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

3

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202 **Abstract**

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

222

223 **Keywords:** carbon sequestration, drylands, decomposition, fertile patch, soil fertility,
224 soil condition, soil health, soil stability

225 **Introduction**

226 Drylands are characterized by a sparse plant cover, with patches of perennial plants
227 nested within an ocean of unvegetated bare soil ^{1,2}. These plant patches and the
228 enriched soil beneath their canopies, act as biogeochemical hotspots, critical for the
229 maintenance of plant and animal diversity, and essential functions and services related
230 to nutrient mineralisation and storage, and water regulation ^{1,3,4}. Dryland vegetation,
231 and the “fertile islands” they create, are predicted to be affected by livestock grazing,
232 the most pervasive land use in drylands ⁵. Overgrazing by livestock and wild (native)
233 herbivores is known to alter surface soils, suppress the infiltration of water, and
234 increase runoff water and sediment discharge ^{6,7}, potentially intensifying the fertile
235 island effect by exacerbating the loss of resources from the interspaces and its
236 supplementation in nearby islands ⁸. Yet, there is little support for this notion, other
237 than studies showing that overgrazing leads to a greater relative effect of woody
238 island soils over interspace soils, but that severe overgrazing leads to total collapse ⁹.
239 Globally, there is little empirical support for the putative importance of grazing as a
240 causal agent of the fertile island effect ^{10,11}, particularly when considering the wide
241 range of plant types characterizing drylands, from grasses to shrubs and trees. This
242 makes it difficult to disentangle grazing effects from the inherent effects of those
243 plants that form the islands. This is an important knowledge gap, as predicted declines
244 in rainfall, changes in the structure of island plants, and forecasted increases of
245 grazing over the next century will likely place increasing pressure on drylands and
246 their perennial components, compromising their ability to sustain livestock, people,
247 and their cultures ¹².

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

257 We examined the fertile island effect by comparing 24 soil physical, chemical
258 and functional attributes beneath the canopy of perennial vegetation compared with
259 their adjacent unvegetated interspaces across global drylands. The 24 attributes were
260 assembled into three synthetic functions that represent the capacity of soils to
261 mineralise organic matter (Decomposition), enhance fertility (Fertility), and conserve
262 water and maintain stability (Conservation, see Methods). We gathered data from 288
263 dryland sites across 25 countries on six continents (Fig. 1) to test the following two
264 contrasting hypotheses. First, we expected that the magnitude of the fertile island
265 effect would increase with increasing levels of both recent (standardised dung mass)
266 and long-term or historic (heuristic assessment; ungrazed to high) grazing pressure
267 (Hypothesis 1a). This prediction is based on the understanding that greater grazing

268 pressure will destabilise surface soils, mobilising sediment, seed, nutrients, and
269 organic matter from unvegetated interspaces to plant patches, strengthening fertile
270 islands^{14,15}. Additionally, livestock might be expected to have a greater effect than
271 wild herbivores because they have not co-evolved with indigenous vegetation and
272 therefore have more deleterious effects on both island plants and their soils⁶,
273 Hypothesis 1b). Alternatively, changes in climate and plant traits, factors that operate
274 at much larger (regional and global) scales, could overwhelm the impacts of grazing,
275 a factor that operates at the local scale, on fertile islands (Hypothesis 2a). More
276 specifically, irrespective of grazing pressure, we would expect that plants would make
277 a greater contribution to fertile islands in arid and hyper-arid ecosystems where soils
278 are extremely bare and infertile compared with less arid ecosystems where the
279 influence of plants would be relatively lower. For example, reduced rainfall and/or
280 increased temperature would increase the harshness of the interspaces compared with
281 the vegetated and more protected islands, thereby strengthening the fertile island
282 effect. Plant effects might also be expected to vary among broad functional groups
283 (tree vs shrub vs grass; Hypothesis 2b). These broad groups could have varying
284 effects on soil biogeochemistry because of marked differences in shape, size, and
285 structural complexity. Quantifying the contribution of grazing by different herbivores
286 at different pressures, plant traits, climate, and soil properties on fertile islands
287 allowed us to assess current and future impacts of grazing on ecosystem structure and
288 functioning across global drylands, where woody vegetation is a predominant plant
289 form¹².

290

291 **Results and Discussion**

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

298 Prior to exploring potential effects of grazing, plant traits, or environmental
299 conditions, we examined the RII relationships of the 24 attributes distributed among
300 the three synthetic functions. This exploration gives us a better understanding of how
301 individual biogeochemical attributes and their three synthetic ecosystem functions
302 might differ between islands and their interspaces (the fertile island effect). We found
303 strong empirical evidence of a pervasive fertile island effect across all sites and
304 continents and for 16 (67%) of the 24 attributes (Fig. 2). Our results are consistent
305 with findings from empirical local studies revealing greater resource accumulation
306 beneath perennial plant canopies for attributes as diverse as soil geochemistry
307^{11,13,16,17}, soil physical properties⁹, hydrology^{18,19} and microbial community structure
308⁴. Of all possible effects, the Decomposition function (which comprised C, N and P
309 mineralisation), was the most strongly developed function within the islands (Fig. 2),

310 likely due to greater litter inputs^{4,20}, microbial activity and plant biomass²¹ beneath
311 perennial plant canopies^{22,23}. The fertile island effect for the other functions was
312 mixed, with strong positive effects for C, and to a lesser extent P, but not for
313 micronutrients (Fig. 2). The fertile island effect for C and N was also greater in more
314 arid drylands. These findings reinforce the view that perennial plant patches are
315 hotspots of biological activity in drylands⁴, and this likely accounts for their potential
316 role as facilitators of protégé plant species through resource supplementation²⁴.

