biogeochemical hotspots are likely to be more important as Earth's climate becomes hotter and drier.

Methods

Study area

We surveyed 288 plots at 88 sites in 25 countries on all continents except Antarctica (Algeria, Argentina, Australia, Botswana, Brazil, Canada, Chile, China, Ecuador, Hungary, Iran, Israel, Kazakhstan, Kenya, Mexico, Mongolia, Namibia, Niger, Palestine, Peru, Portugal, South Africa, Spain, Tunisia and the USA; Fig. 1). We used the sites described in ref. 12 but excluded 10 sites that did not have sufficient trait data. Site selection aimed to capture as much as possible the wide variety of abiotic (climate, soil type, slope) and biotic (vegetation type, cover and species richness) features characterizing dryland ecosystems (for example, grasslands, shrublands, savannas, open woodlands) found in drylands worldwide[12,44]. Elevation varied between 12 m and 2,214 m above sea level, and slope from 0° to 31.6°. The surveyed sites encompassed a wide variety of the representative vegetation physiognomies, including grasslands, shrublands, savannas and open woodlands (Fig. 1) found in drylands. Sites were surveyed between January 2016 and September 2019[12,44].

Establishing and defining local grazing gradients

At each of the 88 sites, multiple 45 m × 45 m plots were sampled across a gradient in grazing pressure that was determined by local experts and compared with dung counts, livestock tracks and livestock density data when available. Plots were selected from grazing gradients (distance to water measured using geographic information systems) or specific paddocks that represented ungrazed, low, medium or high levels of known grazing pressure. Thirty-five per cent of sites had an ungrazed plot (for example, an exclosure). All plots were established in areas representative of the vegetation and soil types found, so the impacts of grazing pressure could be assessed at each site without confounding factors associated with differences in climate, soil type or vegetation.

Field surveyors, who were all intimately associated with the long-term grazing history of these sites, characterized their plots using this four-scale heuristic category (ungrazed, low, moderate, high). Grazing pressure gradients were confirmed by measuring the mass of herbivore dung in situ[6]. Dung production is known to be closely linked to animal activity, time spent grazing and therefore grazing pressure[45,46], although more studies are needed in arid systems to validate these relationships. To measure dung, we collected the dung of different herbivores from within two 25 m² (where herbivores were large bodied, for example, cattle, horses, large ungulates) or 1 m² (when herbivores were smaller bodied, for example, goats, sheep, rabbit, guanaco) quadrats[44]. Dung was oven dried and expressed as mass per area. Where herbivores produced pellets, dung was counted from different herbivores, a subsample collected and, following oven drying, used to calculate the relationship between counts and oven-dry dung mass (Supplementary Text 1).

The mass of dung from each plot was then used to develop a continuous measure of grazing pressure. Dung mass represents the signature of grazing over periods of 1 year to 5 years, depending on the presence

of detritivores and litter-decomposing invertebrates such as termites and dung beetles[47]. Dung decay rates will also likely vary across our sites due to differences in climatic conditions, the presence of exotic invertebrate decomposers, trampling and other factors[48]. Although these differences could potentially alter the amount of dung detected within a plot, this would have minimal impact on our measure of recent grazing pressure given the standardization process we applied to dung mass across plots within a site.

For each plot, we standardized the value of the mass of dung of all herbivores within a plot by the maximum dung mass at that particular site (collection of plots). Standardized values ranged from 0 to 1 (0.30 ± 0.01, mean ± s.e.) across the 88 sites. A value of 1 for a particular plot indicates that this plot had the greatest grazing pressure for that site, and 0 was ungrazed. This approach to standardizing dung mass within sites ensures the equivalence of sites that might have markedly different levels of dung production, due to variation in site productivity, but have the same level of grazing pressure (for example, moderate grazing pressure). The method has also been validated multiple times in grazing studies[49,50]. Across our global study we recorded 29 different herbivore types, of which 5 were livestock (cattle, goat, sheep, donkey, horse)[12].

