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

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Abstract

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. 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.

Introduction

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 mineralisation 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 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, for the first time, 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].

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 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). This prediction is based on the understanding that greater grazing

282 pressure will destabilise surface soils, mobilising sediment, seed, nutrients, and
283 organic matter from unvegetated interspaces to plant patches, strengthening fertile
284 islands [14,15]. Additionally, livestock might be expected to have a greater effect than
285 wild herbivores because they have not co-evolved with indigenous vegetation and
286 therefore have more deleterious effects on both island plants and their soils [6],
287 Hypothesis 1b). Alternatively, changes in climate and plant traits, factors that operate
288 at much larger (regional and global) scales, could overwhelm the impacts of grazing,
289 a factor that operates at the local scale, on fertile islands (Hypothesis 2a). More
290 specifically, irrespective of grazing pressure, we would expect that plants would make
291 a greater contribution to fertile islands in arid and hyper-arid ecosystems where soils
292 are extremely bare and infertile compared with less arid ecosystems where the
293 influence of plants would be relatively lower. For example, reduced rainfall and/or
294 increased temperature would increase the harshness of the interspaces compared with
295 the vegetated and more protected islands, thereby strengthening the fertile island
296 effect. Plant effects might also be expected to vary among broad functional groups
297 (tree vs shrub vs grass; Hypothesis 2b). These broad groups could have varying
298 effects on soil biogeochemistry because of marked differences in shape, size, and
299 structural complexity. Quantifying the contribution of grazing by different herbivores
300 at different pressures, plant traits, climate, and soil properties on fertile islands
301 allowed us to assess current and future impacts of grazing on ecosystem structure and
302 functioning across global drylands, where woody vegetation is a predominant plant
303 form [12].

304

Results and Discussion

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

312 *Global fertile island effects*

313 Prior to exploring potential effects of grazing, plant traits, or environmental
314 conditions, we examined the RII relationships of the 24 attributes distributed among
315 the three synthetic functions. This exploration gives us a better understanding of how
316 individual biogeochemical attributes and their three synthetic ecosystem functions
317 might differ between islands and their interspaces (the fertile island effect). We found
318 strong empirical evidence of a pervasive fertile island effect across all sites and
319 continents and for 16 (67%) of the 24 attributes (Fig. 2). Our results are consistent
320 with findings from empirical local studies revealing greater resource accumulation
321 beneath perennial plant canopies for attributes as diverse as soil geochemistry
322 [11,13,16,17], soil physical properties [9], hydrology [18,19] and microbial community structure
323 [4]. Of all possible effects, the Decomposition function (which comprised C, N and P

324 mineralisation), was the most strongly developed function within the islands (Fig. 2),
325 likely due to greater litter inputs [4,20], microbial activity and plant biomass [21] beneath
326 perennial plant canopies [22,23]. The fertile island effect for the other functions was
327 mixed, with strong positive effects for C, and to a lesser extent P, but not for
328 micronutrients (Fig. 2). The fertile island effect for C and N was also greater in more
329 arid drylands. These findings reinforce the view that perennial plant patches are
330 hotspots of biological activity in drylands [4], and this likely accounts for their potential
331 role as facilitators of protégé plant species through resource supplementation [24].

The influence of grazing, island type and plant traits

333 We then sought to quantify the importance of potential associations among
334 measures of grazing and fertile islands. Using hierarchical linear mixed modelling
335 (see Methods) we found no consistent influence of grazing, either recent (standardized
336 grazing pressure) or long-term (ungrazed, low, medium, high) grazing pressure on the
337 mean (overall) fertile island effect (the average standardized value of all 24 attributes
338 shown in Table S1 in Supplementary Information). We also found a consistent, but
339 extremely weak negative effect of recent grazing pressure on Decomposition, contrary
340 to the results of global meta-analyses [25]. There were no significant effects of
341 increasing recent grazing pressure on either the Fertility or Conservation function
342 (Fig. 3a, Table S2). There were no significant effects of long-term (historic) grazing
343 pressure (ungrazed, low, medium, high) on any measures (Fig. S1, Table S2).