317 We then sought to quantify the importance of potential associations among
318 measures of grazing and fertile islands. Using hierarchical linear mixed modelling
319 (see Methods) we found no consistent influence of grazing, either recent (standardized
320 grazing pressure) or long-term (ungrazed, low, medium, high) grazing pressure on the
321 mean (overall) fertile island effect (the average standardized value of all 24 attributes
322 shown in Table S1 in Supplementary Information). We also found a consistent, but
323 extremely weak negative effect of recent grazing pressure on Decomposition, contrary
324 to the results of global meta-analyses²⁵. There were no significant effects of
325 increasing recent grazing pressure on either the Fertility or Conservation function
326 (Fig. 3a, Table S2). There were no significant effects of long-term (historic) grazing
327 pressure (ungrazed, low, medium, high) on any measures (Fig. S1, Table S2).

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

336 Our results provide fresh insights into the links between grazing and fertile
337 islands, demonstrating that, across global drylands, grazing cannot be considered a
338 causal agent of the fertile island effect. Thus, placed in a global context, the local
339 influence of grazing on fertile islands is overshadowed by global environmental
340 variability. This result challenges the view of fertile islands and their formation,
341 which posits that islands are a byproduct of grazing¹¹. This view has largely been
342 shaped by studies from the Chihuahuan Desert in the western United States where
343 increases in woody plant (generally shrub) density are linked to a dominance of
344 woody plant islands and ensuing desertification²⁶. Undoubtedly, grazing-induced
345 disturbance can aggravate differences between perennial plants and their interspaces
346 in some situations by disturbing interspaces and intensifying the movement of
347 resources from interspace to island patches²⁷. However, neither short- nor long-term
348 grazing pressure, nor herbivore type, were associated with the fertile island effect
349 under the conditions experienced across our extensive global dryland survey.

350 Given the importance of plant traits, a Random Forest algorithm was then used to
351 examine the degree to which a comprehensive suite of 15 functional traits of island

352 woody plant species explained differences in the fertile island effect for the three
353 synthetic functions studied. These traits, which are related to plant size and structure,
354 leaf characteristics, and the ability to respond to environmental stimuli (palatability,
355 resprouting, deciduousness, allelopathy, see Methods) potentially influence the way
356 nutrients are stored, mineralized, and made available to plants, and how soil and water
357 are conserved beneath plant canopies²⁸. Our trait data, which represent the most
358 comprehensive dataset gathered to date across global drylands, were used to evaluate
359 the relative importance of island plant structure. We used site-specific trait values
360 rather than global averages, allowing us to account for potential differences in the
361 morphology of island plants under different grazing pressure, herbivore type and
362 environmental conditions. The extent to which different plant traits affected the three
363 synthetic functions varied depending on the function considered (Fig. S4 in
364 Supplementary Information). We found that the relative fertile effect for our three
365 synthetic functions was generally greater when the islands were dominated by taller
366 and wider plants, and to a lesser extent, by plants with larger leaves. Plant height was
367 important for all functions, while the Decomposition function responded mostly to
368 plant and leaf size, and the Fertility function was driven mostly by changes in plant
369 size and leaf characteristics (Fig. S4 in Supplementary Information).

370 We then used Structural Equation Modelling²⁹ to explore potential associations
371 among biotic and abiotic factors and the fertile island effect. Our *a priori* model (Fig.
372 S5 in Supplementary Information) included environmental drivers (aridity,
373 temperature, rainfall seasonality), soil (sand content, pH) and vegetation (perennial
374 plant richness, relative cover of woody plants) properties, plant traits (the nine most
375 important plant traits related to size, leaf characteristics, and inherent properties of
376 woody plants such as the type of roots or whether they are allelopathic; identified
377 using the Random Forest analyses, see Methods), and grazing (recent grazing, long-
378 term grazing, and herbivore type). Grazing was included to test its potential indirect
379 effects on the relative fertile island effect for the three soil functions evaluated. Our
380 models revealed that decomposition was enhanced in areas of greater aridity
381 (consistent with the hierarchical linear modelling, though not for carbon
382 mineralisation, Fig. S2 Supplementary Information), more sandy soils, and where
383 focal island species were more palatable (Fig. 4; Fig. S6 Supplementary Information).
384 Fertility tended to be greater in sandy soils and with taller palatable species. Soils
385 with larger values of the Conservation function (more stable, with greater water
386 holding capacity) tended to be associated with taller island plants, potentially through
387 mechanisms involving hydraulic lift³⁰, and at plots supporting more perennial plant
388 species (Fig. S6 Supplementary Information). A potential explanation for the link
389 between the Conservation function, and both plant height and richness could relate to
390 a greater leaf area³¹ of larger island plants and therefore reduced surface evaporation
391³². After accounting for all direct and indirect pathways from both abiotic and biotic
392 factors, our SEMs confirm that grazing had no effects on the three functions
393 evaluated.