Dung mass was a good proxy of grazing pressure using two approaches (Supplementary Text 1). First, there was a significant positive relationship between dung mass and livestock density for a subset of sites in Iran, Australia and Argentina for which we had data on dung mass and animal density[12]. Second, we performed a cluster analysis[51] to identify the optimum number of dung-based clusters, based on dung mass, and found that this aligned well with the four heuristic levels of grazing pressure[12].

Third, we linked the four heuristic measures of long-term (decadal to multi-decadal) grazing pressure to the presence of livestock tracks, semi-permanent features created by livestock when they traverse the same path to and from water[52]. The density and size of these tracks is a useful indicator of the history of livestock grazing[53]. We measured the width and depth of all livestock tracks crossing each of the 45 m transects to derive a total cross-sectional area of tracks for each plot and expressed this as the total track density and cross-sectional area per 100 m of transect (Fig. S8). In summary, these three comprehensive measures of grazing intensity by herbivores showed very similar trends, irrespective of whether we used dung mass as a measure of recent grazing pressure or the expert heuristic site classification as a measure of long-term grazing pressure. This gives us a high degree of confidence that the gradients we observed are true gradients in grazing pressure.

Vegetation and plant trait measurements

Field surveys followed a standardized sampling protocol[44]. Briefly, within each plot, we located four 45 m transects oriented downslope, spaced 10 m apart across the slope, for the vegetation surveys. Along each 45 m transect we assessed the cover of perennial plants, by species, within 25 contiguous 1.5 m by 1.5 m quadrats. Perennial plants were then recorded every 10 cm along this transect to obtain a measure of perennial plant cover. Total plot-level plant richness was calculated as the total number of unique perennial plant species found within at least one of the survey methods (transects or quadrats) used. In each site, we measured the height and lateral spread of five randomly selected individuals of the dominant island plants. Lateral spread (canopy width), a proxy of plant area, was assessed by measuring plant diameter in two orthogonal directions through the plant centre. Fresh leaves were collected from the same plants to assess an additional four plant traits in the laboratory (leaf length, leaf area and leaf carbon and nitrogen contents). These six traits describe the size and leaf characteristic of the 162 perennial species in the vegetation patch that was dominated by trees, shrubs or large perennial grasses and which we assessed as potential fertile islands (see detailed measurements in Supplementary Text 2). Twenty-three per cent of plots supported two co-dominant island species (that is, two different tree, shrub or grass species). For

these plots, soil biogeochemical and plant trait data were weighted according to the mean cover of the co-dominant species within a plot.

We compiled information on eight additional plant traits (that is, plant canopy shape, whether foliage reached the ground surface, N-fixation, deciduousness, allelopathy, palatability, resprouting, root type) using information from online plant trait databases such as BROT[54], PLANTS[55], Woody Plants Database (http://woodyplants.cals.cornell.edu) and TRY[56]. The eight categorical traits above were ranked numerically such that a larger value equated with greater function in terms of its own growth or its facilitatory effect on surrounding neighbours and conditions. This procedure is described in detail in Supplementary Text 2.

Soil properties and sampling
Soils were sampled during the dry season. In each plot, five sampling points were randomly located in open areas devoid of perennial vascular plants (<5% plant cover, hereafter 'open' microsite) and another five placed beneath the canopy of five randomly selected individuals of the dominant island plant (Supplementary Text 3). A composite sample of five 145 cm^3 soil cores (0–7.5 cm depth) was collected from beneath each plant or bare area, bulked and homogenized in the field. Soil samples were air dried for 1 month, sieved (<2 mm) and stored for physico-chemical analyses. The samples were then bulked to obtain one composite sample per plot for vegetated areas (island) and a separate composite sample for open areas. All analyses described here are for two composite samples per plot. We assessed soil pH (1:2.5 soil:water suspension, sand content[57] and the values of 24 soil ecological attributes that are linked to three ecosystem functions (Supplementary Table 1).

