

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

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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 <sup>1,2</sup>. 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 <sup>1,3,4</sup>. 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 <sup>5</sup>. 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 <sup>6,7</sup>, potentially intensifying the fertile  
235 island effect by exacerbating the loss of resources from the interspaces and its  
236 supplementation in nearby islands <sup>8</sup>. 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 <sup>9</sup>.  
239 Globally, there is little empirical support for the putative importance of grazing as a  
240 causal agent of the fertile island effect <sup>10,11</sup>, 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 <sup>12</sup>.

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 <sup>8,13</sup>.

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 <sup>14,15</sup>. 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 soils <sup>6</sup>,  
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, a  
275 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 form <sup>12</sup>.

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 <sup>11,13,16,17</sup>, soil physical properties <sup>9</sup>, hydrology <sup>18,19</sup> and microbial community structure  
308 <sup>4</sup>. 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 <sup>4,20</sup>, microbial activity and plant biomass <sup>21</sup> beneath  
311 perennial plant canopies <sup>22,23</sup>. 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 drylands <sup>4</sup>, and this likely accounts for their potential  
316 role as facilitators of protégé plant species through resource supplementation <sup>24</sup>.

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-analyses<sup>25</sup>. 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 grazing<sup>11</sup>. 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 desertification<sup>26</sup>. 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 patches<sup>27</sup>. 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 canopies<sup>28</sup>. 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 Modelling<sup>29</sup> 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 with  
385 larger values of the Conservation function (more stable, with greater water holding  
386 capacity) tended to be associated with taller island plants, potentially through  
387 mechanisms involving hydraulic lift<sup>30</sup>, 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 area<sup>31</sup> of larger island plants and therefore reduced surface evaporation  
391<sup>32</sup>. 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 resources<sup>33</sup> and enhancing hydrological functions<sup>34,35</sup> and may be a  
399 response to declining landscape productivity<sup>36</sup>. Larger plants may be avoided more  
400 by herbivores due to higher concentrations of tannins and secondary compounds<sup>37</sup>.  
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 surface<sup>38</sup>, provide more varied  
404 habitat<sup>39</sup> and concentrate more resources excreted by canopy-resident invertebrates<sup>40</sup>,  
405 potentially accounting for greater fertility<sup>20</sup>. Finally, larger shrubs would support a  
406 greater density of understorey protégé species<sup>41</sup> and have a larger legacy effect on  
407 soils after death<sup>42</sup>. 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 herbivores<sup>39</sup>, leading to declines in soil structure<sup>43</sup>, 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 provides

419 refugia for plants and animals. Our results dispel the long-term assumption that  
420 increasing grazing pressure, either recent or longer term, or differences in herbivore  
421 type, can explain the magnitude of fertile island effects in drylands. Plant size, with  
422 taller and wider shrubs and grasses, supported stronger island effects. Stable and  
423 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<sup>12,44</sup>. 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<sup>12,44</sup>.

### 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*<sup>6</sup>. Dung production is known to be  
458 closely linked to animal activity, time spent grazing, and therefore grazing pressure  
459<sup>45,46</sup>, though more studies are needed in arid systems to validate these relationships. To  
460 measure dung, we collected the dung of different herbivores from within two 25 m<sup>2</sup>  
461 (where herbivores were large bodied, e.g., cattle, horses, large ungulates) or 1 m<sup>2</sup>  
462 (when herbivores were smaller bodied e.g., goats, sheep, rabbit, guanaco) quadrats<sup>44</sup>.  
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<sup>47</sup>. 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<sup>48</sup>. 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 ( $0.30 \pm 0.01$ , 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<sup>49,50</sup>. Across our global study we recorded  
485 29 different herbivore types, of which five were livestock (cattle, goat, sheep, donkey,  
486 horse)<sup>12</sup>.

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 density<sup>12</sup>. Second, we  
491 performed a cluster analysis<sup>51</sup> 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 pressure<sup>12</sup>.

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 water<sup>52</sup>. The  
497 density and size of these tracks is a useful indicator of the history of livestock grazing  
498<sup>53</sup>. 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 protocol<sup>44</sup>. 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 BROT<sup>54</sup>, PLANTS<sup>55</sup>, Woody Plants Database  
531 (<http://woodyplants.cals.cornell.edu>) and TRY<sup>56</sup>. 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 cm<sup>3</sup> 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 content<sup>57</sup>, 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 interval<sup>58</sup> 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 <sup>59</sup> 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 [ $\beta$ -glucosidase, phosphatase, cellobiosidase,  $\beta$ -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,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , total P,  
570 Mn, K, Zn, Mg, Fe, Cu and soil C, hereafter ‘Fertility’), and 3) resource conservation  
571 (water regulation, using measures of soil water holding capacity, soil porosity,  
572 stability of macro-aggregates  $>250 \mu\text{m}$  and mean weight diameter of soil aggregates  
573 (hereafter ‘Conservation’). Detailed measurements on these 24 soil ecological  
574 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/>) <sup>60</sup> database,  
578 which provides global climate data ( $0'30'' \times 0'30''$ ) 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://cgiaresi.community/2019/01/24/global-aridity-index-and-potential-  
582 evapotranspiration-climate-database-v2/](https://cgiaresi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/)) <sup>61</sup>, which includes global aridity data ( $0'30''$   
583  $\times 0'30''$ ) 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 <sup>62</sup>.  
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 <sup>63</sup>. 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’ <sup>64</sup> within R <sup>59</sup>. A  
621 hierarchical model provides several benefits over simple averaging of standardised  
622 indicators or multiple separate models <sup>65</sup>: (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 <sup>29</sup>) 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], resprouting  
632 [RESP], deciduousness [DECID], and allelopathy [ALLELO]), and grazing  
633 (standardised grazing pressure) on the fertile island effect (RII) after accounting for  
634 the effects of location (latitude, cosine longitude, sine longitude) across the globe. All  
635 explanatory variables were standardized (z-transformed) in the SEM analyses. The  
636 nine plant traits used in these analyses were selected from a potential pool of 15  
637 potential traits using the significance of percentage increase in mean square error  
638 using Random Forest analyses (Fig. S3 in Supplementary Information). With these  
639 analyses we aimed to determine which traits are the most influential in describing the  
640 relative difference between islands and their interspaces (as measured with the RII)  
641 for each of the three synthetic functions (Decomposition, Fertility, Conservation).  
642 Random Forest is a robust approach when working with continuous and categorical  
643 variables. The 15 traits considered, which relate to plant size and structure, leaf  
644 characteristics, and ability to respond to environmental stimuli (palatability,  
645 resprouting, deciduousness, allelopathy) potentially influence: 1) how nutrients are  
646 mineralized and made available to plants (Decomposition), 2) contribute to soil  
647 nutrient (including carbon) pools (Fertility) and 3) how soil and water are conserved  
648 (Conservation). Random forest analyses were conducted with the rfPermute package  
649 <sup>66</sup>.

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  $\chi^2$   
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.,  
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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.

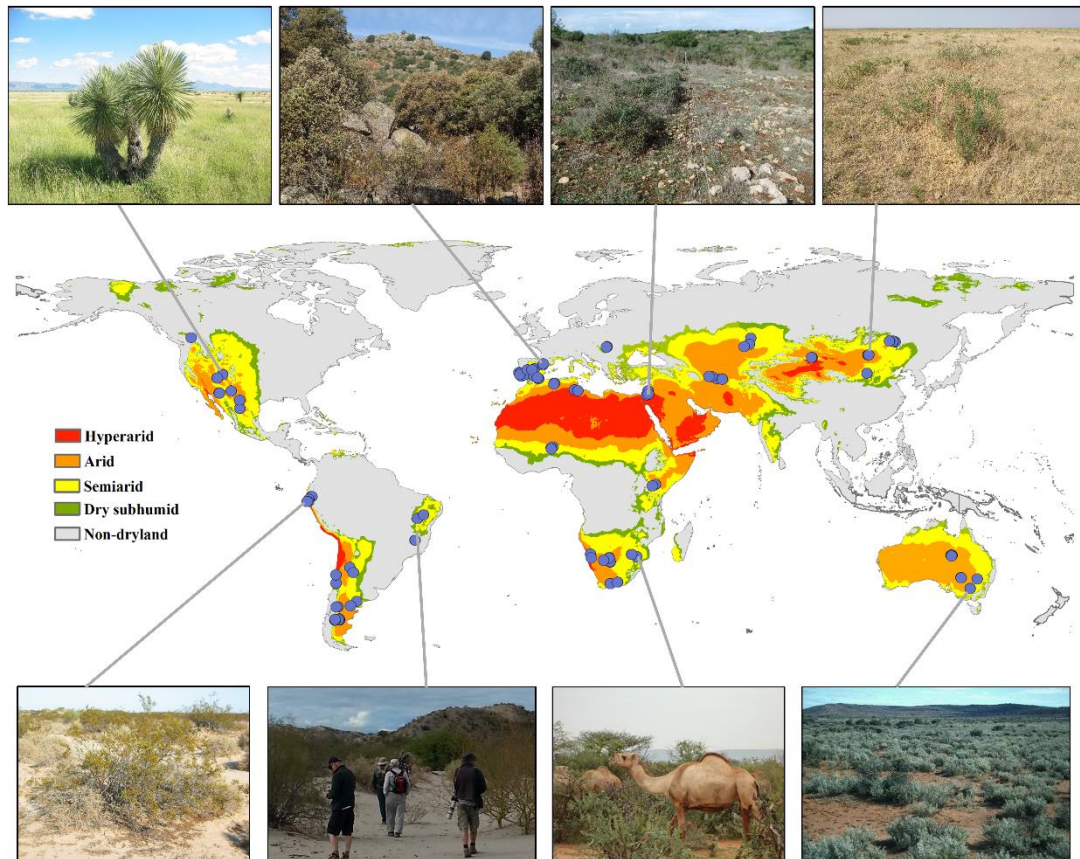
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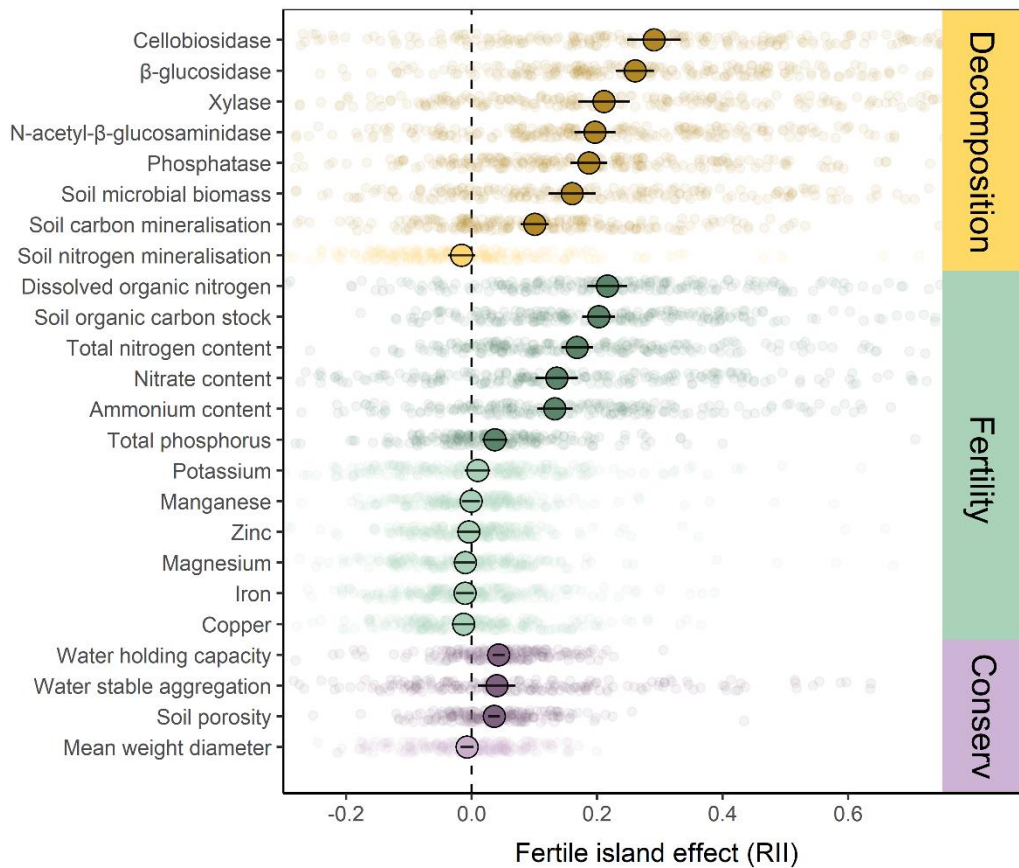
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884 **Figure 1.** Average function (mean relative interaction effect value across 24 soil  
 885 attributes, see Methods) for the 288 plots at 88 sites across global drylands and  
 886 examples of fertile islands at selected sites. The background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

