

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

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## ► To cite this version:

David Eldridge, Jingyi Ding, Josh Dorrough, Manuel Delgado-Baquerizo, Osvaldo Sala, et al.. Hotspots of biogeochemical activity linked to aridity and plant traits across global drylands. Nature Plants, 2024, 10 (5), pp.760-770. 10.1038/s41477-024-01670-7 . hal-04593756

## HAL Id: hal-04593756 https://amu.hal.science/hal-04593756v1

Submitted on 18 Sep 2024  $\,$ 

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## **1** Hotspots of biogeochemical activity linked to aridity and plant traits across

## 2 global drylands

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#### 202 Abstract

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

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

#### 225 Introduction

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

Yet, despite the extensive body of knowledge dedicated to their study, the relative 248 249 importance of grazing, climate, and the traits of the focal island species on the distribution and magnitude of fertile islands across global drylands remains virtually 250 unknown. To address this knowledge gap, we assess, for the first time, the relative 251 association between grazing, plant traits, climate and soil properties, and fertile 252 253 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 vegetation, particularly as grasslands are likely to contract and woody dominated 255 systems increase in a drier and more heavily grazed world<sup>8,13</sup>. 256

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

pressure will destabilise surface soils, mobilising sediment, seed, nutrients, and 268 organic matter from unvegetated interspaces to plant patches, strengthening fertile 269 islands <sup>14,15</sup>. Additionally, livestock might be expected to have a greater effect than 270 wild herbivores because they have not co-evolved with indigenous vegetation and 271 therefore have more deleterious effects on both island plants and their soils <sup>6</sup>, 272 273 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 factor that operates at the local scale, on fertile islands (Hypothesis 2a). More 275 specifically, irrespective of grazing pressure, we would expect that plants would make 276 a greater contribution to fertile islands in arid and hyper-arid ecosystems where soils 277 are extremely bare and infertile compared with less arid ecosystems where the 278 279 influence of plants would be relatively lower. For example, reduced rainfall and/or increased temperature would increase the harshness of the interspaces compared with 280 the vegetated and more protected islands, thereby strengthening the fertile island 281 effect. Plant effects might also be expected to vary among broad functional groups 282 (tree vs shrub vs grass; Hypothesis 2b). These broad groups could have varying 283 effects on soil biogeochemistry because of marked differences in shape, size, and 284 285 structural complexity. Quantifying the contribution of grazing by different herbivores at different pressures, plant traits, climate, and soil properties on fertile islands 286 287 allowed us to assess current and future impacts of grazing on ecosystem structure and functioning across global drylands, where woody vegetation is a predominant plant 288 form  $^{12}$ . 289

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#### 291 Results and Discussion

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

Prior to exploring potential effects of grazing, plant traits, or environmental 298 conditions, we examined the RII relationships of the 24 attributes distributed among 299 the three synthetic functions. This exploration gives us a better understanding of how 300 301 individual biogeochemical attributes and their three synthetic ecosystem functions might differ between islands and their interspaces (the fertile island effect). We found 302 303 strong empirical evidence of a pervasive fertile island effect across all sites and continents and for 16 (67%) of the 24 attributes (Fig. 2). Our results are consistent 304 with findings from empirical local studies revealing greater resource accumulation 305 beneath perennial plant canopies for attributes as diverse as soil geochemistry 306 <sup>11,13,16,17</sup>, soil physical properties <sup>9</sup>, hydrology <sup>18,19</sup> and microbial community structure 307 308 <sup>4</sup>. Of all possible effects, the Decomposition function (which comprised C, N and P mineralisation), was the most strongly developed function within the islands (Fig. 2), 309

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likely due to greater litter inputs <sup>4,20</sup>, microbial activity and plant biomass <sup>21</sup> beneath
perennial plant canopies <sup>22,23</sup>. The fertile island effect for the other functions was
mixed, with strong positive effects for C, and to a lesser extent P, but not for
micronutrients (Fig. 2). The fertile island effect for C and N was also greater in more
arid drylands. These findings reinforce the view that perennial plant patches are
hotspots of biological activity in drylands <sup>4</sup>, and this likely accounts for their potential
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 measures of grazing and fertile islands. Using hierarchical linear mixed modelling 318 (see Methods) we found no consistent influence of grazing, either recent (standardized 319 grazing pressure) or long-term (ungrazed, low, medium, high) grazing pressure on the 320 321 mean (overall) fertile island effect (the average standardized value of all 24 attributes shown in Table S1 in Supplementary Information). We also found a consistent, but 322 323 extremely weak negative effect of recent grazing pressure on Decomposition, contrary to the results of global meta-analyses <sup>25</sup>. There were no significant effects of 324 increasing recent grazing pressure on either the Fertility or Conservation function 325 (Fig. 3a, Table S2). There were no significant effects of long-term (historic) grazing 326 pressure (ungrazed, low, medium, high) on any measures (Fig. S1, Table S2). 327