Assessment of ecosystem functions
We calculated a RII and its 95% confidence interval[58] for the 24 ecological attributes as measures of the fertile island effect. A positive (or negative) value indicates a greater (or lesser) value of that attribute, respectively, in island soils. The RII is defined as the relative difference between attributes beneath the perennial plant islands and their open interspaces and was calculated as RII $= (X_I - X_O)/(X_I + X_O)$, where X_I and X_O represent the mean values of a given ecological attribute beneath a perennial plant patch (island) and in the open interspace, respectively. Values of the RII range from −1 to 1, with positive values indicating greater levels of a given attribute beneath the island and vice versa. Evidence of the fertile island effect (either positive or negative) is based on whether the 95% confidence intervals (95% CIs), calculated using 'Rmisc' package in R[59], cross the zero line.

We focussed on three proxies of function derived from the average RII of different combinations of the 24 soil attributes: (1) organic matter decomposition, quantified using the activity of five soil extracellular enzymes related to the degradation of organic matter (β-glucosidase, phosphatase, cellobiosidase, β-N-acetylglucosaminidase and xylase) and measurements of soil carbon (hereafter 'Decomposition', (2) soil fertility, evaluated using multiple proxies of soil nutrient availability and carbon (contents of dissolved organic and total N, NH_4^+, NO_3^-, total P, Mn, K, Zn, Mg, Fe, Cu and soil C, hereafter 'Fertility') and (3) resource conservation (water regulation, using measures of soil water holding capacity, soil porosity, stability of macro-aggregates >250 μm and mean weight diameter of soil aggregates (hereafter 'Conservation'). Detailed measurements on these 24 soil ecological attributes are described in Supplementary Table 1.

Data compilation and statistical analysis
Rainfall seasonality (coefficient of variation of 12 monthly rainfall totals) data were extracted from the WorldClim Version 2.0 (http://www.worldclim.org/)[60] database, which provides global climate data (0′30′ × 0′30′) for the 1970–2000 period. Aridity was identified as precipitation/potential evapotranspiration and was derived from the Global Aridity Index and Potential Evapotranspiration Climate

Database v2 aridity database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/)[61], which includes global aridity data (0′30′ × 0′30′) for the 1970–2000 period. Soil texture is a major determinant of water holding capacity, and pH is a major driver of plant and soil function in drylands[62]. Sand content and pH data used in this study were obtained from samples taken from the open areas (to ensure that their effects on the ecosystem functions measured are as independent from those of organisms as possible). Relative woody cover was included to account for different levels of woody plants so that this would not bias any results. Standardized dung mass (dung mass in a plot/maximum dung mass within the site) was used as a measure of recent grazing pressure.

Statistical analyses
We fitted a Bayesian hierarchical linear mixed model to evaluate whether the fertile island effect differed (1) with increasing grazing pressure (continuous data: standardized dung mass), (2) with long-term grazing pressure (categorical data: ungrazed, low, moderate, high grazing) and (3) among herbivore types (categorical data: sites dominated by either livestock, native or mixed groups of native and livestock). Our RII values were modelled with a Gaussian (normal) distribution, with all individual ecosystem attributes (n = 24) estimated simultaneously in a single model. Note that RII values are calculated at the plot level, whereas grazing pressure is calculated at the site level. The standardized response variable (RII) was modelled hierarchically as a function of recent grazing pressure (standardized dung), long-term grazing pressure (high, medium, low, ungrazed), herbivore type (livestock, native, mixed), aridity, island type (tree, shrub, grass), and functional category (Decomposition, Fertility, Conservation). The model fitted individual ecosystem functional attributes as groups (random intercepts) with varying slopes associated with each of the main covariates (grazing and aridity). The model also included interactions between ecosystem function category and grazing, island type and aridity to account for potential differences in the effects of each covariate within each ecosystem function category. We included site as a random intercept, accounting for the non-independence of data gathered from the same site.