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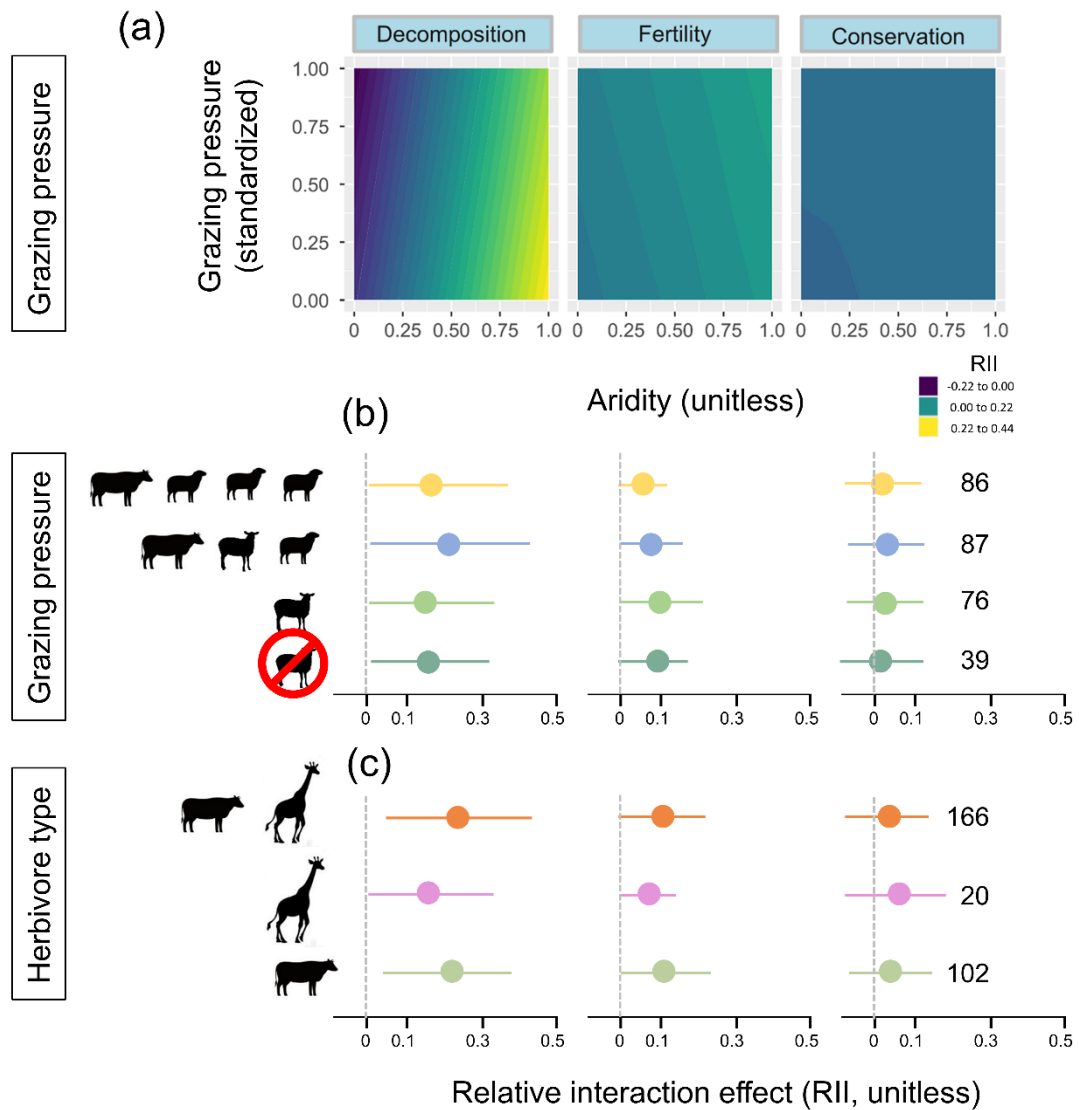
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893 **Figure 2.** The fertile island effect, as measured with the relative interaction effect  
894 (RII), beneath perennial dryland plants for the 24 soil attributes measured across three  
895 functions. Conserv = Conservation. Error bars are 95%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

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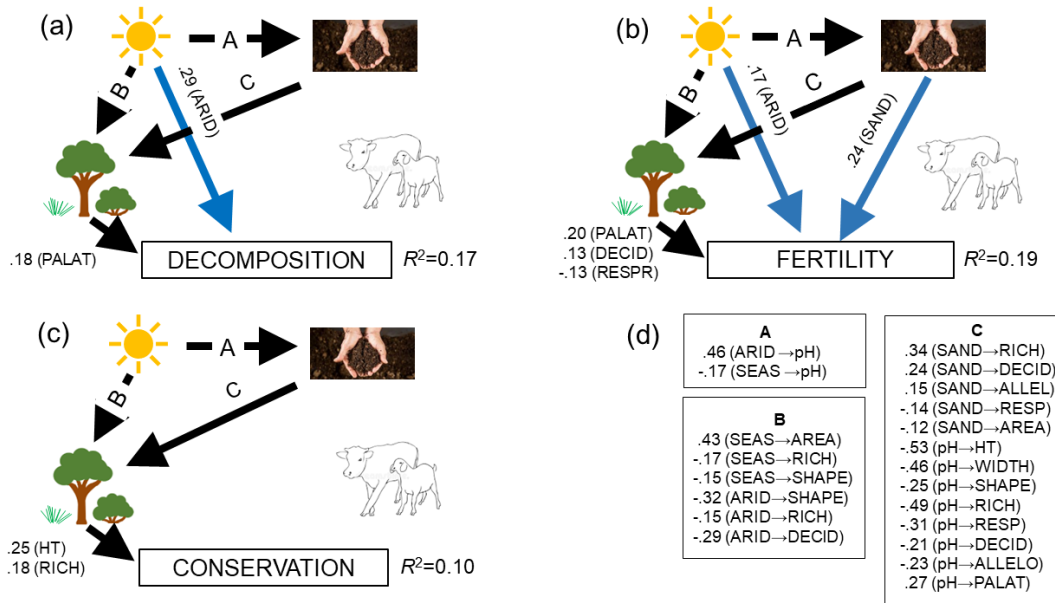
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901 **Figure 3.** Impacts of recent grazing and climate on the fertile island effect. (a)  
 902 Relative interaction effect (RII) value surfaces for the three measures of ecosystem  
 903 function (Decomposition, Fertility, Conservation) in relation 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).



908

909

910 **Figure 4.** Structural equation modelling assessing the direct and indirect effects of  
 911 climate (aridity [ARID], rainfall seasonality [SEAS]), soil (pH and sand [SAND]  
 912 content), plants (perennial cover [COV], perennial plant richness [RICH]), plant  
 913 height [HT], plant shape [SHAPE], leaf area [AREA], leaf length [LNGTH], canopy  
 914 width [WIDTH], palatability [PALAT], deciduousness [DECID], resprouting ability  
 915 [RESP], and allelopathy [ALLEL]), and grazing (standardized grazing pressure) on  
 916 the fertile island effect for soil decomposition (Decomposition), soil fertility (Fertility)  
 917 and soil and water conservation (Conservation), after accounting for the effects of  
 918 location (latitude, cosine longitude, sine longitude). Standardised path coefficients,  
 919 adjacent to the arrows, are analogous to partial correlation coefficients, and indicative  
 920 of the effect size of the relationship. Pathways are significantly negative (red  
 921 unbroken line), significant positive (blue unbroken line) or mixed significant negative  
 922 and significant positive (black unbroken lines). Non-significant pathways are not  
 923 shown in the models. Model fit: (a) organic matter decomposition:  $\chi^2 = 31.9$ ,  $df = 26$ ,  
 924  $P = 0.20$ ,  $R^2=0.17$ , root mean error of approximation (RMSEA) < 0.001, Bollen-Stine  
 925 = 0.40 (2000 bootstrap); (b) Fertility:  $\chi^2 = 31.9$ ,  $df = 26$ ,  $P = 0.20$ ,  $R^2=0.19$ , root mean  
 926 error of approximation (RMSEA) < 0.001, Bollen-Stine = 0.40 (2000 bootstrap); (c)  
 927 Conservation:  $\chi^2 = 31.9$ ,  $df = 26$ ,  $P = 0.20$ ,  $R^2=0.10$ , root mean error of approximation  
 928 (RMSEA) < 0.001, Bollen-Stine = 0.40 (2000 bootstraps). N=288 for all analyses.

929



930 **Supplementary Information for**  
931  
932 **Hotspots of biogeochemical activity linked to aridity and plant traits across**  
933 **global drylands**  
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937 **This PDF file includes:**  
938 **Supplementary Tables S1 to S3**  
939 **Figures S1 to S8**  
940 **Supplementary Text S1 to S3**  
941 **Supplementary References**  
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944 **A1. Supplementary Tables**

945

946 **Table S1** Soil attributes comprising the three synthetic groups of functions.

947

<b>Groups of functions</b>	<b>Soil attribute</b>	<b>Abbreviation</b>	<b>Units</b>
Decomposition	Activity of cellobiosidase	CB	nmol activity·g <sup>-1</sup> ·h <sup>-1</sup>
	Activity of β-glucosidase	BG	μmol PnP·g <sup>-1</sup> ·h <sup>-1</sup>
	Activity of xylanase	XYL	nmol activity·g <sup>-1</sup> ·h <sup>-1</sup>
	Activity of β-N-acetylglucosaminidase	NAG	nmol activity·g <sup>-1</sup> ·h <sup>-1</sup>
	Activity of phosphatase	PHOS	μmol PnP·g <sup>-1</sup> ·h <sup>-1</sup>
	Soil microbial biomass	MICBIOM	μg C mic·g soil·dw <sup>-1</sup>
	Soil carbon mineralization	CARBMIN	μg CO <sub>2</sub> -C·g soil <sup>-1</sup> ·day <sup>-1</sup>
	Soil nitrogen mineralization	NITMIN	mg N·kg soil <sup>-1</sup> ·day <sup>-1</sup>
Fertility	Dissolved organic N content	DON	mg N·kg <sup>-1</sup> soil
	Total N content	TOTN	g N·kg <sup>-1</sup> soil
	NO <sub>3</sub> <sup>-</sup> content	NO3	mg N·kg <sup>-1</sup> soil
	NH <sub>4</sub> <sup>+</sup> content	NH4	mg N·kg <sup>-1</sup> soil
	Total P content	P	mg P·kg <sup>-1</sup> soil
	Mn content	MN	mg Mn·kg <sup>-1</sup> soil
	K content	K	mg K·kg <sup>-1</sup> soil
	Zn content	ZN	mg Zn·kg <sup>-1</sup> soil
	Mg content	MG	mg Mg·kg <sup>-1</sup> soil
	Fe content	FE	mg Fe·kg <sup>-1</sup> soil
	Cu content	CU	mg Cu·kg <sup>-1</sup> soil
	Soil organic C stock	SOC	g C·kg <sup>-1</sup> soil
Conservation	Soil water holding capacity	WHC	g H <sub>2</sub> O·g soil <sup>-1</sup>
	Soil porosity	POROS	%
	Stability of macro-aggregates >250 μm	WSA	%
	Mean weight diameter of soil aggregates	MWD	mm

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949

950 **Table S2.** Summary of the results of hierarchical linear mixed modelling. Coef = coefficient, pd (%) = probability of direction. Coefficients with  
 951 a probability of either a positive or negative effect >95% are shown in **bold**. High, medium, and low refer to historic (long-term) grazing  
 952 pressure assigned to plots based on expert knowledge of the history of grazing at these plots (heuristic assessment).  
 953  
 954

Effect	Parameter	Ecological effects of grazing	Coef	95% CI	pd%
Overall	Aridity	Not significant	0	-0.1 to 0.19	51.2
	Grazing pressure	Not significant	-0.01	-0.0 to 0.05	60.3
	Herbivore Mixed	Not significant	0.05	-0.0 to 0.12	88.1
	Herbivore Native	Not significant	-0.08	-0.2 to 0.05	87.9
	Grazing pressure High	Not significant	-0.02	-0.0 to 0.05	69.5
	Grazing pressure Medium	Not significant	-0.04	-0.1 to 0.02	88.8
	Grazing pressure Low	Not significant	-0.04	-0.1 to 0.02	88.6
	Shrub	Not significant	-0.01	-0.0 to 0.06	60.7
	Tree	Not significant	0.03	-0.0 to 0.12	70.2
	Fertility	Not significant	-0.02	-0.1 to 0.09	62.2
	Decomposition	Not significant	-0.03	-0.1 to 0.08	68.3
	Intercept	Not significant	0.03	-0.1 to 0.17	64.9
Aridity effect	Aridity * Fertility	Not significant	0.06	-0.1 to 0.22	78.0
	<b>Aridity * Decomposition</b>	Strong positive effect of aridity on decomposition	<b>0.31</b>	0.13 to 0.47	100.0
Grazing effect	Fertility * Grazing pressure	Not significant	0.01	-0.0 to 0.06	63.3
	Fertility * Herbivores mixed	Not significant	0	-0.0 to 0.05	55.1
	<b>Fertility * Herbivore native</b>	Weak decline in fertility under native grazing	<b>-0.06</b>	-0.1 to 0.00	95.5
	Fertility * High grazing	Not significant	-0.05	-0.1 to 0.01	92.7
	Fertility * Medium grazing	Not significant	-0.03	-0.0 to 0.02	84.6

	Fertility * Low grazing	Not significant	0	-0.0 to 0.05	50.3
	<b>Decomposition * Grazing pressure</b>	Weak decline in decomposition with increasing pressure	<b>-0.07</b>	-0.1 to -0.0	98.5
	Decomp * Herbivore mixed	Not significant	0.01	-0.0 to 0.06	58.3
	Decomp * Herbivore native	Not significant	-0.06	-0.1 to 0.01	94.7
	Decomp * High grazing	Not significant	0	-0.0 to 0.06	51.1
	Decomp * Medium grazing	Not significant	0.04	-0.0 to 0.10	91.3
	Decomp * Low grazing	Not significant	-0.03	-0.0 to 0.03	79.8
Patch effect	<b>Fertility * Shrub</b>	Weakly greater fertility beneath shrubs	<b>0.04</b>	-0.0 to 0.08	96.7
	<b>Fertility * Tree</b>	Greater fertility beneath trees	<b>0.06</b>	-0.0 to 0.12	97.0
	Decomp * Shrub	Not significant	0	-0.0 to 0.05	52.7
	<b>Decomp * Tree</b>	Lower decomposition beneath trees	<b>-0.06</b>	-0.1 to 0.01	95.4
Patch*Grazing	Shrub * Grazing pressure	Not significant	0	-0.0 to 0.05	52.7
	<b>Shrub * Herbivore mixed</b>	Lower effect beneath shrubs under mixed than native herbivores	<b>-0.07</b>	-0.1 to -0.0	98.5
	<b>Shrub * Herbivore native</b>	Lower effect beneath shrubs under mixed than native herbivores	<b>0.11</b>	-0.0 to 0.23	95.8
	<b>Shrub * High grazing</b>	Consistently weak effect of historical low grazing beneath shrubs	<b>0.08</b>	0.00 to 0.14	98.9
	<b>Shrub * Medium grazing</b>	Consistently weak effect of historical medium grazing beneath shrubs	<b>0.09</b>	0.02 to 0.15	99.7
	<b>Shrub * Low grazing</b>	Consistently weak effect of historical high grazing beneath shrubs	<b>0.07</b>	0.01 to 0.12	99.4
	Tree * Grazing pressure	Not significant	0.04	-0.0 to 0.10	92.1
	<b>Tree * Herbivore mixed</b>	Lower effect beneath trees under mixed grazing	<b>-0.07</b>	-0.1 to 0.01	95.2

	Tree * Herbivore native	Not significant	0.09	-0.0 to 0.23	90.1
	Tree * High grazing	Not significant	-0.03	-0.0 to 0.04	78.1
	Tree * Medium grazing	Not significant	0.06	-0.0 to 0.12	94.3
	<b>Tree * Low grazing</b>	Greater effect beneath trees at low historical grazing	<b>0.07</b>	0.00 to 0.13	98.4

955

956

957 **Table S3** Rationale for the inclusion of different pathways (Path) into our *a priori*  
 958 structural equation model (see Fig. S5 in Supplementary Material) and supporting  
 959 references.  
 960

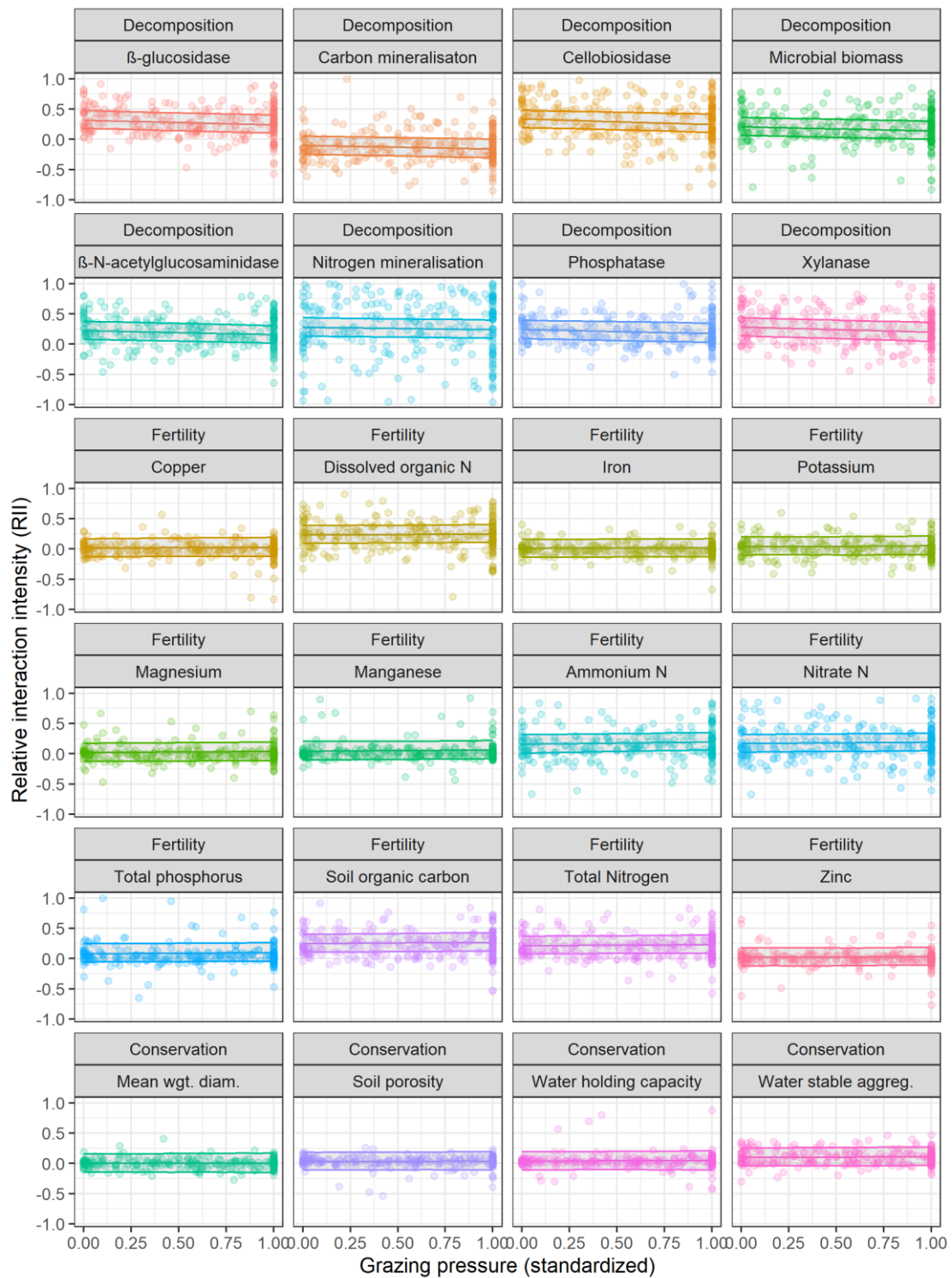
<b>Path</b>	<b>Associations</b>	<b>Rationale</b>
1	Climate → Soil <sup>67,68</sup>	Climate regulates soil properties by affecting physical and chemical processes. For example, aridity affects sand content and soil pH by influencing the magnitude of aeolian processes and soil leaching processes, respectively.
2	Climate → Grazing <sup>69</sup>	Grazing intensity is known to vary with different climatic regimes due to changes in forage production.
3	Climate → Fertile Island effect <sup>70</sup>	The fertile island effect is expected to be higher in arid areas as biological processes of resource accumulation supplanting abiotic processes of redistribution under drying conditions.
4	Climate → Plant <sup>65,71</sup>	Aridity and rainfall seasonality affect plant traits by regulating plant growth and filtering plant species. For example, as aridity increases, plant diversity reduces and plants become sparser and smaller, with deeper roots and higher leaf dry matter content because of adaptation to water limitation and drought.
5	Soil → Plant <sup>72,73</sup>	Soil texture (sand content) and pH are fundamental variables influencing plant growth. For example, neutral soils enhance enzyme activities on breaking down organic matter, thus promoting the growth of plant height and lateral spread. Alkaline soils are likely to reduce species richness by filtering plants with low tolerance.
6	Soil → Fertile Island effect <sup>74,75</sup>	Soil properties affect the accumulation of soil nutrients. For example, soil pH influences soil nutrition cycling by affecting microbe activities, and soil sand content is associated with a higher microbe carbon use efficiency, which enhancing the accumulation of labile carbon.

7	Grazing → Plant <sup>76</sup>	Grazing affects plant traits by selecting species. Plants with taller stem and deeper roots are more resistance to grazing. Our model links increased grazing pressure and herbivore type to plant height and width only.
8	Plant → Fertile Island effect <sup>4,77</sup>	Vegetation attributes and plant traits affect the magnitude of resource accumulation. For example, larger canopies and deeper roots have great capacity of producing litter and scavenge resources, and plants with the ability to fix nitrogen can enhance nutrient availability.
9	Grazing → Fertile Island effect <sup>9</sup>	Grazing is thought to be related to the exacerbation of the fertile island effect by degrading the open interspace and exacerbating the difference between interspace and islands.

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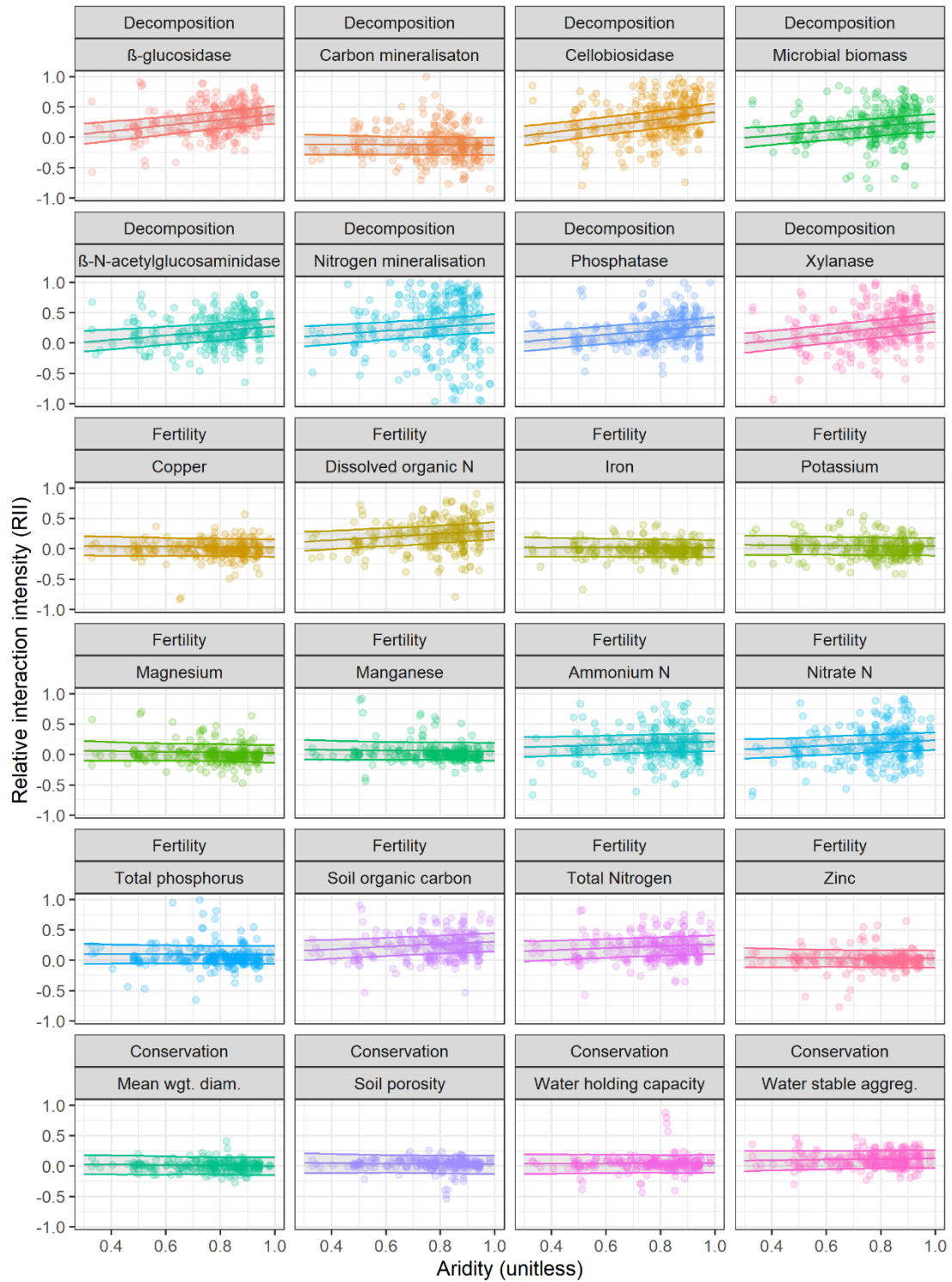
## A2. Supplementary Figures



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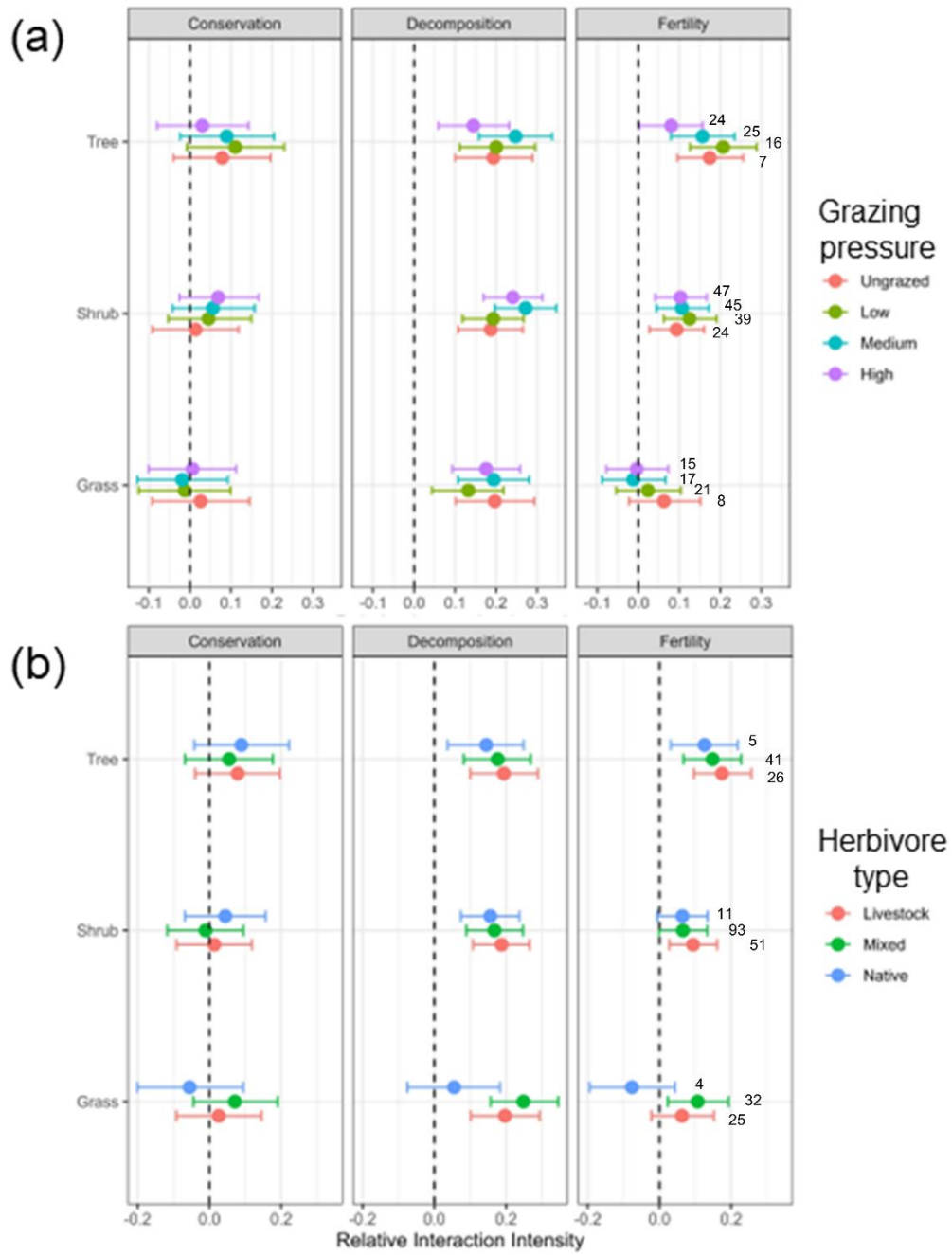
**Figure S1.** Predicted mean (+ 95% CI) and observed fertile island effect, as measured with the relative interaction intensity (RII) index, for each of the 24 soil attributes measured in relation to recent grazing pressure (standardized dung mass). See Supplementary Table S1 and Supplementary Text S3 for descriptions of the 24 attributes evaluated.





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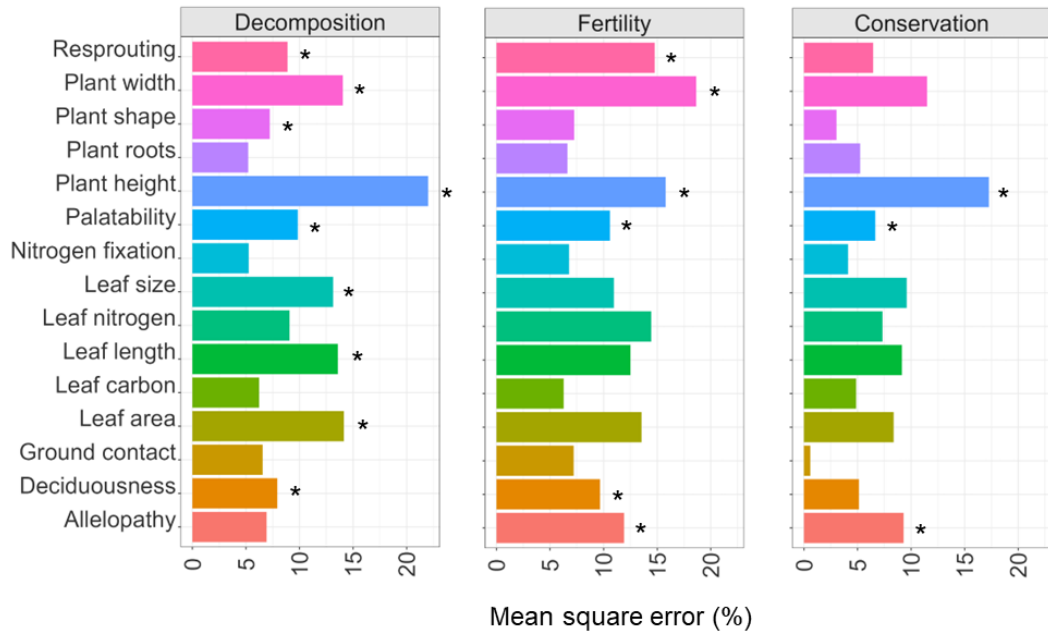
**Figure S2.** Predicted mean (+ 95% CI) and observed fertile island effect, as measured with the relative interaction intensity (RII) index, for each of the 24 soil attributes measured in relation to aridity. See Supplementary Table S1 and Supplementary Text S3 for descriptions of the 24 attributes.



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**Figure S3.** Predicted mean relative interaction intensity (RII) index (+ 95% CI) for Conservation, Decomposition and Fertility for trees, shrubs, and grasses in relation to (a) Grazing pressure and (b) Herbivore type.

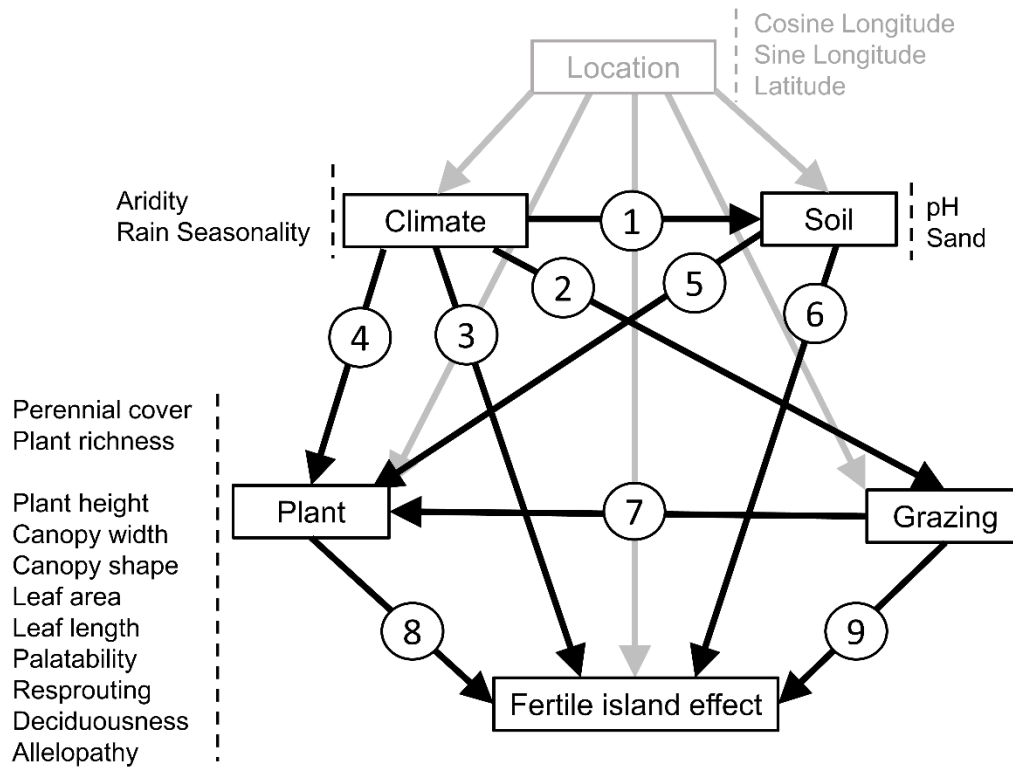




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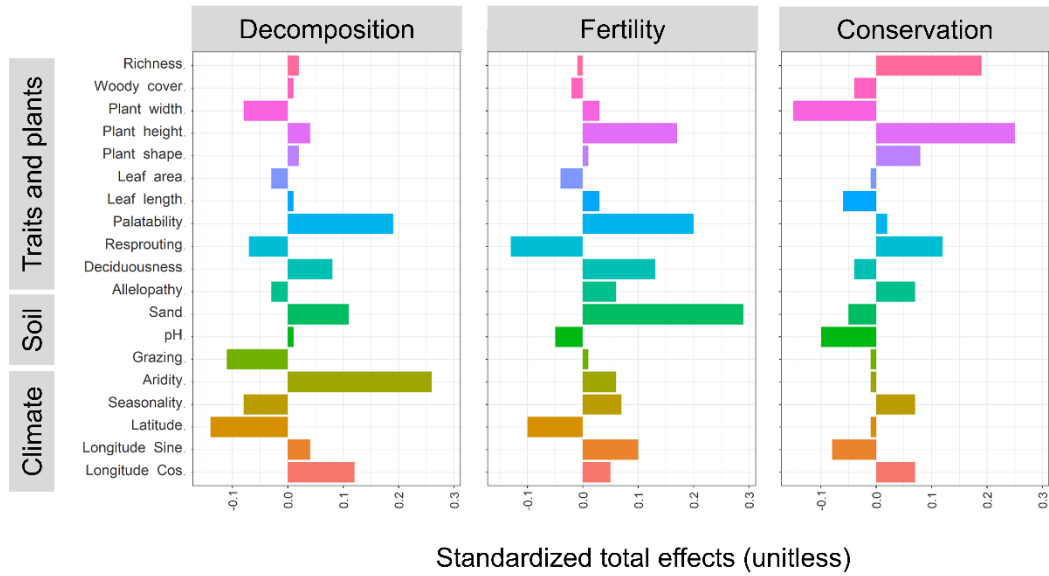
991 **Figure S4.** Results of the Random Forest analyses of the 15 plant traits considered as  
 992 candidate predictors in the structural equation models. \*indicates significant predictor  
 993 of the fertile island effect, as measured with the relative interaction intensity (RII)  
 994 index. N = 288 for all attributes.

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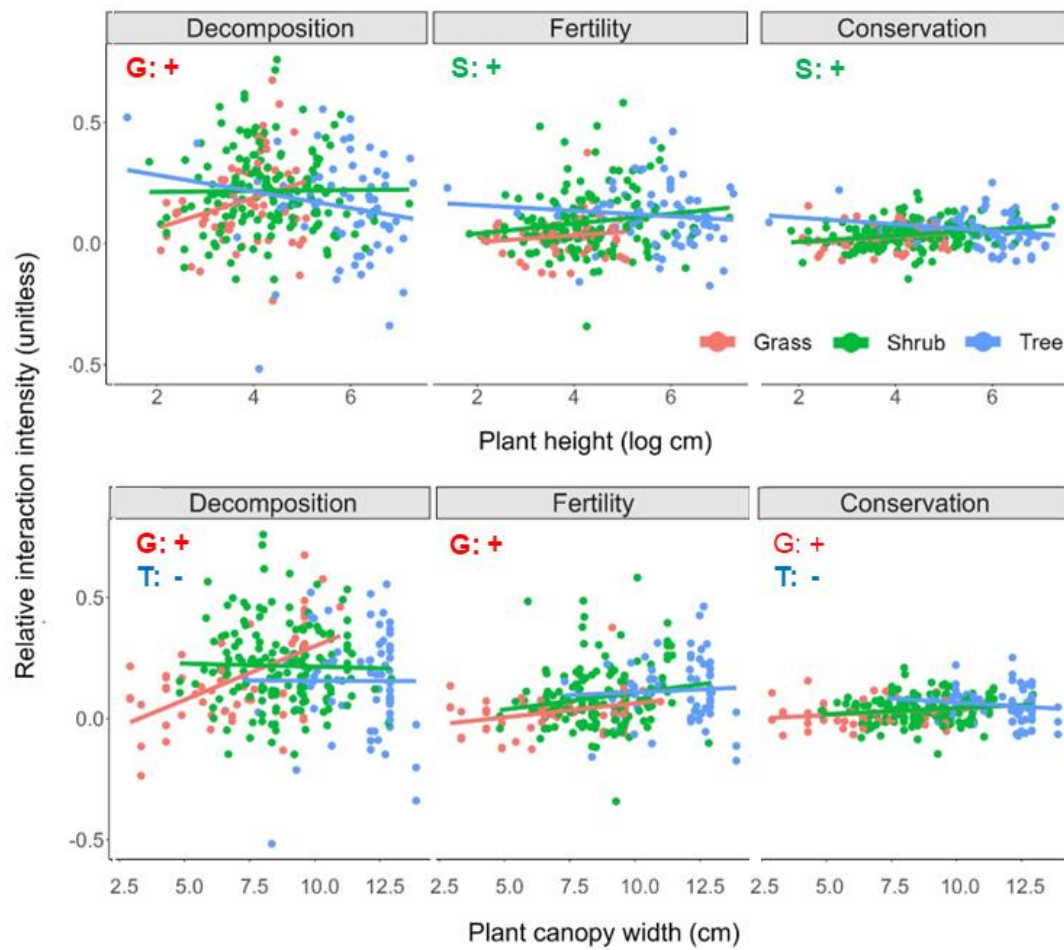
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**Figure S5.** *A priori* structural equation modelling assessing the direct and indirect effect of climate (aridity, rainfall seasonality), soil (pH and sand content), plant (landscape-level vegetation attributes [perennial cover and perennial plant richness] and plant traits [plant height, dry leaf matter content [LDMC], lateral spread, N-fixation, root types]), and grazing (standardised grazing pressure) on the fertile island effect (RII) after taking account of the effect of location (latitude, cosine longitude, sine longitude).



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**Figure S6.** Standardised total effect (sum of direct and indirect effects) for location (cosine longitude, sine longitude, and latitude), climate (rainfall seasonality, and aridity), soils (pH and sand), grazing, traits of the island species (allelopathy, deciduousness, resprouting, palatability, leaf length, leaf area, plant shape, plant height, and plant canopy width) and plot-level total woody cover and plant richness on the fertile island effect (RII index) of 24 ecological attributes grouped into the three groups of functions (organic matter decomposition, soil fertility, conservation). The 24 soil attributes evaluated are described in Supplementary Table S1 and Supplementary Text S3.



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**Figure S7.** Relationships between tree (T), shrub (S) and grass (G) height and canopy width, and the fertile island effects, as measured with the relative interaction intensity (RII) index, for each of the three groups of functions.  $G^+$  = significant increase in the fertile island effect (RII) in the soil beneath grasses.

1029

1030 **Supplementary Information Text**

1031

1032 **Text S1. Assessment of grazing pressure**

1033

1034 At each of the 88 sites surveyed, multiple 45 m x 45 m plots were sampled across a  
1035 local grazing pressure gradient (low, medium and high grazing pressure, plus another  
1036 plot in an ungrazed area whenever possible), as described in ref. 12. All plots were  
1037 established in areas representative of the vegetation and soil types found, so the  
1038 impacts of grazing intensification could be assessed at each site without confounding  
1039 factors associated with differences in climate, soil type or vegetation <sup>12,44</sup>.

1040 To quantify grazing pressure, we used the amount of herbivore dung, which is  
1041 used widely to evaluate recent grazing pressure and abundance of large mammalian  
1042 herbivores <sup>78</sup>, cattle and sheep <sup>79</sup>, deer <sup>80</sup> and kangaroos <sup>81</sup>. To measure it, we placed a  
1043 25 m<sup>2</sup> (5 m x 5 m) quadrat, within which was nested a smaller 1 m<sup>2</sup> (1 m by 1 m)  
1044 quadrat, at distances of 10 m and 30 m along each 45 m transect. Within the larger  
1045 quadrat we counted the dung of large-bodied herbivores (e.g., giraffe, cattle and  
1046 horses), and in the smaller quadrat, the dung or pellets of smaller-bodied herbivores  
1047 (e.g., goats, sheep, lagomorphs), and classified it accordingly to the species producing  
1048 it. Experienced field operators were familiar with the dung of different herbivores and  
1049 were therefore able to identify and separate dung in the field. This was particularly  
1050 important in Namibia, which the sites supported the greatest herbivore richness ( $n =$   
1051 9). Field guides are available to allow operators to identify dung in different regions  
1052 (e.g., antelope spp. in Africa <sup>82</sup> or different herbivores in Australia <sup>83</sup>). However, not all  
1053 groups could successfully separate the dung of sheep and goats, except where they  
1054 occurred separately, largely because of the high degree of overlap in morphological  
1055 features of the dung <sup>84</sup>.

1056

1057 *Dung counts of herbivores*

1058

1059 We calculated dung/pellet ('dung' hereafter) mass based on dung counts using  
1060 algorithm relationships between dung counts and the dry mass of each herbivore.  
1061 Field surveyors counted dung of each herbivore in all quadrats but collected it from  
1062 only a subsample of the quadrats surveyed, generally four large (25 m<sup>2</sup>) or small (1  
1063 m<sup>2</sup>) quadrats (depending on herbivore type), to derive relationships between dung  
1064 counts and mass for separate herbivore types. This estimation technique is highly  
1065 effective for those herbivores that produce pellets, such as goats (*Capra hircus*), sheep  
1066 (*Ovis aries*), deer (*Capreolus capreolus*, *Cervus elapus*), various antelope species  
1067 including Gemsbok (*Oryx gazelle*), Springbok (*Antidorcus marsupialis*) and Greater  
1068 kudu (*Tragelaphus strepsiceros*), various kangaroos (*Macropus* spp.), European  
1069 rabbit (*Oryctolagus cuniculus*), and the European hare (*Lepus* sp.). Grazing pressure  
1070 was estimated based on the dry mass of herbivores per hectare <sup>6</sup>, and we standardized  
1071 the dung counts within each site as a measure of standardized grazing pressure.



1072  
1073 *Validating the use of herbivore dung as a measure of grazing pressure*  
1074

1075 As an initial test of the validity of herbivore dung as a measure of recent grazing  
1076 pressure (grazing intensity), we examined three sites from our study (Argentina,  
1077 Australia, Iran) that were all grazed by sheep and from which we had data on the mass  
1078 of dung collected in the field and empirical data on long-term stocking rates obtained  
1079 from experimental studies or from pastoralists or herders. We plotted total dry mass of  
1080 livestock dung against grazing pressure (which was adjusted to a common scale of dry  
1081 sheep equivalents [DSE ha<sup>-1</sup>], the value of one non-lactating ewe without a lamb<sup>85</sup>.  
1082 Results for these four sites, shown in ref. 12, demonstrate a positive linear relationship  
1083 between livestock density (DSE ha<sup>-1</sup>) and dung mass (kg·ha<sup>-1</sup>). Experimental studies  
1084 of sheep grazing in arid South Australia show a strong relationship between time that  
1085 livestock spend grazing and amount of dung produced<sup>86</sup>. Other studies from  
1086 Zimbabwe<sup>87</sup>, Kenya<sup>88</sup>, South Africa<sup>46</sup> and southern Mongolia<sup>89</sup> have linked dung  
1087 counts to herbivore grazing pressure.  
1088

1089 We tested the relationship between dung measurements (kg ha<sup>-1</sup>) and the heuristic  
1090 assessment of grazing pressure (ungrazed, low, medium, high) using two analyses.  
1091 This heuristic measure represents the longer-term assessment of grazing pressure.  
1092 First, we tested the relationship between these grazing pressure levels and dung  
1093 measurements using a general linear model that considered study sites as a random  
1094 effect. Increases in grazing pressure were associated with increasing levels of dung  
1095 production ( $F = 37.0$ ,  $df = 3$ ,  $P = 0.0017$ , on  $\log_{10}(x+1)$  data). Tukey's *post-hoc* LSD  
1096 test indicated a significant difference among all grazing pressure levels except  
1097 medium and high, which did not differ significantly. Second, we performed a cluster  
1098 analysis validation. In this analysis, we first standardized the dung density values by  
1099 dividing them by the maximum dung density found within each site. Standardization  
1100 yielded a value ranging from 1 (maximum density within a site) to 0 (minimum  
1101 possible dung density). We then performed a cluster analysis, using the Elbow method<sup>51</sup>,  
1102 to identify the optimum number of clusters that can be obtained using dung data  
1103 only (hereafter 'dung-based clusters'). This analysis identified four clusters as being  
1104 optimum, which is consistent with our assignment of four categorical classes under  
1105 the expert-derived heuristic method<sup>44</sup>. To test the veracity and accuracy of this  
1106 clustering approach, we assigned clusters to the plots based on the mass of dung and  
1107 compared the match with the classification made by individual experts (ungrazed and  
1108 low, medium and high grazing pressure). Total accuracy of expert assignment was  
1109 39.2%, with a significant association between dung-based and expert-based grazing  
1110 levels ( $\chi^2 = 95.05$ ,  $df = 9$ ,  $P = 0.00425$ ). Low accuracy was driven mainly by a  
1111 similarity among low and ungrazed plots, which are not well distinguished in terms of  
1112 dung clusters. When this process was repeated without ungrazed plots, the match  
1113 between expert-based assignment and dung-based assignment increased to 53.2% ( $\chi^2$   
1114 = 46.01,  $df = 4$ ,  $P = 0.0022$ ). For this reduced analysis, the greatest mismatch

1115 between expert-based and dung-based approaches occurred under medium grazing  
1116 pressure plots, which sometimes had dung levels close to high grazing pressure and  
1117 others close to low grazing pressure plots. See ref. 44 for additional results of the  
1118 clustering approach followed.

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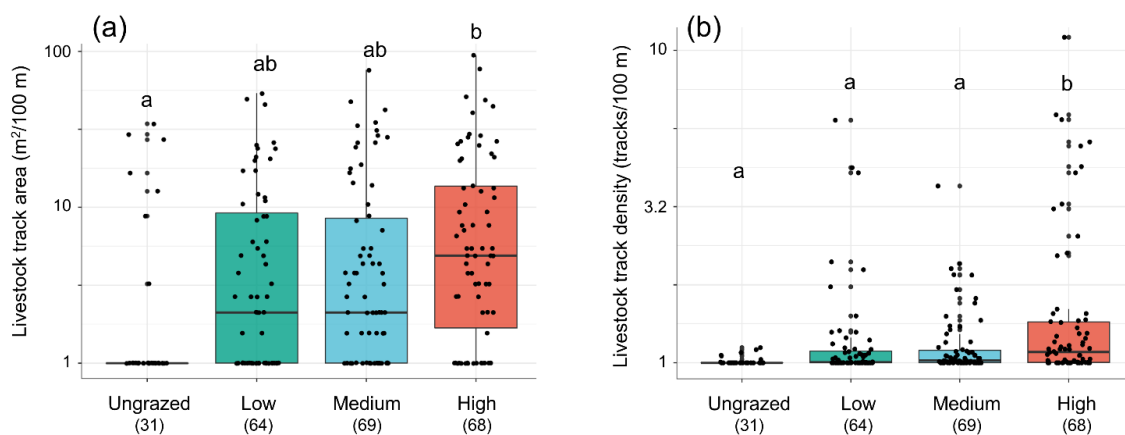
### 1120 *Assessment of historic livestock grazing pressure*

1121

1122 Our measure of long-term grazing pressure is highly correlated with data we obtained  
1123 on the size and intensity of livestock tracks. Livestock tracks are semi-permanent  
1124 landscape features that are formed when livestock traverse the same path to and from  
1125 water<sup>52</sup>. These compacted tracks are clearly visible over many decades, and tracks  
1126 become wider and deeper as the pressure of livestock grazing increases. The density  
1127 and size of livestock tracks is therefore a useful indicator of the history of livestock  
1128 grazing<sup>53,89</sup>. Livestock tracks, however, fail to form on sandy soils<sup>90</sup>, so we could  
1129 only explore potential relationships between tracks and our measure of historic  
1130 grazing could only use those sites where tracks are evident. We measured the width  
1131 and depth of all livestock tracks crossing each of the 45 m transects to derive a total  
1132 cross-sectional area of tracks for each site. These values were then scaled to a total  
1133 area per 100 m of transect. We also calculated the total number of tracks per 100 m of  
1134 transect. Using a general linear model that considered study site as a random effect,  
1135 we found a strong and significant difference in the area of livestock tracks among the  
1136 four expert-derived levels of grazing pressure (ungrazed and low, medium and high  
1137 grazing pressure;  $F_{3,163} = 14.95$ ,  $P < 0.001$  on  $\log_{10}(x+1)$ -transformed data; Fig. S8).  
1138 In summary, these comprehensive analyses of the intensity with which sites were  
1139 grazed by herbivores showed very similar trends, irrespective of whether we used  
1140 dung mass as a measure of recent grazing pressure, or the expert heuristic site  
1141 classification as a measure of long-term grazing pressure. This gives us a high degree  
1142 of confidence that the gradients we observed are true gradients in grazing pressure.

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1145

1146

1147 **Figure S8.** Box plots of the area (a) and density (b) of livestock tracks for the four  
1148 levels of grazing pressure evaluated. Boxes show the median, 25th and 75th  
1149 percentiles. Lowercase letters indicate significant differences at  $P = 0.00113$  for area  
1150 and  $P = 0.0047$  for density (using Tukey's LSD tests). The total number of plots used  
1151 for these analyses was 232. All tests were two-sided.  
1152  
1153

1154 **Text S2. Detailed plant trait measurements**

1155

1156 We measured *in situ* six traits of the 162 dominant perennial plants that acted as  
1157 fertile islands either in the field or the laboratory: plant height, plant canopy width,  
1158 leaf length, leaf area, and leaf carbon and nitrogen. These traits were measured  
1159 following the protocols detailed in refs. 12 and 44). They describe the size, leaf  
1160 characteristics and leaf chemistry of perennial species (including trees, shrubs, and  
1161 large woody grasses) beneath which we assessed the fertile island effect. Canopy size  
1162 was measured, with a tape measure, across the largest distance on the lateral width of  
1163 perennial canopies. For each selected individual plant, we sampled the last mature and  
1164 undamaged leaves at the top of the plant (sampled leaf surface was always > 2 cm<sup>2</sup>).  
1165 Leaves were then stored in moisturized plastic bags and brought to the lab for  
1166 rehydration. Leaf area and leaf length was quantified by taking photographs of the  
1167 collected leaves and analysing them using the ImageJ <https://imagej.nih.gov/ij/>.

1168

1169 We also compiled data on an additional eight categorical plant traits (i.e., plant  
1170 canopy shape, whether plant foliage reached the surface [ground contact],  
1171 deciduousness, allelopathy, N fixation, root type, resprouting, palatability). Values for  
1172 these traits were taken from online plant trait databases such as BROT<sup>54</sup>, PLANTS<sup>55</sup>,  
1173 Woody Plants Database (<http://woodyplants.cals.cornell.edu>) and TRY<sup>56</sup>. The seven  
1174 categorical traits were ranked numerically such that a larger number equated with  
1175 greater function in terms of its own growth or its ability to facilitate surrounding  
1176 conditions. (1) Plant canopy shape: ranked according to a greater ability to obtain  
1177 resources (water and light) for the understorey, with greater resource accumulation  
1178 under v-shaped plants but greater rainfall accumulation under pyramid-shaped  
1179 (inverted v-shaped) plants (v-shaped = 1, weeping/round = 2, pyramid = 3<sup>91</sup>). (2)  
1180 Foliage reaching the ground soil surface [ground contact]: high values were ranked  
1181 according to the ability to protect habitat for understorey species (no = 1, yes = 2  
1182<sup>92,93</sup>). (3) Deciduousness: higher values relate to the ability of species to benefit their  
1183 growth conditions, such as greater litter inputs to the soil nutrient pool (evergreen = 1,  
1184 deciduous = 2; <sup>94</sup>). (4) Allelopathy: lower values for species that exclude or compete  
1185 with protégé species (allelopathic = 1, no-allelopathy = 2<sup>95</sup>). (5) Nitrogen fixation:  
1186 higher value for N-fixing plants (non-N fixing = 1, N-fixing = 2<sup>96</sup>). (6) Root type:  
1187 higher values relate to potentially greater nutrient cycling and water infiltration (tap  
1188 roots = 1, lateral roots = 2, tap and lateral roots = 3<sup>97</sup>). (7) Resprout: a higher value  
1189 was associated with resprouting species being able to sustain woody plant habitat  
1190 (non-resprouting = 1, resprouting = 2<sup>98</sup>). (8) Palability: higher values for woody  
1191 species that maintain their structure (palatable = 1, unpalatable = 2<sup>49</sup>).

1192

1193 **Text S3 Soils and soil attributes**

1194

1195 **Sampling, analysis, and assessment of the 24 attributes and three functions**

1196

1197 To avoid problems associated with the use of multiple laboratories when analysing the  
1198 soils from different sites, and to facilitate the comparison of results between them,  
1199 dried and frozen soil samples from all the countries were shipped to the laboratory of  
1200 Rey Juan Carlos University (URJC) in Móstoles (Spain), where they were either  
1201 analysed or distributed to other laboratories. Thus, all soil samples were analysed in  
1202 the same laboratory by the same personnel using the same protocols. Once in the  
1203 laboratory, we created a composite sample per microsite (vegetated patches and bare  
1204 open patches) and plot using equal amounts of all the replicate samples collected in  
1205 the field and all the laboratory analyses were carried out on these composite samples.  
1206

1207 Soil pH was measured in all the soil samples with a pH meter, in a 1:2.5 soil: to water  
1208 suspension ratio. Soil sand content was measured according to ref. <sup>57</sup>). These physico-  
1209 chemical properties widely differed among the 288 plots surveyed: sand content and  
1210 pH ranged from 11% to 99% and from 3.73 to 9.85, respectively.

1211

1212 **Soil attributes and functions**

1213

1214 We measured in all plots a total of 24 soil ecological attributes linked to three  
1215 ecosystem services (organic matter decomposition, soil fertility, and soil and water  
1216 conservation) to assess the fertile island effect under perennial plants (see Table S1).

1217

1218 *Organic matter decomposition (Decomposition)*

1219

1220 To quantify organic matter decomposition, we measured five soil extracellular  
1221 enzyme activities related to the degradation of organic matter [cellobiase,  $\beta$ -  
1222 glucosidase, phosphatase,  $\beta$ -N-acetylglucosaminidase and xylanase], soil carbon and  
1223 nitrogen mineralization and microbial biomass. These variables are either direct  
1224 proxies or linked to the mineralization of essential elements (C, N and P), and are  
1225 involved in the degradation of compounds such as sugars, chitin, cellulose, and  
1226 hemicellulose <sup>99</sup>. Therefore, they are good proxies of the capacity of a given  
1227 ecosystem to decompose organic matter and return available nutrients from organic  
1228 sources to the soil <sup>100</sup>.

1229 ).

1230

1231 Phosphatase activity was measured by determining the amount of p-nitrophenol  
1232 (PNF) released from 0.5 g soil after incubation at 37 °C for 1 h with the substrate p-  
1233 nitrophenyl phosphate in MUB buffer (pH 6.5 <sup>101</sup>. The activity of  $\beta$ -glucosidase was  
1234 assayed according to ref. <sup>101</sup> following the procedure for phosphatase but using p-  
1235 nitrophenyl- $\beta$ -D-glucopyranoside as substrate and Trishydroxymethyl aminomethane

1236 instead of NaOH. The activities of  $\beta$ -N-acetylglucosaminidase, cellobiase and  
1237 xylanase were measured from 1g of soil using fluorometry as described in ref. <sup>102</sup>.

1238  
1239 Carbon mineralization rate ( $\mu\text{g CO}_2\text{-C g}^{-1}$  dry soil  $\text{day}^{-1}$ ) was measured as  $\text{CO}_2$   
1240 evolved after 48 h of incubation at  $25^\circ\text{C}$  and 60% of water holding capacity (WHC) in  
1241 soil samples from each plot. We waited 48 h to make sure that an equilibrium in the  
1242 soil atmosphere was reached after disruption and water adjustment to achieve 60% of  
1243 WHC <sup>103</sup>. We measured soil  $\text{CO}_2$  exchange by placing 10.5 g of each soil sample  
1244 inside a 30 mL plastic jar with a tight sealed lid connected to a portable, closed-  
1245 chamber soil respiration system (EGM-4, PP systems, MA, USA) during 60 s. We  
1246 monitored  $\text{CO}_2$  concentration every second and fitted to a linear model ( $R^2 > 0.95$  in  
1247 all cases). Afterwards, the ideal gas law equation was used to convert and calculate  
1248 the net  $\text{CO}_2$  increase (ppm) to mass of C (m) in the headspace of the jar:

$$m = \frac{\text{ppm} \times P \times V \times M}{R \times T}$$

1251  
1252 where P (atm) and V (L) are, respectively, the air pressure and the known headspace  
1253 volume in the jar, M is the atomic mass of carbon ( $\text{g mol}^{-1}$ ), R is the universal gas  
1254 constant ( $0.08206 \text{ ATM l mol}^{-1} \text{ K}^{-1}$ ) and T is the temperature ( $^\circ\text{K}$ ) at the  
1255 measurement time. The headspace volume in the jar (L) was measured as the total  
1256 volume of the jar minus the volume of the soil. The mass of  $\text{CO}_2$  evolved from each  
1257 flask was calculated according to ref. <sup>104</sup> and expressed as  $\mu\text{g CO}_2\text{-C s}^{-1}$ . Finally, we  
1258 express soil carbon mineralization on a dry mass basis ( $\mu\text{g CO}_2\text{-C g}^{-1}$  soil  $\text{day}^{-1}$ ).

1259  
1260 Potential N mineralization rate was measured by determination of total  $\text{K}_2\text{SO}_4^-$   
1261 extractable  $\text{NO}_3^-$  before and after incubation in the laboratory at 80% of field water  
1262 holding capacity and  $30^\circ\text{C}$  for 14 days <sup>105</sup>.

1263  
1264 Soil microbial biomass C was assessed using an automated  $\text{O}_2$  micro-compensation  
1265 system <sup>106</sup> by substrate-induced respiration, i.e., the respiratory response of  
1266 microorganisms to glucose addition <sup>107</sup>. To saturate catabolic microbial enzymes, 4  
1267 mg glucose  $\text{g}^{-1}$  dry soil was added as aqueous solution to the soil samples. Prior to the  
1268 measurement, and to prevent a respiration peak due to water addition, the dry soil  
1269 samples were rewetted 24 h before so that they reached 40% water holding capacity.  
1270 The final measurements were done at 60% water holding capacity by adding a  
1271 specific amount of water and glucose to reach 4 mg glucose  $\text{g}^{-1}$  soil dry weight. The  
1272 mean of the three lowest hourly measurements was taken as the maximum initial  
1273 respiratory response (MIRR) – a period where microbial growth has not started to  
1274 calculate microbial biomass C. Microbial biomass C ( $\text{mg C g}^{-1}$ ) was calculated as  $38$   
1275  $\times \text{MIRR}$  ( $\text{ml O}_2 \text{ g}^{-1}$  dry soil) <sup>108</sup>. All these measurements were conducted at  $20^\circ\text{C}$  in an  
1276 air-conditioned laboratory using the same analytical devices.

1278 *Soil fertility (Fertility)*

1279

1280 We quantified soil fertility by measuring the contents of dissolved organic N, total N,  
1281  $\text{NO}_3^-$  and  $\text{NH}_4^+$ , and total P, Mn, K, Zn, Mg, Fe, Cu, and soil organic C, which are  
1282 strongly related to plant growth and productivity in drylands<sup>109-112</sup>. Total N was  
1283 determined on ball-milled soils by dry combustion, gas chromatography and thermal  
1284 conductivity detection<sup>113</sup>. Dissolved organic N concentrations were measured from  
1285  $\text{K}_2\text{SO}_4$  0.5 M soil extracts in a ratio 1:5. Soil extracts were shaken in an orbital shaker  
1286 at 200 rpm for 1 h at 20°C and filtered to pass a 0.45- $\mu\text{m}$  Millipore filter<sup>114</sup>. The  
1287 filtered extract was kept at 2 °C until colorimetric analyses, which were conducted  
1288 within the 24 h following the extraction. Sub-samples of each extract were taken for  
1289 measurements of ammonium and nitrate. Ammonium concentration was directly  
1290 estimated by the indophenol blue method using a microplate reader<sup>115</sup>. Nitrate was  
1291 first reduced to  $\text{NH}_4^+$ -N with Devarda alloy, and its concentration was determined by  
1292 the indophenol blue method. Total P, Mn, K, Zn, Mg, Fe, and Cu were extracted by  
1293 open-vessel nitric-perchloric acid wet digestion, re-suspended in water and measured  
1294 by inductively coupled plasma optical emission spectrometry (ICP-OES Perkin Elmer  
1295 Optima 4300 DV)<sup>82,116</sup>. Soil organic C is a major terrestrial C reservoir and a major  
1296 source sink of atmospheric  $\text{CO}_2$ <sup>117,118</sup>. Soil organic C stocks were calculated as the  
1297 product of soil organic C concentration, bulk density and sampling depth. Organic C  
1298 concentration was determined on ball-milled soils by dry combustion, gas  
1299 chromatography and thermal conductivity detection, after removing carbonates by  
1300 acid fumigation<sup>113</sup>. Bulk density was measured at each plot following the cylindrical  
1301 core method<sup>119</sup>.

1302

1303 *Soil and water conservation (Conservation)*

1304

1305 We combined four measures, two relating to water regulation, and two related to soil  
1306 stability, as our measure of soil conservation i.e., the capacity of soils to retain water  
1307 and to maintain their structural stability. Water holding capacity is relevant to many  
1308 aspects of soil water management<sup>120</sup>, is an important determinant of aboveground  
1309 primary productivity in rangelands<sup>121</sup> and is linked to essential water-related  
1310 ecosystem processes such as plant-water provision<sup>122</sup>. Soil porosity is also an  
1311 important physical variable that controls multiple key soil hydrological properties,  
1312 including infiltration and water storage capacity<sup>123-125</sup>.

1313

1314 To measure water holding capacity, we weighted 10 g of dry soil per sample and  
1315 added them to a funnel with moist filter paper. We then added 10 ml of deionized  
1316 water to each sample and covered every funnel with parafilm to avoid evaporation.  
1317 The soils were allowed to drain for 24 h into a test tube. After 24 h, we weighted the  
1318 soils to calculate their water holding capacity. Soil porosity was estimated as  $1 -$   
1319  $(\text{Db}/\text{Dp})$ , where Db and Dp are bulk density and particle density, respectively<sup>126</sup>.  
1320 Bulk density was estimated for every plot as described above. Particle density was

1321 estimated using a constant value of 2.65 g cm<sup>-3</sup> (a typical value used when estimating  
1322 soil porosity and/or soil particle properties in soils such as those surveyed here <sup>127-131</sup> .

1323

1324 Soil aggregation and aggregate stability are good proxies for erosion control <sup>132-134</sup> ,  
1325 are strongly linked to soil quality <sup>135</sup> and together play an important role in the  
1326 production of forage in rangelands <sup>136-138</sup> . Soil aggregation was determined by  
1327 measuring both the mean weight diameter of the whole sample and the water stability  
1328 of the macro-aggregate fraction > 250µm. Each sample was passed through a stack of  
1329 sieves (1mm, 212µm, 53µm, <53µm) to separate the sample into five fractions of  
1330 decreasing particle size. The fraction weights were used to calculate the mean weight  
1331 diameter (in mm) as follows:

1332

$$\text{MWD} = \sum_{i=1}^n \underline{x}_i w_i$$

1333 where  $\underline{x}_i$  is the mean diameter of size fraction  $i$  and  $w_i$  is the weight of fraction  $i$

1334 standardized by the overall sample mass.

1335

1336 Water stable aggregation was tested following a modified protocol of ref. <sup>139</sup> .  
1337 Following the MWD measurements, samples were carefully mixed, and 4.0 g placed  
1338 on small sieves of 250µm mesh size. Samples were allowed to capillary wetting  
1339 before being introduced to the sieving machine (Agrisearch Equipment, Eijkelkamp,  
1340 Giesbeek, Netherlands). Samples were then moved vertically for 3 min in deionized  
1341 water to separate samples into their water-stable and water-unstable fractions. The  
1342 water-stable fraction was then washed to extract sand particles and organic debris  
1343 (i.e., the coarse matter fraction). The percentage of water-stable aggregates was  
1344 calculated as follows:

1345

1346 WSA (%) = (water stable fraction-coarse matter) / (4g-coarse matter).

1347

1348 All soil analyses were conducted with dry samples, as commonly carried out with  
1349 global surveys conducted in drylands and mesic ecosystems <sup>73,140-141</sup> . Previous studies  
1350 have shown that in drylands such as those we studied, air drying and further storage of  
1351 soils does not appreciably alter functions such as those studied here <sup>142,143</sup> . It is also  
1352 important to note that our sampled soils would have remained dry for a large portion  
1353 of the year <sup>144-147</sup> , and that most samples were collected when the soil was in this very  
1354 dry state. Thus, the potential bias induced by our drying treatment is expected to be  
1355 minimal.

1356

1357 Soil stability analyses were carried out at the laboratories of the Institute of Biology at  
1358 Free University Berlin (Germany). Microbial biomass and C mineralization analyses  
1359 were conducted in the laboratories of the Institute of Biology at Leipzig University  
1360 (Germany). ARG analyses, C mineralization, soil organic C and total N, P, K, Mg, Fe,  
1361 Mn, Cu and Zn analyses were conducted at the laboratories of the Institute of



1362 Agricultural Sciences-CSIC (Madrid). The remaining analyses were carried out at the  
1363 laboratory of the Biology and Geology Department, Rey Juan Carlos University  
1364 (Móstoles, Spain).  
1365

1366 **A4. Supplementary References**

1367

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