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

336 Our results provide fresh insights into the links between grazing and fertile islands, demonstrating that, across global drylands, grazing cannot be considered a 337 causal agent of the fertile island effect. Thus, placed in a global context, the local 338 influence of grazing on fertile islands is overshadowed by global environmental 339 variability. This result challenges the view of fertile islands and their formation, 340 which posits that islands are a biproduct of grazing <sup>11</sup>. This view has largely been 341 shaped by studies from the Chihuahuan Desert in the western United States where 342 increases in woody plant (generally shrub) density are linked to a dominance of 343 woody plant islands and ensuing desertification <sup>26</sup>. Undoubtedly, grazing-induced 344 disturbance can aggravate differences between perennial plants and their interspaces 345 346 in some situations by disturbing interspaces and intensifying the movement of resources from interspace to island patches <sup>27</sup>. However, neither short- nor long-term 347 grazing pressure, nor herbivore type, were associated with the fertile island effect 348 349 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

woody plant species explained differences in the fertile island effect for the three 352 synthetic functions studied. These traits, which are related to plant size and structure. 353 leaf characteristics, and the ability to respond to environmental stimuli (palatability, 354 resprouting, deciduousness, allelopathy, see Methods) potentially influence the way 355 nutrients are stored, mineralized, and made available to plants, and how soil and water 356 are conserved beneath plant canopies <sup>28</sup>. Our trait data, which represent the most 357 comprehensive dataset gathered to date across global drylands, were used to evaluate 358 the relative importance of island plant structure. We used site-specific trait values 359 rather than global averages, allowing us to account for potential differences in the 360 morphology of island plants under different grazing pressure, herbivore type and 361 environmental conditions. The extent to which different plant traits affected the three 362 363 synthetic functions varied depending on the function considered (Fig. S4 in Supplementary Information). We found that the relative fertile effect for our three 364 synthetic functions was generally greater when the islands were dominated by taller 365 and wider plants, and to a lesser extent, by plants with larger leaves. Plant height was 366 important for all functions, while the Decomposition function responded mostly to 367 plant and leaf size, and the Fertility function was driven mostly by changes in plant 368 369 size and leaf characteristics (Fig. S4 in Supplementary Information).

We then used Structural Equation Modelling<sup>29</sup> to explore potential associations 370 among biotic and abiotic factors and the fertile island effect. Our a priori model (Fig. 371 S5 in Supplementary Information) included environmental drivers (aridity, 372 temperature, rainfall seasonality), soil (sand content, pH) and vegetation (perennial 373 plant richness, relative cover of woody plants) properties, plant traits (the nine most 374 important plant traits related to size, leaf characteristics, and inherent properties of 375 woody plants such as the type of roots or whether they are allelopathic; identified 376 using the Random Forest analyses, see Methods), and grazing (recent grazing, long-377 378 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 models revealed that decomposition was enhanced in areas of greater aridity 380 (consistent with the hierarchical linear modelling, though not for carbon 381 mineralisation, Fig. S2 Supplementary Information), more sandy soils, and where 382 383 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 larger values of the Conservation function (more stable, with greater water 385 holding capacity) tended to be associated with taller island plants, potentially through 386 mechanisms involving hydraulic lift <sup>30</sup>, and at plots supporting more perennial plant 387 species (Fig. S6 Supplementary Information. A potential explanation for the link 388 between the Conservation function, and both plant height and richness could relate to 389 a greater leaf area <sup>31</sup> of larger island plants and therefore reduced surface evaporation 390 <sup>32</sup>. After accounting for all direct and indirect pathways from both abiotic and biotic 391 factors, our SEMs confirm that grazing had no effects on the three functions 392 evaluated. 393

Among plant traits, plant size (height and canopy) was particularly important, 394 with larger canopies associated with greater RII values of all three functions (but only 395 for grasses), and taller grasses with greater RII values of the Decomposition function 396 (Fig. S7 in Supplementary Information. Larger grasses are functionally more efficient 397 at capturing resources <sup>33</sup> and enhancing hydrological functions <sup>34,35</sup> and may be a 398 response to declining landscape productivity <sup>36</sup>. Larger plants may be avoided more 399 by herbivores due to higher concentrations of tannins and secondary compounds <sup>37</sup>. 400 Similarly, taller shrubs were associated with larger values of the Conservation and 401 Fertility, but not Decomposition, functions (Fig. S7 in Supplementary Information). 402 Taller shrubs would return more litter to the soil surface <sup>38</sup>, provide more varied 403 habitat <sup>39</sup> and concentrate more resources excreted by canopy-resident invertebrates 404 <sup>40</sup>, potentially accounting for greater fertility <sup>20</sup>. Finally, larger shrubs would support a 405 greater density of understorey protégé species <sup>41</sup> and have a larger legacy effect on 406 soils after death <sup>42</sup>. Interestingly, trees with larger canopies were associated with 407 lower values of the Decomposition and Conservation functions (Fig. S7 in 408 Supplementary Information). Large tree canopies are often preferred camping sites for 409 herbivores <sup>39</sup>, leading to declines in soil structure <sup>43</sup>, and reductions in soil water 410 holding capacity due to the proliferation of surface roots. Our results could suggest a 411 waning of the fertile island effect under large trees. 412

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

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
- 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
- drylands. Sites were surveyed between January 2016 and September 2019<sup>12,44</sup>.

## 444 Establishing and defining local grazing gradients

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

454 Field surveyors, who were all intimately associated with the long-term grazing history of these sites, characterised their plots using this four-scale heuristic category 455 (ungrazed, low, moderate, high). Grazing pressure gradients were confirmed by 456 measuring the mass of herbivore dung *in situ*<sup>6</sup>. Dung production is known to be 457 closelv linked to animal activity, time spent grazing, and therefore grazing pressure 458 <sup>45,46</sup>, though more studies are needed in arid systems to validate these relationships. 459 To measure dung, we collected the dung of different herbivores from within two 25 460  $m^2$  (where herbivores were large bodied, e.g., cattle, horses, large ungulates) or 1  $m^2$ 461 (when herbivores were smaller bodied e.g., goats, sheep, rabbit, guanaco) quadrats <sup>44</sup>. 462 Dung was oven dried and expressed as a mass per area. Where herbivores produced 463 pellets, dung was counted from different herbivores, a subsample collected, and 464 following oven drying, used to calculate the relationship between counts and oven-dry 465 dung mass (Text S1 in Supplementary Information). 466

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

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

- Standardized values ranged from 0 to 1 ( $0.30 \pm 0.01$ , mean  $\pm$  SE) across the 88 sites. 478 A value of 1 for a particular plot indicates that this plot had the greatest grazing 479 pressure for that site and zero was ungrazed. This approach to standardising dung 480 mass within sites ensures the equivalence of sites that might have markedly different 481 levels of dung production, due to variation in site productivity, but have the same 482 483 level of grazing pressure (e.g., moderate grazing pressure). The method has also been validated multiple times in grazing studies <sup>49,50</sup>. Across our global study we recorded 484 29 different herbivore types, of which five were livestock (cattle, goat, sheep, donkey, 485 horse)<sup>12</sup>. 486
- Dung mass was a good proxy of grazing pressure using two approaches (see Text S1 in Supplementary Information). First, there was a significant positive relationship between dung mass and livestock density for a subset of sites in Iran, Australia, and Argentina for which we had data on dung mass and animal density <sup>12</sup>. Second, we performed a cluster analysis <sup>51</sup> to identify the optimum number of dung-based clusters, based on dung mass, and found that this aligned well with the four heuristic levels of grazing pressure <sup>12</sup>.
- 494 Third, we linked the four heuristic measures of long-term (decadal to multidecadal) grazing pressure to the presence of livestock tracks; semi-permanent features 495 created by livestock when they traverse the same path to and from water <sup>52</sup>. The 496 density and size of these tracks is a useful indicator of the history of livestock grazing 497  $^{53}$ . We measured the width and depth of all livestock tracks crossing each of the 45 m 498 transects to derive a total cross-sectional area of tracks for each plot and expressed 499 500 this as the total track density and cross-sectional area per 100 m of transect (Fig. S8). In summary, these three comprehensive measures of grazing intensity by herbivores 501 showed very similar trends, irrespective of whether we used dung mass as a measure 502 of recent grazing pressure, or the expert heuristic site classification as a measure of 503 long-term grazing pressure. This gives us a high degree of confidence that the 504 gradients we observed are true gradients in grazing pressure. 505

#### 506 Vegetation and plant trait measurements

Field surveys followed a standardised sampling protocol <sup>44</sup>. Briefly, within each plot, 507 we located four 45 m transects oriented downslope, spaced 10 m apart across the 508 slope, for the vegetation surveys. Along each 45 m transect we assessed the cover of 509 perennial plants, by species, within 25 contiguous 1.5 m by 1.5 m quadrats. Perennial 510 plants were then recorded every 10 cm along this transect to obtain a measure of 511 perennial plant cover. Total plot-level plant richness was calculated as the total 512 513 number of unique perennial plant species found within at least one of the survey methods (transects or quadrats) employed. In each site, we measured the height and 514 lateral spread of five randomly selected individuals of the dominant island plants. 515 Lateral spread (canopy width), a proxy of plant area, was assessed by measuring plant 516 517 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

- traits describe the size and leaf characteristic of the 162 perennial species in the vegetation patch that was dominated by trees, shrubs, or large perennial grasses, and which we assessed as potential fertile islands (see detailed measurements in Text S2 in Supplementary Information). Twenty-three percent of plots supported two codominant island species (i.e., two different tree, shrub, or grass species). For these plots, soil biogeochemical and plant trait data were weighted according to the mean cover of the co-dominant species within a plot.
- 527 We compiled information on eight additional plant traits (i.e., plant canopy shape, whether foliage reached the ground surface, N-fixation, deciduousness, 528 529 allelopathy, palatability, resprouting, root type) using information from online plant trait databases such as BROT <sup>54</sup>, PLANTS <sup>55</sup>, Woody Plants Database 530 (http://woodyplants.cals.cornell.edu) and TRY <sup>56</sup>. The eight categorical traits above 531 were ranked numerically such that a larger value equated with greater function in 532 533 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 Information. 535

#### 536 Soil properties and sampling

Soils were sampled during the dry season. In each plot, five sampling points were 537 538 randomly located in open areas devoid of perennial vascular plants (< 5% plant cover, hereafter 'open' microsite), and another five placed beneath the canopy of five 539 randomly selected individuals of the dominant island plant (Text S3 in Supplementary 540 Information). A composite sample of five 145 cm<sup>3</sup> soil cores (0-7.5 cm depth) was 541 collected from beneath each plant or bare area, bulked, and homogenized in the field. 542 Soil samples were air-dried for 1 month, sieved (< 2 mm) and stored for physico-543 544 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 analyses described here are for two composite samples per plot. We assessed soil pH 546 (1:2.5 soil water suspension, sand content <sup>57</sup>, and the values of 24 soil ecological 547 attributes that are linked to three ecosystem functions (Table S1 in Supplementary 548 Information). 549

#### 550 Assessment of ecosystem functions

We calculated a relative interaction index (RII) and its 95% confidence interval <sup>58</sup> for 551 the 24 ecological attributes as measures of the fertile island effect. A positive (or 552 negative) value indicates a greater (or lesser) value of that attribute, respectively, in 553 island soils. The RII is defined as the relative difference between attributes beneath 554 555 the perennial plant islands and their open interspaces and was calculated as  $RII = (X_I)$ 556  $(X_{I} + X_{O})$ , where X<sub>I</sub> and X<sub>O</sub> represent the mean values of a given ecological attribute beneath a perennial plant patch (island) and in the open interspace, 557 respectively. Values of the RII range from -1 to 1, with positive values indicating 558 greater levels of a given attribute beneath the island and vice versa. Evidence of the 559 fertile island effect (either positive or negative) is based on whether the 95% 560

confidence intervals (95% CIs), calculated using 'Rmisc' package in R <sup>59</sup> cross the
 zero line.

We focussed on three proxies of function derived from the average RII of 563 different combination of the 24 soil attributes: 1) organic matter decomposition, 564 quantified using the activity of five soil extracellular enzymes related to the 565 degradation of organic matter [\beta-glucosidase, phosphatase, cellobiosidase, β-N-566 acetylglucosaminidase and xylase], and measurements of soil carbon (hereafter 567 568 'Decomposition' (2) soil fertility, evaluated using multiple proxies of soil nutrient availability and carbon (contents of dissolved organic and total N, NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, total 569 P. Mn, K, Zn, Mg, Fe, Cu and soil C, hereafter 'Fertility'), and 3) resource 570 conservation (water regulation, using measures of soil water holding capacity, soil 571 porosity, stability of macro-aggregates >250 µm and mean weight diameter of soil 572 aggregates (hereafter 'Conservation'). Detailed measurements on these 24 soil 573

574 ecological attributes are described in Table S1 in Supplementary Information.

### 575 Data compilation and statistical analysis

Rainfall seasonality (coefficient of variation of 12 monthly rainfall totals) data were 576 extracted from the WorldClim Version 2.0 (http://www.worldclim.org/)<sup>60</sup> database, 577 which provides global climate data  $(0'30'' \times 0'30'')$  for the 1970-2000 period. Aridity 578 579 was identified as precipitation/potential evapotranspiration and was derived from the Global Aridity Index and Potential Evapotranspiration Climate Database v2 aridity 580 database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-581 evapotranspiration-climate-database-v2/)<sup>61</sup>, which includes global aridity data (0'30" 582  $\times$  0'30") for the 1970-2000 period. Soil texture is a major determinant of water 583 holding capacity and pH is a major driver of plant and soil function in drylands <sup>62</sup>. 584 585 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 to account for different levels of woody plants so that this would not bias any results. 588 Standardized dung mass (dung mass in a plot/maximum dung mass within the site) 589 was used as a measure of recent grazing pressure. 590

#### 591 Statistical analyses

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

602 grazing pressure (high, medium, low, ungrazed), herbivore type (livestock, native,

- mixed), aridity, island type (tree, shrub, grass), and functional category 603 (Decomposition, Fertility, Conservation). The model fitted individual ecosystem 604 functional attributes as groups (random intercepts) with varying slopes associated 605 with each of the main covariates (grazing and aridity). The model also included 606 interactions between ecosystem function category and grazing, island type, and aridity 607 608 to account for potential differences in the effects of each covariate within each ecosystem function category. We included site as a random intercept, accounting for 609 the non-independence of data gathered from the same site. 610
- We specified weakly informative normally distributed priors for the intercept and 611 all regression coefficients (mean = 0 and scale = 2.5). Default priors were used for 612 sigma (exponential, rate =1) and variance-covariance matrix of the varying intercepts 613 and slope parameters (shape and scale of 1). Posterior simulations of model 614 parameters were undertaken using the No-U-Turn Hamiltonian Monte Carlo sampler 615 within Stan<sup>63</sup>. Posterior distributions were estimated from four chains, each with 616 617 1000 iterations, after discarding the preliminary 1000 iterations. The convergence of models was assessed using visual diagnostics (autocorrelation, trace plots, and 618 posterior predictive checks) and inspection of effective sample sizes (min. 1000) and 619 r hat values (<1.01). Models were fitted using the package 'rstanarm' <sup>64</sup> within R <sup>59</sup>. A 620 hierarchical model provides several benefits over simple averaging of standardised 621 indicators or multiple separate models <sup>65</sup>: (i) simultaneous modelling of multiple 622 attributes improves precision and estimates of uncertainty for each ecosystem function 623 category; (ii) non-independence of multiple attributes within sites is explicitly 624 accounted for; (iii) enables simultaneous estimation of overall fertile island effect for 625 626 each ecosystem functional category and the individual soil attributes within these.

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

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

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

668

#### 669 Data Availability

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

672

## 673 Acknowledgments

674 Funding: This research was supported by the European Research Council [ERC grant

675 647038 (BIODESERT) awarded to F.T.M] and Generalitat Valenciana

676 (CIDEGENT/2018/041). D.E. was supported by the Hermon Slade Foundation

677 (HSF21040). J.DING was supported by the National Natural Science Foundation of

678 China Project (41991232) and the Fundamental Research Funds for the Central

- 679 Universities of China. M.D-B. acknowledges support from TED2021-130908B-
- 680 C41/AEI/10.13039/501100011033/Unión Europea Next Generation EU/PRTR and
- the Spanish Ministry of Science and Innovation for the I + D + i project PID2020-
- 682 115813RA-I00 funded by MCIN/AEI/10.13039/501100011033. O.S. was supported
- by US National Science Foundation (Grants DEB 1754106, 20-25166), and Y.L.B.-P.
- 684 by a Marie Sklodowska-Curie Actions Individual Fellowship (MSCA-1018 IF) within
- the European Program Horizon 2020 (DRYFUN Project 656035). K.G. and N.B.
- acknowledge support from the German Federal Ministry of Education and Research

- 687 (BMBF) SPACES projects OPTIMASS (FKZ: 01LL1302A) and ORYCS
- 688 (FKZ: FKZ01LL1804A). B.B. was supported by the Taylor Family-Asia Foundation
- Endowed Chair in Ecology and Conservation Biology, and M.A.B. by funding from
  the School of Forestry, Northern Arizona University. C.B. acknowledges funding
- from the National Natural Science Foundation of China (41971131). D.B.
- acknowledges support from the Hungarian Research, Development and Innovation
- 693 Office (NKFI KKP 144096) and A.F. support from ANID PIA/BASAL FB 210006
- and the Millennium Science Initiative Program NCN2021-050. M.F. and H.E.
- 695 received funding from Ferdowsi University of Mashhad (Grant 39843). A.N. and
- 696 M.K. acknowledge support from FCT (CEECIND/02453/2018/CP1534/CT0001,
- 697 SFRH/BD/130274/2017, PTDC/ASP-SIL/7743/2020, UIDB/00329/2020), EEA 698 (10/CALL#5), AdaptForGrazing (PRR-C05-i03-I-000035) and LTsER Montado
- 699 platform (LTER EU PT 001) grants. O.V. acknowledges support from the
- 700 Hungarian Research, Development and Innovation Office (NKFI KKP 144096). L.W.
- 701 was supported by the US National Science Foundation (EAR 1554894). Z.Z. and X.Z.
- were supported by the National Natural Science Foundation of China (U2003214).
- 703 H.S. is supported by a María Zambrano fellowship funded by the Ministry of
- 704 Universities and European Union-Next Generation plan. The use of any trade, firm, or
- 705 product names does not imply endorsement by any agency, institution or government.
- Finally, we thank the many people who assisted with field work, and the landowners, corporations and national bodies that allowed us access to their land.

## 708 Author contributions

- F.T.M. designed and coordinated the field survey. D.J.E. and J.DING conceived the
- 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
- managed field data collection. D.J.E. and J.DING wrote the draft manuscript in
- 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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Figure 1. Average function (mean relative interaction effect value across 24 soil
attributes, see Methods) for the 288 plots at 88 sites across global drylands and
examples of fertile islands at selected sites. The background map shows the
distribution of aridity (1- [precipitation/potential evapotranspiration]) across global
drylands.



Fertile island effect (RII)

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



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

904 pressure (standardized dung mass) and aridity, and mean ( $\pm$  95% CI) predicted RII

- value for the three functions in relation to (b) long-term (historic) measure of
   herbivore grazing pressure (ungrazed, low, medium, high), and (c) herbivore type
- 907 (livestock, native, mixed).



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Figure 4. Structural equation modelling assessing the direct and indirect effects of 910 climate (aridity [ARID], rainfall seasonality [SEAS]), soil (pH and sand [SAND] 911 912 content), plants (perennial cover [COV], perennial plant richness [RICH]), plant height [HT], plant shape [SHAPE], leaf area [AREA], leaf length [LNGTH], canopy 913 width [WIDTH], palatability [PALAT], deciduousness [DECID], resprouting ability 914 [RESP], and allelopathy [ALLEL]), and grazing (standardized grazing pressure) on 915 the fertile island effect for soil decomposition (Decomposition), soil fertility 916 (Fertility) and soil and water conservation (Conservation), after accounting for the 917 effects of location (latitude, cosine longitude, sine longitude). Standardised path 918 coefficients, adjacent to the arrows, are analogous to partial correlation coefficients, 919 and indicative of the effect size of the relationship. Pathways are significantly 920 negative (red unbroken line), significant positive (blue unbroken line) or mixed 921 significant negative and significant positive (black unbroken lines). Non-significant 922 pathways are not shown in the models. Model fit: (a) organic matter decomposition: 923  $\gamma^2 = 31.9$ , df = 26, P = 0.20,  $R^2 = 0.17$ , root mean error of approximation (RMSEA) < 924 0.001, Bollen-Stine = 0.40 (2000 bootstrap); (b) Fertility:  $\gamma^2 = 31.9$ , df = 26, P = 0.20, 925  $R^2$ =0.19, root mean error of approximation (RMSEA) < 0.001, Bollen-Stine = 0.40 926 (2000 bootstrap); (c) Conservation:  $\chi^2 = 31.9$ , df = 26, P = 0.20,  $R^2 = 0.10$ , root mean 927 error of approximation (RMSEA) < 0.001, Bollen-Stine = 0.40 (2000 bootstraps). 928 N=288 for all analyses. 929