We specified weakly informative normally distributed priors for the intercept and all regression coefficients (mean = 0 and scale = 2.5). Default priors were used for sigma (exponential, rate = 1) and variance–covariance matrix of the varying intercepts and slope parameters (shape and scale of 1). Posterior simulations of model parameters were undertaken using the No-U-Turn Hamiltonian Monte Carlo sampler within Stan[63]. Posterior distributions were estimated from four chains, each with 1,000 iterations, after discarding the preliminary 1,000 iterations. The convergence of models was assessed using visual diagnostics (autocorrelation, trace plots and posterior predictive checks) and inspection of effective sample sizes (minimum 1,000) and r hat values (<1.01). Models were fitted using the package 'rstanarm'[64] within R[59]. A hierarchical model provides several benefits over simple averaging of standardized indicators or multiple separate models[65]: (1) simultaneous modelling of multiple attributes improves precision and estimates of uncertainty for each ecosystem function category; (2) non-independence of multiple attributes within sites is explicitly accounted for and (3) it enables simultaneous estimation of overall fertile island effect for each ecosystem functional category and the individual soil attributes within these.

SEM[29] was used to explore the direct and indirect impacts of climate (aridity (ARID), rainfall seasonality (SEAS)), soil pH (pH), sand content (SAND), vegetation attributes (plot-level perennial plant cover (COV) and plant richness (RICH), plant height (HT), canopy width (WIDTH), shape (SHAPE), leaf length (LNGTH), leaf area (AREA), palatability (PALAT), resprouting (RESP), deciduousness (DECID) and allelopathy (ALLELO)) and grazing (standardized grazing pressure) on the fertile island effect (RII) after accounting for the effects of location

(latitude, cosine longitude, sine longitude) across the globe. All explanatory variables were standardized (z-transformed) in the SEM analyses. The nine plant traits used in these analyses were selected from a potential pool of 15 potential traits using the significance of percentage increase in mean square error using random forest analyses (Supplementary Fig. 3). With these analyses, we aimed to determine which traits are the most influential in describing the relative difference between islands and their interspaces (as measured with the RII) for each of the three synthetic functions (Decomposition, Fertility, Conservation). Random forest is a robust approach when working with continuous and categorical variables. The 15 traits considered, which relate to plant size and structure, leaf characteristics and ability to respond to environmental stimuli (palatability, resprouting, deciduousness, allelopathy) potentially influence the following: (1) how nutrients are mineralized and made available to plants (Decomposition), (2) how nutrients contribute to soil nutrient (including carbon) pools (Fertility) and (3) how soil and water are conserved (Conservation). Random forest analyses were conducted with the rfPermute package[66].

SEM allowed us to test hypothesized relationships among predictors and the fertile island effect based on an a priori model that constructs pathways among model terms based on a priori knowledge (Supplementary Fig. 5). This model predicted that spatial location would affect all the predictors such as climate, plant attributes (including site-level vegetation attributes and plant traits), soil attributes and grazing. Climate would influence the fertile island effect through its influence on soil properties, grazing and plant attributes. Grazing and soil properties would affect the fertile island effect directly or indirectly by altering plant attributes. We ran the SEM on the RII of the three functional categories (Decomposition, Fertility and Conservation; Supplementary Fig. 4). To obtain the values for these three average functions, we used the concept of the multifunctionality index and averaged the values of the RII for all individual attributes that comprised each function. Models with low χ^2 and root mean error of approximation (r.m.s.e.a. < 0.05), and high goodness of fit index (GFI) and R^2 were selected as the best fit model for our data. In addition, we calculated the standardized total effects of each explanatory variable to show its total effect. SEM analyses were performed using SPSS AMOS 22 (IBM) software.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data used for this study are available via Figshare[67] at https://doi.org/10.6084/m9.figshare.25283074.v1. The other databases used in this study are: Global Aridity Index and Potential Evapotranspiration Climate Database v2 aridity database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/), WorldClim version 2.0 (http://www.worldclim.org/), Woody Plants Database (http://woodyplants.cals.cornell.edu), TRY Database (https://www.try-db.org/TryWeb/Home.php), PLANTS Database (https://plants.usda.gov/) and BROT Database (https://www.uv.es/jgpausas/brot.htm). Source data are provided with this paper.

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Competing interests

The authors declare no competing interests.