394 Among plant traits, plant size (height and canopy) was particularly important,
395 with larger canopies associated with greater RII values of all three functions (but only
396 for grasses), and taller grasses with greater RII values of the Decomposition function
397 (Fig. S7 in Supplementary Information. Larger grasses are functionally more efficient
398 at capturing resources³³ and enhancing hydrological functions^{34,35} and may be a
399 response to declining landscape productivity³⁶. Larger plants may be avoided more
400 by herbivores due to higher concentrations of tannins and secondary compounds³⁷.
401 Similarly, taller shrubs were associated with larger values of the Conservation and
402 Fertility, but not Decomposition, functions (Fig. S7 in Supplementary Information).
403 Taller shrubs would return more litter to the soil surface³⁸, provide more varied
404 habitat³⁹ and concentrate more resources excreted by canopy-resident invertebrates
405⁴⁰, potentially accounting for greater fertility²⁰. Finally, larger shrubs would support a
406 greater density of understorey protégé species⁴¹ and have a larger legacy effect on
407 soils after death⁴². Interestingly, trees with larger canopies were associated with
408 lower values of the Decomposition and Conservation functions (Fig. S7 in
409 Supplementary Information). Large tree canopies are often preferred camping sites for
410 herbivores³⁹, leading to declines in soil structure⁴³, and reductions in soil water
411 holding capacity due to the proliferation of surface roots. Our results could suggest a
412 waning of the fertile island effect under large trees.

413 Overall, our work provides solid evidence that factors such as climate and plant
414 traits can overshadow the influence of factors such as grazing pressure on the capacity
415 of plants to create fertile islands across global drylands. Our findings indicate that
416 fertile islands will prevail in more arid environments regardless of grazing pressure
417 and the composition of herbivores. In these environments, fertile islands sustain
418 healthy and functional soils, moderate adverse environmental conditions, and
419 provides refugia for plants and animals. Our results dispel the long-term assumption
420 that increasing grazing pressure, either recent or longer term, or differences in
421 herbivore type, can explain the magnitude of fertile island effects in drylands. Plant
422 size, with taller and wider shrubs and grasses, supported stronger island effects. Stable
423 and functional soils were also linked to species-rich sites with taller plants. The
424 overwhelming importance of aridity and plant traits suggests that fertile islands may
425 represent an autogenic response to drying and warming climates. These
426 biogeochemical hotspots are likely to be more important as Earth's climate becomes
427 hotter and drier.

428

429 **Methods**

430 **Study area**

431 We surveyed 288 plots at 88 sites in 25 countries on all continents except Antarctica
432 (Algeria, Argentina, Australia, Botswana, Brazil, Canada, Chile, China, Ecuador,
433 Hungary, Iran, Israel, Kazakhstan, Kenya, Mexico, Mongolia, Namibia, Niger,
434 Palestine, Peru, Portugal, South Africa, Spain, Tunisia, and United States of America,
435 Fig. 1). We used the sites described in ref. 12, but excluded 10 sites that did not have

436 sufficient trait data (see below). Site selection aimed to capture as much as possible of
437 the wide variety of abiotic (climate, soil type, slope) and biotic (vegetation type, cover
438 and species richness) features characterizing dryland ecosystems (e.g., grasslands,
439 shrublands, savannas, open woodlands) found in drylands worldwide ^{12,44}. Elevation
440 varied between 12 m and 2214 m a.s.l, and slope from 0° to 31.6°. The surveyed sites
441 encompassed a wide variety of the representative vegetation physiognomies,
442 including grasslands, shrublands, savannas and open woodlands (Fig. 1) found in
443 drylands. Sites were surveyed between January 2016 and September 2019 ^{12,44}.

444 **Establishing and defining local grazing gradients**

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

454 Field surveyors, who were all intimately associated with the long-term grazing
455 history of these sites, characterised their plots using this four-scale heuristic category
456 (ungrazed, low, moderate, high). Grazing pressure gradients were confirmed by
457 measuring the mass of herbivore dung *in situ* ⁶. Dung production is known to be
458 closely linked to animal activity, time spent grazing, and therefore grazing pressure
459 ^{45,46}, though more studies are needed in arid systems to validate these relationships.
460 To measure dung, we collected the dung of different herbivores from within two 25
461 m² (where herbivores were large bodied, e.g., cattle, horses, large ungulates) or 1 m²
462 (when herbivores were smaller bodied e.g., goats, sheep, rabbit, guanaco) quadrats ⁴⁴.
463 Dung was oven dried and expressed as a mass per area. Where herbivores produced
464 pellets, dung was counted from different herbivores, a subsample collected, and
465 following oven drying, used to calculate the relationship between counts and oven-dry
466 dung mass (Text S1 in Supplementary Information).

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

476 For each plot, we standardised the value of the mass of dung of all herbivores
477 within a plot by the maximum dung mass at that particular site (collection of plots).