344 Of all effects, aridity was by far the strongest (Table S2), with a strong positive
345 effect on the Decomposition function, weak effects on the Fertility, but no effect on
346 the Conservation function (Fig. S3a, Table S2). Although the effects of island type
347 (tree, shrub, grass) were minor compared with the large aridity effect, we did identify
348 some trends. For example, there were consistent positive, though weak, fertile island
349 effects beneath shrubs, and to a lesser extent trees, irrespective of grazing pressure.
350 The only other noteworthy grazing-related effect was the negative interaction between
351 shrubs, and to a lesser extent trees, and mixed herbivores (Table S2).

352 Our results provide fresh insights into the links between grazing and fertile
353 islands, demonstrating that, across global drylands, grazing cannot be considered a
354 causal agent of the fertile island effect. Thus, placed in a global context, the local
355 influence of grazing on fertile islands is overshadowed by global environmental
356 variability. This result challenges the view of fertile islands and their formation,
357 which posits that islands are a biproduct of grazing [11]. This view has largely been
358 shaped by studies from the Chihuahuan Desert in the western United States where
359 increases in woody plant (generally shrub) density are linked to a dominance of
360 woody plant islands and ensuing desertification [26]. Undoubtedly, grazing-induced
361 disturbance can aggravate differences between perennial plants and their interspaces
362 in some situations by disturbing interspaces and intensifying the movement of
363 resources from interspace to island patches [27]. However, neither short- nor long-term
364 grazing pressure, nor herbivore type, were associated with the fertile island effect
365 under the conditions experienced across our extensive global dryland survey.

366   Given the importance of plant traits, a Random Forest algorithm was then used to
367   examine the degree to which a comprehensive suite of 15 functional traits of island
368   woody plant species explained differences in the fertile island effect for the three
369   synthetic functions studied. These traits, which are related to plant size and structure,
370   leaf characteristics, and the ability to respond to environmental stimuli (palatability,
371   resprouting, deciduousness, allelopathy, see Methods) potentially influence the way
372   nutrients are stored, mineralized, and made available to plants, and how soil and water
373   are conserved beneath plant canopies [28]. Our trait data, which represent the most
374   comprehensive dataset gathered to date across global drylands, were used to evaluate
375   the relative importance of island plant structure. We used site-specific trait values
376   rather than global averages, allowing us to account for potential differences in the
377   morphology of island plants under different grazing pressure, herbivore type and
378   environmental conditions. The extent to which different plant traits affected the three
379   synthetic functions varied depending on the function considered (Fig. S4 in
380   Supplementary Information). We found that the relative fertile effect for our three
381   synthetic functions was generally greater when the islands were dominated by taller
382   and wider plants, and to a lesser extent, by plants with larger leaves. Plant height was
383   important for all functions, while the Decomposition function responded mostly to
384   plant and leaf size, and the Fertility function was driven mostly by changes in plant
385   size and leaf characteristics (Fig. S4 in Supplementary Information).

386   *Direct and indirect drivers of the fertile island effect*

387   We then used Structural Equation Modelling [29] to explore potential associations
388   among biotic and abiotic factors and the fertile island effect. Our *a priori* model (Fig.
389   S5 in Supplementary Information) included environmental drivers (aridity,
390   temperature, rainfall seasonality), soil (sand content, pH) and vegetation (perennial
391   plant richness, relative cover of woody plants) properties, plant traits (the nine most
392   important plant traits related to size, leaf characteristics, and inherent properties of
393   woody plants such as the type of roots or whether they are allelopathic; identified
394   using the Random Forest analyses, see Methods), and grazing (recent grazing, long-
395   term grazing, and herbivore type). Grazing was included to test its potential indirect
396   effects on the relative fertile island effect for the three soil functions evaluated. Our
397   models revealed that decomposition was enhanced in areas of greater aridity
398   (consistent with the hierarchical linear modelling, though not for carbon
399   mineralisation, Fig. S2 Supplementary Information), more sandy soils, and where
400   focal island species were more palatable (Fig. 4; Fig. S6 Supplementary Information).
401   Fertility tended to be greater in sandy soils and with taller palatable species. Soils
402   with larger values of the Conservation function (more stable, with greater water
403   holding capacity) tended to be associated with taller island plants, potentially through
404   mechanisms involving hydraulic lift [30], and at plots supporting more perennial plant
405   species (Fig. S6 Supplementary Information. A potential explanation for the link
406   between the Conservation function, and both plant height and richness could relate to
407   a greater leaf area [31] of larger island plants and therefore reduced surface evaporation
408   [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 RII values of all three functions (but only for grasses), and taller grasses with greater RII values of the Decomposition function (Fig. S7 in Supplementary Information. 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 (Fig. S7 in Supplementary Information). 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 (Fig. S7 in Supplementary Information). 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, moderate adverse environmental conditions, and provides 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,

451   Palestine, Peru, Portugal, South Africa, Spain, Tunisia, and United States of America,
452   Fig. 1). We used the sites described in ref. 12, but excluded 10 sites that did not have
453   sufficient trait data (see below). Site selection aimed to capture as much as possible of
454   the wide variety of abiotic (climate, soil type, slope) and biotic (vegetation type, cover
455   and species richness) features characterizing dryland ecosystems (e.g., grasslands,
456   shrublands, savannas, open woodlands) found in drylands worldwide [12,44]. Elevation
457   varied between 12 m and 2214 m a.s.l, and slope from 0º to 31.6º. The surveyed sites
458   encompassed a wide variety of the representative vegetation physiognomies,
459   including grasslands, shrublands, savannas and open woodlands (Fig. 1) found in
460   drylands. Sites were surveyed between January 2016 and September 2019 [12,44].

461   *Establishing and defining local grazing gradients*

462   At each of the 88 sites, multiple 45 m x 45 m plots were sampled across a gradient in
463   grazing pressure that was determined by local experts and compared with dung
464   counts, livestock tracks, and livestock density data when available. Plots were
465   selected from grazing gradients (distance to water measured using GIS) or specific
466   paddocks that represented ungrazed, low, medium, or high levels of known grazing
467   pressure. Thirty-five percent of sites had an ungrazed plot (e.g., an exclosure). All
468   plots were established in areas representative of the vegetation and soil types found,
469   so the impacts of grazing pressure could be assessed at each site without confounding
470   factors associated with differences in climate, soil type or vegetation.

471   Field surveyors, who were all intimately associated with the long-term grazing
472   history of these sites, characterised their plots using this four-scale heuristic category
473   (ungrazed, low, moderate, high). Grazing pressure gradients were confirmed by
474   measuring the mass of herbivore dung *in situ* [6]. Dung production is known to be
475   closely linked to animal activity, time spent grazing, and therefore grazing pressure
476   [45,46], though more studies are needed in arid systems to validate these relationships.
477   To measure dung, we collected the dung of different herbivores from within two 25
478   m^2 (where herbivores were large bodied, e.g., cattle, horses, large ungulates) or 1 m^2
479   (when herbivores were smaller bodied e.g., goats, sheep, rabbit, guanaco) quadrats [44].
480   Dung was oven dried and expressed as a mass per area. Where herbivores produced
481   pellets, dung was counted from different herbivores, a subsample collected, and
482   following oven drying, used to calculate the relationship between counts and oven-dry
483   dung mass (Text S1 in Supplementary Information).

484   The mass of dung from each plot was then used to develop a continuous measure
485   of grazing pressure. Dung mass represents the signature of grazing over periods of
486   one to five years, depending on the presence of detritivores and litter decomposing
487   invertebrates such as termites and dung beetles [47]. Dung decay rates will also likely
488   vary across our sites due to differences in climatic conditions, the presence of exotic
489   invertebrate decomposers, trampling and other factors [48]. Although these differences
490   could potentially alter the amount of dung detected within a plot, this would have
491   minimal impact on our measure of recent grazing pressure given the standardisation
492   process we applied to dung mass across plots within a site.

493   For each plot, we standardised the value of the mass of dung of all herbivores
494   within a plot by the maximum dung mass at that particular site (collection of plots).
495   Standardized values ranged from 0 to 1 (0.30 ± 0.01, mean $\pm$ SE) across the 88 sites.
496   A value of 1 for a particular plot indicates that this plot had the greatest grazing
497   pressure for that site and zero was ungrazed. This approach to standardising dung
498   mass within sites ensures the equivalence of sites that might have markedly different
499   levels of dung production, due to variation in site productivity, but have the same
500   level of grazing pressure (e.g., moderate grazing pressure). The method has also been
501   validated multiple times in grazing studies [49,50]. Across our global study we recorded
502   29 different herbivore types, of which five were livestock (cattle, goat, sheep, donkey,
503   horse)[12].

504   Dung mass was a good proxy of grazing pressure using two approaches (see Text
505   S1 in Supplementary Information). First, there was a significant positive relationship
506   between dung mass and livestock density for a subset of sites in Iran, Australia, and
507   Argentina for which we had data on dung mass and animal density [12]. Second, we
508   performed a cluster analysis [51] to identify the optimum number of dung-based
509   clusters, based on dung mass, and found that this aligned well with the four heuristic
510   levels of grazing pressure [12].

511   Third, we linked the four heuristic measures of long-term (decadal to multi-
512   decadal) grazing pressure to the presence of livestock tracks; semi-permanent features
513   created by livestock when they traverse the same path to and from water [52]. The
514   density and size of these tracks is a useful indicator of the history of livestock grazing
515   [53]. We measured the width and depth of all livestock tracks crossing each of the 45 m
516   transects to derive a total cross-sectional area of tracks for each plot and expressed
517   this as the total track density and cross-sectional area per 100 m of transect (Fig. S8).
518   In summary, these three comprehensive measures of grazing intensity by herbivores
519   showed very similar trends, irrespective of whether we used dung mass as a measure
520   of recent grazing pressure, or the expert heuristic site classification as a measure of
521   long-term grazing pressure. This gives us a high degree of confidence that the
522   gradients we observed are true gradients in grazing pressure.

523   *Vegetation and plant trait measurements*

524   Field surveys followed a standardised sampling protocol [44]. Briefly, within each plot,
525   we located four 45 m transects oriented downslope, spaced 10 m apart across the
526   slope, for the vegetation surveys. Along each 45 m transect we assessed the cover of
527   perennial plants, by species, within 25 contiguous 1.5 m by 1.5 m quadrats. Perennial
528   plants were then recorded every 10 cm along this transect to obtain a measure of
529   perennial plant cover. Total plot-level plant richness was calculated as the total
530   number of unique perennial plant species found within at least one of the survey
531   methods (transects or quadrats) employed. In each site, we measured the height and
532   lateral spread of five randomly selected individuals of the dominant island plants.
533   Lateral spread (canopy width), a proxy of plant area, was assessed by measuring plant
534   diameter in two orthogonal directions through the plant centre. Fresh leaves were

535 collected from the same plants to assess an additional four plant traits in the
536 laboratory (leaf length, leaf area, and leaf carbon and nitrogen contents). These six
537 traits describe the size and leaf characteristic of the 162 perennial species in the
538 vegetation patch that was dominated by trees, shrubs, or large perennial grasses, and
539 which we assessed as potential fertile islands (see detailed measurements in Text S2
540 in Supplementary Information). Twenty-three percent of plots supported two co-
541 dominant island species (i.e., two different tree, shrub, or grass species). For these
542 plots, soil biogeochemical and plant trait data were weighted according to the mean
543 cover of the co-dominant species within a plot.

544   We compiled information on eight additional plant traits (i.e., plant canopy
545 shape, whether foliage reached the ground surface, N-fixation, deciduousness,
546 allelopathy, palatability, resprouting, root type) using information from online plant
547 trait databases such as BROT [54], PLANTS [55], Woody Plants Database
548 (http://woodyplants.cals.cornell.edu) and TRY [56]. The eight categorical traits above
549 were ranked numerically such that a larger value equated with greater function in
550 terms of its own growth or its facilitatory effect on surrounding neighbours and
551 conditions. This procedure is described in detail in Text S2 in Supplementary
552 Information.

Soil properties and sampling

554 Soils were sampled during the dry season. In each plot, five sampling points were
555 randomly located in open areas devoid of perennial vascular plants (< 5% plant cover,
556 hereafter 'open' microsite), and another five placed beneath the canopy of five
557 randomly selected individuals of the dominant island plant (Text S3 in Supplementary
558 Information). A composite sample of five 145 cm^3 soil cores (0-7.5 cm depth) was
559 collected from beneath each plant or bare area, bulked, and homogenized in the field.
560 Soil samples were air-dried for 1 month, sieved (< 2 mm) and stored for physico-
561 chemical analyses. The samples were then bulked to obtain one composite sample per
562 plot for vegetated (island) and a separate composite sample for open areas. All
563 analyses described here are for two composite samples per plot. We assessed soil pH
564 (1:2.5 soil water suspension, sand content [57], and the values of 24 soil ecological
565 attributes that are linked to three ecosystem functions (Table S1 in Supplementary
566 Information).

Assessment of ecosystem functions

568 We calculated a relative interaction index (RII) and its 95% confidence interval [58] for
569 the 24 ecological attributes as measures of the fertile island effect. A positive (or
570 negative) value indicates a greater (or lesser) value of that attribute, respectively, in
571 island soils. The RII is defined as the relative difference between attributes beneath
572 the perennial plant islands and their open interspaces and was calculated as RII = (X_I
573 – X_O) / (X_I + X_O), where X_I and X_O represent the mean values of a given ecological
574 attribute beneath a perennial plant patch (island) and in the open interspace,
575 respectively. Values of the RII range from -1 to 1, with positive values indicating
576 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 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, 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 Table S1 in Supplementary Information.

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 standardised response variable (RII) was modelled hierarchically as a function of recent grazing pressure (standardised dung), long-term

619   grazing pressure (high, medium, low, ungrazed), herbivore type (livestock, native,
620   mixed), aridity, island type (tree, shrub, grass), and functional category
621   (Decomposition, Fertility, Conservation). The model fitted individual ecosystem
622   functional attributes as groups (random intercepts) with varying slopes associated
623   with each of the main covariates (grazing and aridity). The model also included
624   interactions between ecosystem function category and grazing, island type, and aridity
625   to account for potential differences in the effects of each covariate within each
626   ecosystem function category. We included site as a random intercept, accounting for
627   the non-independence of data gathered from the same site.

628   We specified weakly informative normally distributed priors for the intercept and
629   all regression coefficients (mean = 0 and scale = 2.5). Default priors were used for
630   sigma (exponential, rate =1) and variance-covariance matrix of the varying intercepts
631   and slope parameters (shape and scale of 1). Posterior simulations of model
632   parameters were undertaken using the No-U-Turn Hamiltonian Monte Carlo sampler
633   within Stan [63]. Posterior distributions were estimated from four chains, each with
634   1000 iterations, after discarding the preliminary 1000 iterations. The convergence of
635   models was assessed using visual diagnostics (autocorrelation, trace plots, and
636   posterior predictive checks) and inspection of effective sample sizes (min. 1000) and
637   r hat values (<1.01). Models were fitted using the package 'rstanarm' [64] within R [59]. A
638   hierarchical model provides several benefits over simple averaging of standardised
639   indicators or multiple separate models [65]: (i) simultaneous modelling of multiple
640   attributes improves precision and estimates of uncertainty for each ecosystem function
641   category; (ii) non-independence of multiple attributes within sites is explicitly
642   accounted for; (iii) enables simultaneous estimation of overall fertile island effect for
643   each ecosystem functional category and the individual soil attributes within these.

644   Structural Equation Modelling (SEM [29]) was employed to explore the direct and
645   indirect impact of climate (aridity [ARID], rainfall seasonality [SEAS]), soil pH (pH),
646   sand content (SAND), vegetation attributes (plot-level perennial plant cover [COV]
647   and plant richness [RICH], plant height [HT], canopy width [WIDTH], shape
648   [SHAPE], leaf length [LNGTH], leaf area [AREA], palatability [PALAT],
649   resprouting [RESP], deciduousness [DECID], and allelopathy [ALLELO]), and
650   grazing (standardised grazing pressure) on the fertile island effect (RII) after
651   accounting for the effects of location (latitude, cosine longitude, sine longitude)
652   across the globe. All explanatory variables were standardized (z-transformed) in the
653   SEM analyses. The nine plant traits used in these analyses were selected from a
654   potential pool of 15 potential traits using the significance of percentage increase in
655   mean square error using Random Forest analyses (Fig. S3 in Supplementary
656   Information). With these analyses we aimed to determine which traits are the most
657   influential in describing the relative difference between islands and their interspaces
658   (as measured with the RII) for each of the three synthetic functions (Decomposition,
659   Fertility, Conservation). Random Forest is a robust approach when working with
660   continuous and categorical variables. The 15 traits considered, which relate to plant
661   size and structure, leaf characteristics, and ability to respond to environmental stimuli

662 (palatability, resprouting, deciduousness, allelopathy) potentially influence: 1) how
663 nutrients are mineralized and made available to plants (Decomposition), 2) contribute
664 to soil nutrient (including carbon) pools (Fertility) and 3) how soil and water are
665 conserved (Conservation). Random forest analyses were conducted with the
666 rfPermute package [66].

667 Structural equation modelling allowed us to test hypothesized relationships
668 among predictors and the fertile island effect based on an *a priori* model that
669 constructs pathways among model terms based on *a priori* knowledge (Fig. S5 in
670 Supplementary Information). This model predicted that spatial location would affect
671 all the predictors such as climate, plant attributes (including site-level vegetation
672 attributes and plant traits), soil attributes and grazing. Climate would influence the
673 fertile island effect through its influence on soil properties, grazing, and plant
674 attributes. Grazing and soil properties would affect the fertile island effect directly, or
675 indirectly, by altering plant attributes. We ran the SEM on the RII of the three
676 functional categories (Decomposition, Fertility, Conservation, Fig. S4 in
677 Supplementary Information). To obtain the values for these three average functions,
678 we employed the concept of the multifunctionality index and averaged the values of
679 the RII for all individual attributes that comprised each function. Models with low χ^2
680 and Root Mean Error of Approximation (RMSEA < 0.05), and high Goodness of Fit
681 Index (GFI) and R^2 were selected as the best fit model for our data. In addition, we
682 calculated the standardised total effects of each explanatory variable to show its total
683 effect. SEM analyses were performed using SPSS AMOS 22 (IBM, Chicago, IL,
684 USA) software.

685

Data Availability

687 The data used for this study is available via the Figshare repository
688 https://doi.org/10.6084/m9.figshare.25283074.v1.

689 Other databases used in this study is listed as below: Global Aridity Index and
690 Potential Evapotranspiration Climate Database v2 aridity database
691 (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-
692 evapotranspiration-climate-database-v2/); WorldClim Version 2.0
693 (http://www.worldclim.org/); Woody Plants Database
694 (http://woodyplants.cals.cornell.edu); TRY Database (https://www.try-
695 db.org/TryWeb/Home.php); PLANTS Database (https://plants.usda.gov/); BROT
696 Database (https://www.uv.es/jgpausas/brot.htm)

Author Contributions Statement

733 F.T.M. designed and coordinated the field survey. D.J.E. and J.DING conceived the
734 study. J.D. undertook the Bayesian analyses, M.M-C. drafted the figures, and J.DING
735 produced the map. Laboratory analyses were performed by V.O., B.G., B.J.M., S.A.,
736 A.R., P.D.M., C.P., N.E., M.R., S.C. and M.D-B. The remaining authors collected and
737 managed field data collection. D.J.E. and J.DING wrote the draft manuscript in
738 collaboration with F.T.M. and O.S., and with contributions from all authors.

Competing Interests Statement

740 The authors declare no competing interests.

741

Figure Legends

Figure 1. Average function (mean relative interaction effect value across 24 soil attributes, see Methods) 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.

Figure 2. The fertile island effect, as measured with the relative interaction effect (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.

Figure 3. Impacts of recent grazing and climate on the fertile island effect. (a) Relative interaction effect (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 in relation to (b) long-term (historic) measure of herbivore grazing pressure (ungrazed, low, medium, high), and (c) herbivore type (livestock, native, mixed). Numbers in (b-c) are replicates for each category.

Figure 4. Structural equation modelling assessing the direct and indirect 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) on the fertile island effect for soil decomposition (Decomposition), soil fertility (Fertility) and soil and water conservation (Conservation), after accounting for the effects of location (latitude, cosine longitude, sine longitude). Standardised 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), significant positive (blue unbroken line) or mixed significant negative and significant positive (black unbroken lines). Non-significant pathways are not shown in the models. Model fit: (a) organic matter decomposition: $\chi^2 = 31.9$, df = 26, $P = 0.20$, $R^2=0.17$, root mean error of approximation (RMSEA) < 0.001, Bollen-Stine = 0.40 (2000 bootstrap); (b) Fertility: $\chi^2 = 31.9$, df = 26, $P = 0.20$, $R^2=0.19$, root mean error of approximation (RMSEA) < 0.001, Bollen-Stine = 0.40 (2000 bootstrap); (c) Conservation: $\chi^2 = 31.9$, df = 26, $P = 0.20$, $R^2=0.10$, root mean error of approximation (RMSEA) < 0.001, Bollen-Stine = 0.40 (2000 bootstraps). N=288 for all analyses.

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Hyperarid
Arid
Semiarid
Dry subhumid
Non-dryland

(a)

Grazing pressure (standardized)

Decomposition Fertility Conservation

RII
-0.22 to 0.00
0.00 to 0.22
0.22 to 0.44

Aridity (unitless)

(b)

Grazing pressure

86
87
76
39

(c)

Herbivore type

166
20
102

Relative interaction effect (RII, unitless)

(a)

.29 (ARID)

.18 (PALAT)

DECOMPOSITION R^2=0.17

(b)

.17 (ARID)

.24 (SAND)

.20 (PALAT)
.13 (DECID)
-.13 (RESPR)

SOIL FERTILITY R^2=0.19

(c)

.25 (HT)
.18 (RICH)

CONSERVATION R^2=0.10

(d)

A
.46 (ARID →pH)
-.17 (SEAS →pH)

B
.43 (SEAS→AREA)
-.17 (SEAS→RICH)
-.15 (SEAS→SHAPE)
-.32 (ARID→SHAPE)
-.15 (ARID→RICH)
-.29 (ARID→DECID)

C
.34 (SAND→RICH)
.24 (SAND→DECID)
.15 (SAND→ALLEL)
-.14 (SAND→RESP)
-.12 (SAND→AREA)
-.53 (pH→HT)
-.46 (pH→WIDTH)
-.25 (pH→SHAPE)
-.49 (pH→RICH)
-.31 (pH→RESP)
-.21 (pH→DECID)
-.23 (pH→ALLELO)
.27 (pH→PALAT)