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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☒	☐	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

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Software and code

Policy information about availability of computer code

Data collection	Rainfall seasonality (coefficient of variation of 12 monthly rainfall totals) data were extracted from the WorldClim Version 2.0 (http://www.worldclim.org/) database, which provides global climate data (0'30" × 0'30") for the 1970-2000 period. Aridity was identified as precipitation/potential evapotranspiration and was derived from the Global Aridity Index and Potential Evapotranspiration Climate Database v2 aridity database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/). We compiled information on eight additional plant traits (i.e., plant canopy shape, whether foliage reached the ground surface, N-fixation, deciduousness, allelopathy, palatability, resprouting, root type) using information from online plant trait databases: Woody Plants Database (http://woodyplants.cals.cornell.edu); TRY Database (https://www.try-db.org/TryWeb/Home.php); PLANTS Database (https://plants.usda.gov/); BROT Database (https://www.uv.es/jgpausas/brot.htm)
Data analysis	Bayesian hierarchical linear mixed model were fitted using the R package "rstanarm" Random forest analyses were conducted with the R package "rfPermute" All the figures were created using "ggplot2" in R version 4.0.379. SEM analyses were performed using SPSS AMOS 22 (IBM, Chicago, IL, USA) software.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

The data used for this study is available via the Figshare repository https://doi.org/10.6084/m9.figshare.25283074.v1.
Other databases used in this study is listed as below: Global Aridity Index and Potential Evapotranspiration Climate Database v2 aridity database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/); WorldClim Version 2.0 (http://www.worldclim.org/); Woody Plants Database (http://woodyplants.cals.cornell.edu); TRY Database (https://www.try-db.org/TryWeb/Home.php); PLANTS Database (https://plants.usda.gov/); BROT Database (https://www.uv.es/jgpausas/brot.htm)

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	Not applicable
Population characteristics	Not applicable
Recruitment	Not applicable
Ethics oversight	Not applicable

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

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Ecological, evolutionary & environmental sciences study design

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Study description	To characterize fertile islands, we investigated the influence of plants by comparing 24 soil physical, chemical, and functional attributes beneath the canopy of perennial vegetation compared with their adjacent unvegetated interspaces across global drylands. The 24 attributes were assembled into three synthetic functions that represent the capacity of soils to mineralise organic matter (Decomposition), enhance fertility (Fertility), and conserve water and maintain stability (Conservation, see Methods). We gathered data from 288 dryland sites across 25 countries on six continents (Fig. 1) to test the following two contrasting hypotheses. First, we expected that the magnitude of the fertile island effect would increase with increasing levels of both recent (standardised dung mass) and long-term or historic (heuristic assessment; ungrazed to high) grazing pressure (Hypothesis 1a). These factors operate at the local (site) level (see Methods). This prediction is based on the understanding that greater grazing pressure will destabilise surface soils, mobilising sediment, seed, nutrients, and organic matter from unvegetated interspaces to plant patches, strengthening fertile islands (Ridolfi et al. 2008). Additionally, livestock might be expected to have a greater effect than wild herbivores because they have not co-evolved with indigenous vegetation and therefore have more deleterious effects on both island plants and their soils (Eldridge et al. 2017, Hypothesis 1b). Alternatively, changes in climate and plant traits, factors that operate at much large (regional and global) scales, could overwhelm the impacts of grazing, a factor that operates at the local scale, on fertile islands (Hypothesis 2a). Put simply, irrespective of grazing pressure, we would expect that plants would make a greater contribution to fertile islands in arid and hyper-arid ecosystems where soils are extremely bare and infertile compared with less arid ecosystems where the influence of plants would be relatively lower. Plant effects might also be expected to vary among broad functional groups (tree vs shrub vs grass; Hypothesis 2b). These broad groups could have varying effects on soil biogeochemistry because of marked differences in shape, size, and structural complexity. Quantifying the contribution of grazing by different herbivores at different pressures, plant traits, climate, and soil properties on fertile islands allowed us to assess current and future impacts of grazing on ecosystem structure and functioning across global drylands, where woody vegetation is a predominant plant form (Maestre et al. 2016).
Research sample	We calculated a relative interaction index (RII) and its 95% confidence interval (Armas et al. 2004) for the 24 ecological attributes as measures of the fertile island effect. A positive (or negative) value indicates a greater (or lesser) value of that attribute, respectively,