478 Standardized values ranged from 0 to 1 (0.30 ± 0.01 , mean \pm SE) across the 88 sites.
479 A value of 1 for a particular plot indicates that this plot had the greatest grazing
480 pressure for that site and zero was ungrazed. This approach to standardising dung
481 mass within sites ensures the equivalence of sites that might have markedly different
482 levels of dung production, due to variation in site productivity, but have the same
483 level of grazing pressure (e.g., moderate grazing pressure). The method has also been
484 validated multiple times in grazing studies^{49,50}. Across our global study we recorded
485 29 different herbivore types, of which five were livestock (cattle, goat, sheep, donkey,
486 horse)¹².

487 Dung mass was a good proxy of grazing pressure using two approaches (see Text
488 S1 in Supplementary Information). First, there was a significant positive relationship
489 between dung mass and livestock density for a subset of sites in Iran, Australia, and
490 Argentina for which we had data on dung mass and animal density¹². Second, we
491 performed a cluster analysis⁵¹ to identify the optimum number of dung-based
492 clusters, based on dung mass, and found that this aligned well with the four heuristic
493 levels of grazing pressure¹².

494 Third, we linked the four heuristic measures of long-term (decadal to multi-
495 decadal) grazing pressure to the presence of livestock tracks; semi-permanent features
496 created by livestock when they traverse the same path to and from water⁵². The
497 density and size of these tracks is a useful indicator of the history of livestock grazing
498⁵³. We measured the width and depth of all livestock tracks crossing each of the 45 m
499 transects to derive a total cross-sectional area of tracks for each plot and expressed
500 this as the total track density and cross-sectional area per 100 m of transect (Fig. S8).
501 In summary, these three comprehensive measures of grazing intensity by herbivores
502 showed very similar trends, irrespective of whether we used dung mass as a measure
503 of recent grazing pressure, or the expert heuristic site classification as a measure of
504 long-term grazing pressure. This gives us a high degree of confidence that the
505 gradients we observed are true gradients in grazing pressure.

506 **Vegetation and plant trait measurements**

507 Field surveys followed a standardised sampling protocol⁴⁴. Briefly, within each plot,
508 we located four 45 m transects oriented downslope, spaced 10 m apart across the
509 slope, for the vegetation surveys. Along each 45 m transect we assessed the cover of
510 perennial plants, by species, within 25 contiguous 1.5 m by 1.5 m quadrats. Perennial
511 plants were then recorded every 10 cm along this transect to obtain a measure of
512 perennial plant cover. Total plot-level plant richness was calculated as the total
513 number of unique perennial plant species found within at least one of the survey
514 methods (transects or quadrats) employed. In each site, we measured the height and
515 lateral spread of five randomly selected individuals of the dominant island plants.
516 Lateral spread (canopy width), a proxy of plant area, was assessed by measuring plant
517 diameter in two orthogonal directions through the plant centre. Fresh leaves were
518 collected from the same plants to assess an additional four plant traits in the
519 laboratory (leaf length, leaf area, and leaf carbon and nitrogen contents). These six

520 traits describe the size and leaf characteristic of the 162 perennial species in the
521 vegetation patch that was dominated by trees, shrubs, or large perennial grasses, and
522 which we assessed as potential fertile islands (see detailed measurements in Text S2
523 in Supplementary Information). Twenty-three percent of plots supported two co-
524 dominant island species (i.e., two different tree, shrub, or grass species). For these
525 plots, soil biogeochemical and plant trait data were weighted according to the mean
526 cover of the co-dominant species within a plot.

527 We compiled information on eight additional plant traits (i.e., plant canopy
528 shape, whether foliage reached the ground surface, N-fixation, deciduousness,
529 allelopathy, palatability, resprouting, root type) using information from online plant
530 trait databases such as BROT⁵⁴, PLANTS⁵⁵, Woody Plants Database
531 (<http://woodyplants.cals.cornell.edu>) and TRY⁵⁶. The eight categorical traits above
532 were ranked numerically such that a larger value equated with greater function in
533 terms of its own growth or its facilitatory effect on surrounding neighbours and
534 conditions. This procedure is described in detail in Text S2 in Supplementary
535 Information.

536 **Soil properties and sampling**

537 Soils were sampled during the dry season. In each plot, five sampling points were
538 randomly located in open areas devoid of perennial vascular plants (< 5% plant cover,
539 hereafter ‘open’ microsite), and another five placed beneath the canopy of five
540 randomly selected individuals of the dominant island plant (Text S3 in Supplementary
541 Information). A composite sample of five 145 cm³ soil cores (0-7.5 cm depth) was
542 collected from beneath each plant or bare area, bulked, and homogenized in the field.
543 Soil samples were air-dried for 1 month, sieved (< 2 mm) and stored for physico-
544 chemical analyses. The samples were then bulked to obtain one composite sample per
545 plot for vegetated (island) and a separate composite sample for open areas. All
546 analyses described here are for two composite samples per plot. We assessed soil pH
547 (1:2.5 soil water suspension, sand content⁵⁷, and the values of 24 soil ecological
548 attributes that are linked to three ecosystem functions (Table S1 in Supplementary
549 Information).

550 **Assessment of ecosystem functions**

551 We calculated a relative interaction index (RII) and its 95% confidence interval⁵⁸ for
552 the 24 ecological attributes as measures of the fertile island effect. A positive (or
553 negative) value indicates a greater (or lesser) value of that attribute, respectively, in
554 island soils. The RII is defined as the relative difference between attributes beneath
555 the perennial plant islands and their open interspaces and was calculated as $RII = (X_I$
556 $- X_O) / (X_I + X_O)$, where X_I and X_O represent the mean values of a given ecological
557 attribute beneath a perennial plant patch (island) and in the open interspace,
558 respectively. Values of the RII range from -1 to 1, with positive values indicating
559 greater levels of a given attribute beneath the island and vice versa. Evidence of the
560 fertile island effect (either positive or negative) is based on whether the 95%

561 confidence intervals (95% CIs), calculated using ‘Rmisc’ package in R ⁵⁹ cross the
562 zero line.

563 We focussed on three proxies of function derived from the average RII of
564 different combination of the 24 soil attributes: 1) organic matter decomposition,
565 quantified using the activity of five soil extracellular enzymes related to the
566 degradation of organic matter [β -glucosidase, phosphatase, cellobiosidase, β -N-
567 acetylglucosaminidase and xylase], and measurements of soil carbon (hereafter
568 ‘Decomposition’ (2) soil fertility, evaluated using multiple proxies of soil nutrient
569 availability and carbon (contents of dissolved organic and total N, NH_4^+ , NO_3^- , total
570 P, Mn, K, Zn, Mg, Fe, Cu and soil C, hereafter ‘Fertility’), and 3) resource
571 conservation (water regulation, using measures of soil water holding capacity, soil
572 porosity, stability of macro-aggregates $>250 \mu\text{m}$ and mean weight diameter of soil
573 aggregates (hereafter ‘Conservation’). Detailed measurements on these 24 soil
574 ecological attributes are described in Table S1 in Supplementary Information.

575 **Data compilation and statistical analysis**

576 Rainfall seasonality (coefficient of variation of 12 monthly rainfall totals) data were
577 extracted from the WorldClim Version 2.0 (<http://www.worldclim.org/>) ⁶⁰ database,
578 which provides global climate data ($0^{\circ}30'' \times 0^{\circ}30''$) for the 1970-2000 period. Aridity
579 was identified as precipitation/potential evapotranspiration and was derived from the
580 Global Aridity Index and Potential Evapotranspiration Climate Database v2 aridity
581 database ([https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-
582 evapotranspiration-climate-database-v2/](https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/)) ⁶¹, which includes global aridity data ($0^{\circ}30''$
583 $\times 0^{\circ}30''$) for the 1970-2000 period. Soil texture is a major determinant of water
584 holding capacity and pH is a major driver of plant and soil function in drylands ⁶².
585 Sand content and pH data used in this study were obtained from samples taken from
586 the open areas (to ensure that their effects on the ecosystem functions measured are as
587 independent from those of organisms as possible). Relative woody cover was included
588 to account for different levels of woody plants so that this would not bias any results.
589 Standardized dung mass (dung mass in a plot/maximum dung mass within the site)
590 was used as a measure of recent grazing pressure.

591 **Statistical analyses**

592 We fitted a Bayesian hierarchical linear mixed model to evaluate whether the fertile
593 island effect differed (1) with increasing grazing pressure (continuous data:
594 standardized dung mass), 2) with long-term grazing pressure (categorical data:
595 ungrazed, low, moderate, high grazing), and 3) among herbivore types (categorical
596 data: sites dominated by either livestock, native, or mixed groups of native and
597 livestock). Our RII values were modelled with a Gaussian (normal) distribution, with
598 all individual ecosystem attributes ($n = 24$) estimated simultaneously in a single
599 model. Note that RII values are calculated at the plot level whereas grazing pressure is
600 calculated at the site level. The standardised response variable (RII) was modelled
601 hierarchically as a function of recent grazing pressure (standardised dung), long-term
602 grazing pressure (high, medium, low, ungrazed), herbivore type (livestock, native,

603 mixed), aridity, island type (tree, shrub, grass), and functional category
604 (Decomposition, Fertility, Conservation). The model fitted individual ecosystem
605 functional attributes as groups (random intercepts) with varying slopes associated
606 with each of the main covariates (grazing and aridity). The model also included
607 interactions between ecosystem function category and grazing, island type, and aridity
608 to account for potential differences in the effects of each covariate within each
609 ecosystem function category. We included site as a random intercept, accounting for
610 the non-independence of data gathered from the same site.

611 We specified weakly informative normally distributed priors for the intercept and
612 all regression coefficients (mean = 0 and scale = 2.5). Default priors were used for
613 sigma (exponential, rate = 1) and variance-covariance matrix of the varying intercepts
614 and slope parameters (shape and scale of 1). Posterior simulations of model
615 parameters were undertaken using the No-U-Turn Hamiltonian Monte Carlo sampler
616 within Stan ⁶³. Posterior distributions were estimated from four chains, each with
617 1000 iterations, after discarding the preliminary 1000 iterations. The convergence of
618 models was assessed using visual diagnostics (autocorrelation, trace plots, and
619 posterior predictive checks) and inspection of effective sample sizes (min. 1000) and
620 \hat{r} values (<1.01). Models were fitted using the package 'rstanarm' ⁶⁴ within R ⁵⁹. A
621 hierarchical model provides several benefits over simple averaging of standardised
622 indicators or multiple separate models ⁶⁵: (i) simultaneous modelling of multiple
623 attributes improves precision and estimates of uncertainty for each ecosystem function
624 category; (ii) non-independence of multiple attributes within sites is explicitly
625 accounted for; (iii) enables simultaneous estimation of overall fertile island effect for
626 each ecosystem functional category and the individual soil attributes within these.

627 Structural Equation Modelling (SEM ²⁹) was employed to explore the direct and
628 indirect impact of climate (aridity [ARID], rainfall seasonality [SEAS]), soil pH (pH),
629 sand content (SAND), vegetation attributes (plot-level perennial plant cover [COV]
630 and plant richness [RICH], plant height [HT], canopy width [WIDTH], shape
631 [SHAPE], leaf length [LNGTH], leaf area [AREA], palatability [PALAT],
632 resprouting [RESP], deciduousness [DECID], and allelopathy [ALLELO]), and
633 grazing (standardised grazing pressure) on the fertile island effect (RII) after
634 accounting for the effects of location (latitude, cosine longitude, sine longitude)
635 across the globe. All explanatory variables were standardized (z-transformed) in the
636 SEM analyses. The nine plant traits used in these analyses were selected from a
637 potential pool of 15 potential traits using the significance of percentage increase in
638 mean square error using Random Forest analyses (Fig. S3 in Supplementary
639 Information). With these analyses we aimed to determine which traits are the most
640 influential in describing the relative difference between islands and their interspaces
641 (as measured with the RII) for each of the three synthetic functions (Decomposition,
642 Fertility, Conservation). Random Forest is a robust approach when working with
643 continuous and categorical variables. The 15 traits considered, which relate to plant
644 size and structure, leaf characteristics, and ability to respond to environmental stimuli
645 (palatability, resprouting, deciduousness, allelopathy) potentially influence: 1) how

646 nutrients are mineralized and made available to plants (Decomposition), 2) contribute
647 to soil nutrient (including carbon) pools (Fertility) and 3) how soil and water are
648 conserved (Conservation). Random forest analyses were conducted with the
649 rfPermute package ⁶⁶.

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

668

669 **Data Availability**

670 The data used for this study will be make public within the Figshare repository upon
671 publication. <https://doi.org/10.6084/m9.figshare.24873135.v1>

672

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708 **Author contributions**

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

715 **Competing interests**

716 The authors declare no competing interests.

717 **References**

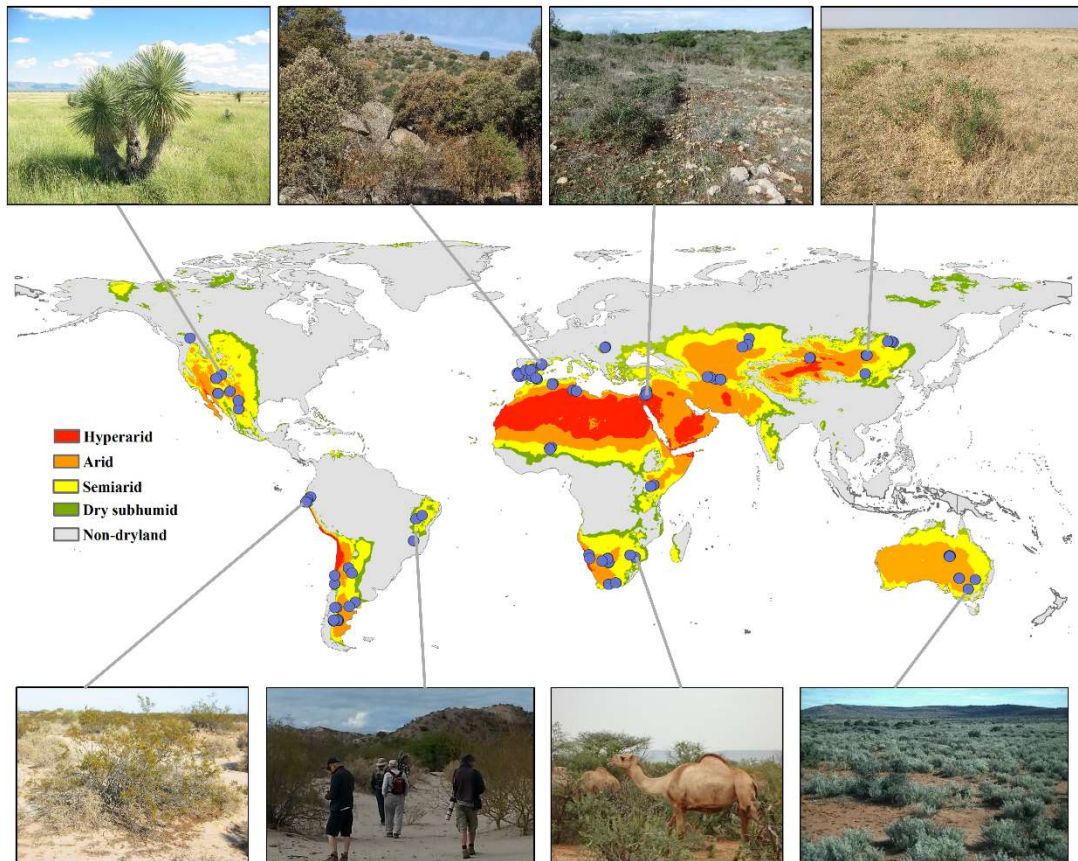
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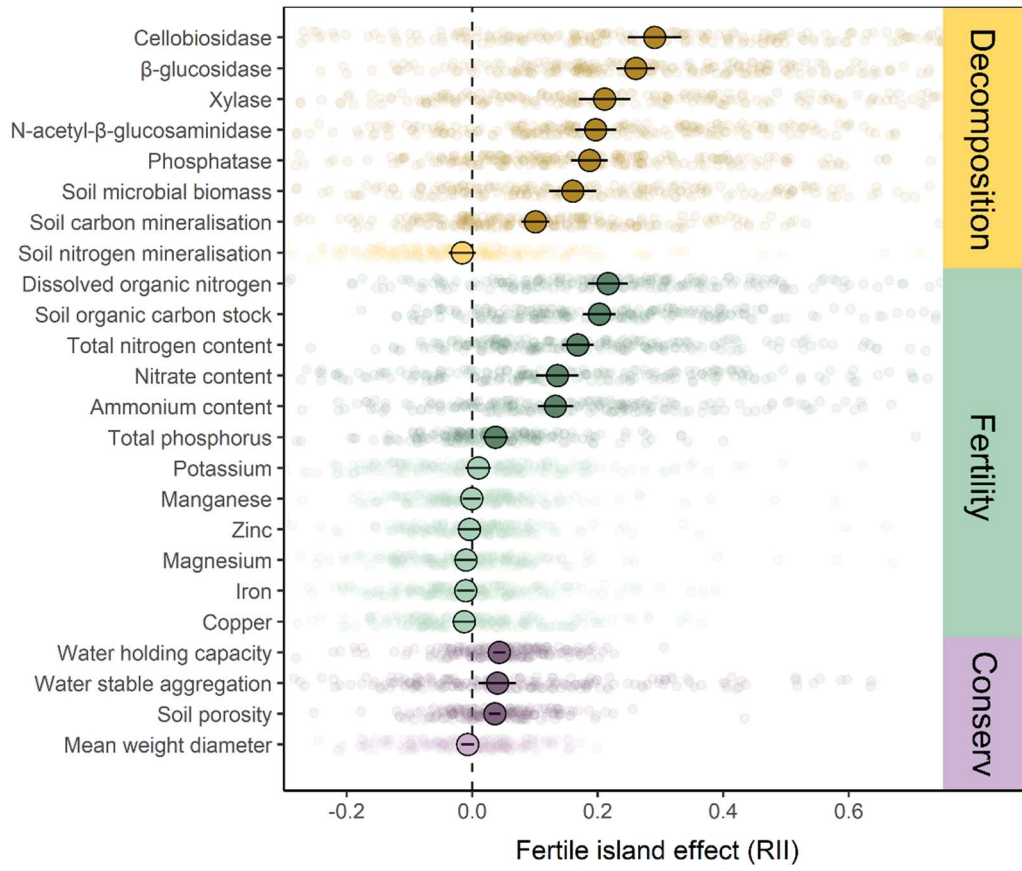


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884 **Figure 1.** Average function (mean relative interaction effect value across 24 soil
 885 attributes, see Methods) for the 288 plots at 88 sites across global drylands and
 886 examples of fertile islands at selected sites. The background map shows the
 887 distribution of aridity ($1 - [\text{precipitation}/\text{potential evapotranspiration}]$) across global
 888 drylands.

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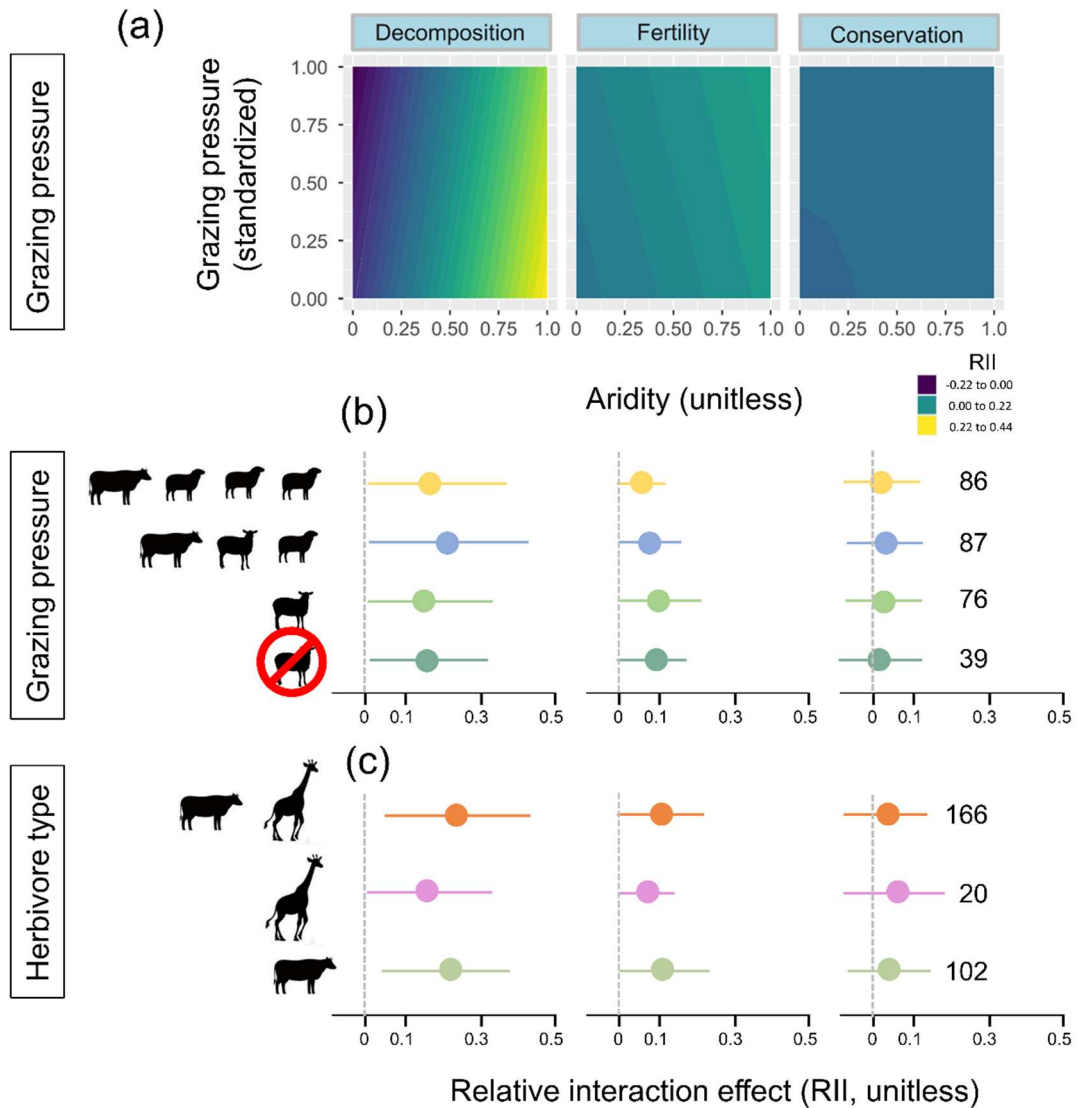
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893 **Figure 2.** The fertile island effect, as measured with the relative interaction effect
 894 (RII), beneath perennial dryland plants for the 24 soil attributes measured across three
 895 functions. Conserv = Conservation. Error bars are 95% CI and darker colours indicate
 896 significant positive effects.

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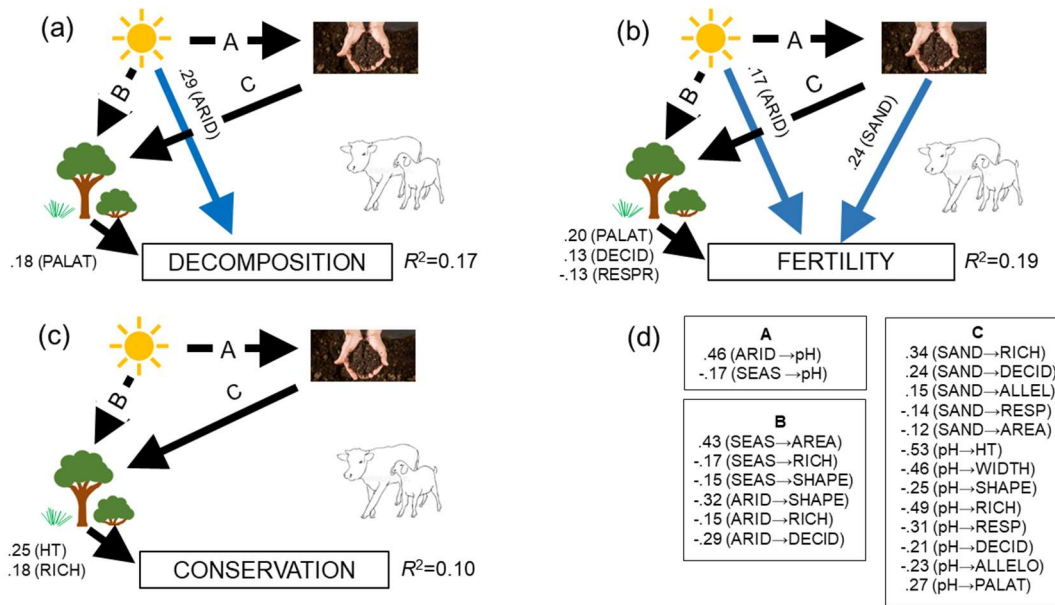
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901 **Figure 3.** Impacts of recent grazing and climate on the fertile island effect. (a)
 902 Relative interaction effect (RII) value surfaces for the three measures of ecosystem
 903 function (Decomposition, Fertility, Conservation) in relation to recent grazing
 904 pressure (standardized dung mass) and aridity, and mean (\pm 95% CI) predicted RII
 905 value for the three functions in relation to (b) long-term (historic) measure of
 906 herbivore grazing pressure (ungrazed, low, medium, high), and (c) herbivore type
 907 (livestock, native, mixed).



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910 **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.