in island soils. The RII is defined as the relative difference between attributes beneath the perennial plant islands and their open interspaces and was calculated as RII = (XI − XO) ∕ (XI + XO), where XI and XO represent the mean values of a given ecological attribute beneath a perennial plant patch (island) and in the open interspace, respectively. Values of the RII range from -1 to 1, with positive values indicating greater levels of a given attribute beneath the island and vice versa. Evidence of the fertile island effect (either positive or negative) is based on whether the 95% confidence intervals (95% CIs), calculated using 'Rmisc' package in R (R Core Team 2018) cross the zero line.

We focussed on three proxies of function derived from the average RII of different combination of the 24 soil attributes: 1) organic matter decomposition, quantified using the activity of five soil extracellular enzymes related to the degradation of organic matter [β-glucosidase, phosphatase, cellobiosidase, β-N-acetylglucosaminidase and xylase], and measurements of soil carbon (hereafter 'Decomposition' (2) soil fertility, evaluated using multiple proxies of soil nutrient availability and carbon (contents of dissolved organic and total N, NH4+, NO3-, total P, Mn, K, Zn, Mg, Fe, Cu and soil C, hereafter 'Fertility'), and 3) resource conservation (water regulation, using measures of soil water holding capacity, soil porosity, stability of macro-aggregates >250 μm and mean weight diameter of soil aggregates (hereafter 'Conservation'). Detailed measurements on these 24 soil ecological attributes are described in Table S1 in Supplementary Information.

Sampling strategy	Soils were sampled during the dry season. In each plot, five sampling points were randomly located in open areas devoid of perennial vascular plants (< 5% plant cover, hereafter 'open' microsite), and another five placed beneath the canopy of five randomly selected individuals of the dominant island plant (Text S3 in Supplementary Information). A composite sample of five 145 cm3 soil cores (0-7.5 cm depth) was collected from beneath each plant or bare area, bulked, and homogenized in the field. Soil samples were air-dried for 1 month, sieved (< 2 mm) and stored for physico-chemical analyses. The samples were then bulked to obtain one composite sample per plot for vegetated (island) and a separate composite sample for open areas. All analyses described here are for two composite samples per plot. We assessed soil pH (1:2.5 soil water suspension, sand content (Kettler et al., 2001), and the values of 24 soil ecological attributes that are linked to three ecosystem functions (Table S1 in Supplementary Information).
Data collection	Rainfall seasonality (coefficient of variation of 12 monthly rainfall totals) data were extracted from the WorldClim Version 2.0 (http://www.worldclim.org/) (Fick and Hijmans 2017) database, which provides global climate data (0'30" × 0'30") for the 1970-2000 period. Aridity was identified as precipitation/potential evapotranspiration and was derived from the Global Aridity Index and Potential Evapotranspiration Climate Database v2 aridity database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/) (Zomer et al. 2019), which includes global aridity data (0'30" × 0'30") for the 1970-2000 period. Soil texture is a major determinant of water holding capacity and pH is a major driver of plant and soil function in drylands (Zhang et al. 2021, Maestre et al. 2022a). Sand content and pH data used in this study were obtained from samples taken from the open areas (to ensure that their effects on the ecosystem functions measured are as independent from those of organisms as possible). Relative woody cover was included to account for different levels of woody plants so that this would not bias any results. Standardized dung mass (dung mass in a plot/maximum dung mass within the site) was used as a measure of recent grazing pressure.
Timing and spatial scale	Timing: field survey: 2016-2018 Spatial scale: Studies were distributed globally across all continents except Antarctica, and covering a wide variety of biomes
Data exclusions	None
Reproducibility	The results of this study can be reproducibility based on the dataset and code that available in Figshare https://doi.org/10.6084/m9.figshare.14923065.v1
Randomization	NA
Blinding	NA

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

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n/a	Involved in the study
☒	Antibodies
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☒	Clinical data
☒	Dual use research of concern

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging