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David Eldridge, Jingyi Ding, Josh Dorrough, Manuel Delgado-Baquerizo, Osvaldo Sala, Nicolas Gross, Yoann Le Bagousse-Pinguet, Max Mallen-Cooper, Hugo Saiz, Sergio Asensio, et al.

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

3  
4 David J. Eldridge<sup>1</sup>, Jingyi Ding<sup>2</sup>, Josh Dorrough<sup>3,4</sup>, Manuel Delgado-Baquerizo<sup>5</sup>,  
5 Osvaldo Sala<sup>6</sup>, Nicolas Gross<sup>7</sup>, Yoann Le Bagousse-Pinguet<sup>8</sup>, Max Mallen-Cooper<sup>9</sup>,  
6 Hugo Saiz<sup>10</sup>, Sergio Asensio<sup>11</sup>, Victoria Ochoa<sup>12</sup>, Beatriz Gozalo<sup>11</sup>, Emilio Guirado<sup>11</sup>,  
7 Miguel García-Gómez<sup>13</sup>, Enrique Valencia<sup>14</sup>, Jaime Martínez-Valderrama<sup>11,15</sup>, César  
8 Plaza<sup>12</sup>, Mehdi Abedi<sup>16</sup>, Negar Ahmadian<sup>16</sup>, Rodrigo J. Ahumada<sup>17</sup>, Julio M.  
9 Alcántara<sup>18</sup>, Fateh Amghar<sup>19</sup>, Luísa Azevedo<sup>20</sup>, Farah Ben Salem<sup>21</sup>, Miguel  
10 Berdugo<sup>14,22</sup>, Niels Blaum<sup>23</sup>, Bazartseren Boldgiv<sup>24</sup>, Matthew Bowker<sup>25,26</sup>, Donaldo  
11 Bran<sup>27</sup>, Chongfeng Bu<sup>28,29</sup>, Rafaella Canessa<sup>30,31,35</sup>, Andrea P. Castillo-Monroy<sup>32</sup>,  
12 Ignacio Castro<sup>33</sup>, Patricio Castro-Quezada<sup>34</sup>, Simone Cesarz<sup>35,36</sup>, Roukaya Chibani<sup>21</sup>,  
13 Abel Augusto Conceição<sup>37</sup>, Anthony Darrouzet-Nardi<sup>38</sup>, Yvonne C. Davila<sup>39</sup>, Balázs  
14 Deák<sup>40</sup>, Paloma Díaz-Martínez<sup>12</sup>, David A. Donoso<sup>32</sup>, Andrew David Dougill<sup>41</sup>, Jorge  
15 Durán<sup>42</sup>, Nico Eisenhauer<sup>35,36</sup>, Hamid Ejtehadi<sup>43</sup>, Carlos Ivan Espinosa<sup>44</sup>, Alex  
16 Fajardo<sup>45</sup>, Mohammad Farzam<sup>46</sup>, Ana Foronda<sup>47</sup>, Jorgelina Franzese<sup>48</sup>, Lauchlan H.  
17 Fraser<sup>49</sup>, Juan Gaitán<sup>50</sup>, Katja Geissler<sup>23</sup>, Sofia Laura Gonzalez<sup>51</sup>, Elizabeth Gusman-  
18 Montalvan<sup>44</sup>, Rosa Mary Hernández<sup>33</sup>, Norbert Hölzel<sup>52</sup>, Frederic Mendes Hughes<sup>37</sup>,  
19 Oswaldo Jadan<sup>34</sup>, Anke Jentsch<sup>53</sup>, Mengchen Ju<sup>29</sup>, Kudzai F. Kaseke<sup>54</sup>, Melanie  
20 Köbel<sup>55</sup>, Anika Lehmann<sup>56</sup>, Pierre Liancourt<sup>30</sup>, Anja Linstädter<sup>57</sup>, Michelle A Louw<sup>58</sup>,  
21 Qianhui Ma<sup>59</sup>, Mancha Mabaso<sup>60</sup>, Gillian Maggs-Kölling<sup>61</sup>, Thulani P.  
22 Makhalanyane<sup>60</sup>, Oumarou Malam Issa<sup>62</sup>, Eugene Marais<sup>61</sup>, Mitchel McClaran<sup>63</sup>,  
23 Betty Mendoza<sup>64</sup>, Vincent Mokoka<sup>65</sup>, Juan P. Mora<sup>45</sup>, Gerardo Moreno<sup>66</sup>, Seth  
24 Munson<sup>67</sup>, Alice Nunes<sup>55</sup>, Gabriel Oliva<sup>27</sup>, Gastón R Oñatibia<sup>68</sup>, Brooke Osborne<sup>69</sup>,  
25 Guadalupe Peter<sup>70</sup>, Margerie Pierre<sup>71</sup>, Yolanda Pueyo<sup>72</sup>, R. Emiliano Quiroga<sup>17</sup>, Sasha  
26 Reed<sup>73</sup>, Ana Rey<sup>74</sup>, Pedro Rey<sup>18</sup>, Víctor Manuel Reyes Gómez<sup>75</sup>, Víctor Rolo<sup>66</sup>,  
27 Matthias C. Rillig<sup>76</sup>, Peter C. le Roux<sup>58</sup>, Jan Christian Ruppert<sup>30</sup>, Ayman Salah<sup>77</sup>,  
28 Phokgedi Julius Sebei<sup>78</sup>, Anarmaa Sharkhuu<sup>24</sup>, Ilan Stavi<sup>79</sup>, Colton Stephens<sup>49</sup>,  
29 Alberto L. Teixido<sup>14</sup>, Andrew David Thomas<sup>80</sup>, Katja Tielbörger<sup>30</sup>, Silvia Torres  
30 Robles<sup>70</sup>, Samantha Travers<sup>1</sup>, Orsolya Valkó<sup>40</sup>, Liesbeth van den Brink<sup>30</sup>, Frederike  
31 Velbert<sup>52</sup>, Andreas von Heßberg<sup>53</sup>, Wanyoike Wamiti<sup>81</sup>, Deli Wang<sup>59</sup>, Lixin Wang<sup>82</sup>,  
32 Glenda M. Wardle<sup>83</sup>, Laura Yahdjian<sup>84</sup>, Eli Zaady<sup>85</sup>, Yuanming Zhang<sup>86</sup>, Xiaobing  
33 Zhou<sup>86</sup>, Fernando T. Maestre<sup>87</sup>

34 **Affiliations**

35 <sup>1</sup>Centre for Ecosystem Science, School of Biological, Earth and Environmental  
36 Sciences, University of New South Wales, Sydney, New South Wales, 2052,  
37 Australia

38 <sup>2</sup>State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of  
39 Geographical Science, Beijing Normal University, Beijing 100875, China

40 <sup>3</sup>Department of Planning and Environment, PO Box 656, Merimbula NSW 2548,  
41 Australia

42 <sup>4</sup>Fenner School of Environment & Society, Australian National University, Canberra,  
43 2601, Australia

44 <sup>5</sup>Laboratorio de Biodiversidad y Funcionamiento Ecosistémico. Instituto de Recursos  
45 Naturales y Agrobiología de Sevilla (IRNAS), CSIC, 41012, Sevilla, Spain

46 <sup>6</sup>Schools of Life Sciences, School of Sustainability, and Global Drylands Center,  
47 Arizona State University, Tempe, AZ 85287

48 <sup>7</sup>Université Clermont Auvergne, INRAE, VetAgro Sup, Unité Mixte de Recherche  
49 Ecosystème Prairial; Clermont-Ferrand, France

50 <sup>8</sup>Aix Marseille Univ, CNRS, Avignon Université, IRD, IMBE; Aix-en-Provence,  
51 France

52 <sup>9</sup>Department of Forest Ecology and Management, Swedish University of Agricultural  
53 Sciences (SLU), Umeå, Sweden

54 <sup>10</sup> Departamento de Ciencias Agrarias y Medio Natural, Escuela Politécnica Superior,  
55 Instituto Universitario de Investigación en Ciencias Ambientales de Aragón (IUCA),  
56 Universidad de Zaragoza, Huesca, Spain.

57 <sup>11</sup>Instituto Multidisciplinar para el Estudio del Medio “Ramón Margalef”, Universidad  
58 de Alicante, Alicante, Spain

59 <sup>12</sup>Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas,  
60 Madrid, Spain

61 <sup>13</sup>Departamento de Ingeniería y Morfología del Terreno, Escuela Técnica Superior de  
62 Ingenieros de Caminos, Canales y Puertos, Universidad Politécnica de Madrid,  
63 Madrid, Spain

64 <sup>14</sup>Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias  
65 Biológicas. Universidad Complutense de Madrid, 28040, Madrid, Spain

66 <sup>15</sup>Estación Experimental de Zonas Áridas (EEZA), CSIC, Campus UAL. Carretera de  
67 Sacramento s/n 04120, La Cañada de San Urbano, Almería, Spain

68 <sup>16</sup>Department of Range Management, Faculty of Natural Resources and Marine  
69 Sciences, Tarbiat Modares University, Noor, Iran

70 <sup>17</sup>Instituto Nacional de Tecnología Agropecuaria, Estación Experimental  
71 Agropecuaria Catamarca, 4700 Catamarca, Argentina

72 <sup>18</sup>Instituto Interuniversitario de Investigación del Sistema Tierra de Andalucía,  
73 Universidad de Jaén, E-23071 Jaén, Spain

74 <sup>19</sup>Laboratoire Biodiversité, Biotechnologie, Environnement et Développement  
75 Durable (Biodev), Université M’hamed Bougara de Boumerdès, Avenue de  
76 l’indépendance 35000 Boumerdès, Algérie

77 <sup>20</sup>Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas  
78 Gerais, Belo Horizonte, MG, 31270-901, Brazil

- 79 <sup>21</sup>Laboratory of Eremology and Combating Desertification (LR16IRA01), IRA,  
80 Institut des Régions Arides Medenine, Tunisia
- 81 <sup>22</sup>Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland.
- 82 <sup>23</sup>Plant Ecology and Nature Conservation, University of Potsdam, Am Mühlberg 3,  
83 14476 Potsdam, Germany
- 84 <sup>24</sup>Laboratory of Ecological and Evolutionary Synthesis, Department of Biology,  
85 School of Arts and Sciences, National University of Mongolia, Ulaanbaatar 14201,  
86 Mongolia.
- 87 <sup>25</sup>School of Forestry, Northern Arizona University, Arizona, USA
- 88 <sup>26</sup>Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff,  
89 Arizona, USA
- 90 <sup>27</sup>Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental  
91 Agropecuaria Bariloche, Bariloche, Río Negro, Argentina
- 92 <sup>28</sup>Institute of Soil and Water Conservation, Northwest A & F University, Yangling,  
93 Shaanxi 712100, China
- 94 <sup>29</sup>Institute of Soil and Water Conservation, Chinese Academy of Sciences and  
95 Ministry of Water Resources, Yangling, Shaanxi, 712100, China
- 96 <sup>30</sup>State Museum of Natural History Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany
- 97 <sup>31</sup>Martin Luther University of Halle-Wittenberg, Halle (Saale), Germany
- 98 <sup>32</sup>Grupo de Investigación en Ecología Evolutiva en los Trópicos-EETROP-  
99 Universidad de las Américas, Quito, Ecuador
- 100 <sup>33</sup>Universidad Simón Rodríguez. Instituto de Estudios Científicos y Tecnológicos  
101 (IDECYT),
- 102 <sup>34</sup>Grupo de Ecología Forestal y Agroecosistemas, Facultad de Ciencias  
103 Agropecuarias, Carrera de Agronomía, Universidad de Cuenca, Ecuador
- 104 <sup>35</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig;  
105 Leipzig, Germany
- 106 <sup>36</sup>Leipzig University, Institute of Biology; Leipzig, Germany
- 107 <sup>37</sup>Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana,  
108 Biológicas, Universidade Estadual de Feira de Santana, Feira de Santana, Bahia,  
109 Brazil
- 110 <sup>38</sup>Department of Biological Sciences, University of Texas at El Paso, Texas, USA
- 111 <sup>39</sup>Faculty of Science, University of Technology Sydney, Sydney New South Wales  
112 2007, Australia
- 113 <sup>40</sup>HUN-REN 'Lendület' Seed Ecology Research Group, Institute of Ecology and  
114 Botany, Centre for Ecological Research, Vácrátót, H-2163, Hungary

115 <sup>41</sup>University of York, UK.

116 <sup>42</sup>Misión Biológica de Galicia, Consejo Superior de Investigaciones Científicas,  
117 Pontevedra, Spain

118 <sup>43</sup>Faculty of Science, Ferdowsi University of Mashhad, Iran

119 <sup>44</sup>Departamento de Ciencias Biológicas, Universidad Técnica Particular de Loja; Loja,  
120 Ecuador.

121 <sup>45</sup> Instituto de Investigación Interdisciplinaria (I3), Vicerrectoría Académica,  
122 Universidad de Talca, Chile.

123 <sup>46</sup>Department of Range and Watershed Management, Faculty of Natural Resources  
124 and Environment, Ferdowsi University of Mashhad, Iran.

125 <sup>47</sup>Veterinary Faculty, University of Zaragoza, Zaragoza, Spain

126 <sup>48</sup>Investigaciones de Ecología en Ambientes Antropizados, Laboratorio Ecotono,  
127 INIBIOMA (Universidad Nacional del Comahue, CONICET), Bariloche 8400, Río  
128 Negro, Argentina.

129 <sup>49</sup>Department of Natural Resource Science, Thompson Rivers University, Kamloops,  
130 BC, V2C 0C8, Canada

131 <sup>50</sup>Universidad Nacional de Luján-CONICET. Luján, Argentina.

132 <sup>51</sup>Instituto de Investigaciones en Biodiversidad y Medioambiente (CONICET),  
133 Universidad Nacional del Comahue, Argentina

134 <sup>52</sup>Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149  
135 Münster, Germany

136 <sup>53</sup>Disturbance Ecology and Vegetation Dynamics, Bayreuth Center of Ecology and  
137 Environmental Research (BayCEER), University of Bayreuth, Universitaetsstrasse 30,  
138 95440 Bayreuth, Germany

139 <sup>54</sup>Earth Research Institute, University of California, Santa Barbara, CA 93106, USA

140 <sup>55</sup>cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE -  
141 Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de  
142 Lisboa, 1749-016 Lisboa, Portugal

143 <sup>56</sup>Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin,  
144 Germany

145 <sup>57</sup>University of Potsdam, Biodiversity Research / Systematic Botany, Potsdam,  
146 Germany

147 <sup>58</sup>Department of Plant and Soil Sciences, University of Pretoria, South Africa

148 <sup>59</sup>Key Laboratory of Vegetation Ecology of the Ministry of Education, Jilin Songnen  
149 Grassland Ecosystem National Observation and Research Station, Institute of  
150 Grassland Science, Northeast Normal University, Changchun 130024, China

151 <sup>60</sup>Department of Biochemistry, Genetics and Microbiology, DSI/NRF SARCHI in  
152 Marine Microbiomics, University of Pretoria, Hatfield, Lynnwood Road, Pretoria,  
153 South Africa, 0029

154 <sup>61</sup>Gobabeb – Namib Research Institute, Walvis Bay, Namibia

155 <sup>62</sup>Institute of Ecology and Environmental Sciences of Paris,  
156 SU/IRD/CNRS/INRAE/UPEC, Bondy, France

157 <sup>63</sup>School of Natural Resources and the Environment, University of Arizona, Tucson,  
158 AZ, USA

159 <sup>64</sup>Departamento de Biología y Geología, Física y Química Inorgánica, Universidad  
160 Rey Juan Carlos; Móstoles, Spain

161 <sup>65</sup>Risk and Vulnerability Science Centre, University of Limpopo, South Africa

162 <sup>66</sup>INDEHESA, Forestry School, Universidad de Extremadura, Plasencia 10600, Spain

163 <sup>67</sup>U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, Arizona,  
164 USA

165 <sup>68</sup>Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura  
166 (IFEVA-CONICET), Cátedra de Ecología, Facultad de Agronomía, Universidad de  
167 Buenos Aires, C1418DSE Ciudad Autónoma de Buenos Aires, Argentina

168 <sup>69</sup>Department of Environment and Society, Utah State University, Moab, UT, USA

169 <sup>70</sup>Universidad Nacional de Río Negro, Sede Atlántica, Centro de Estudios  
170 Ambientales desde la NorPatagonia (CEANPa). Viedma, Río Negro, Argentina. -  
171 CONICET

172 <sup>71</sup>Normandie Universite, Unirouen, Inrae, Ecodiv, 76000 Rouen, France.

173 <sup>72</sup>Instituto Pirenaico de Ecología (IPE, CSIC), Zaragoza, Spain

174 <sup>73</sup>U.S. Geological Survey, Southwest Biological Science Center, Moab, Utah, USA

175 <sup>74</sup>Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones  
176 Científicas; Madrid, Spain

177 <sup>75</sup>Instituto de Ecología, A.C. Chihuahua, Chihuahua, Mexico

178 <sup>76</sup>Institute of Biology, Freie Universität Berlin, Berlin, Germany

179 <sup>77</sup>Al Quds University, Abu Dis, Palestine.

180 <sup>78</sup>Mara Research Station, Limpopo Department of Agriculture and Rural  
181 Development, Makhado, 0920, South Africa

182 <sup>79</sup>The Dead Sea and Arava Science Center, Yotvata, 88820, Israel, and Eilat Campus,  
183 Ben-Gurion University of the Negev, Eilat 88100, Israel

184 <sup>80</sup>Department of Geography and Earth Science, Aberystwyth University, Wales, UK.

185 <sup>81</sup>Zoology Department, National Museums of Kenya, P.O. Box 40658-00100,  
186 Nairobi, Kenya.

187 <sup>82</sup>Department of Earth Sciences, Indiana University Indianapolis (IUI), Indianapolis,  
188 Indiana 46202, USA

189 <sup>83</sup>Desert Ecology Research Group, School of Life and Environmental Sciences, The  
190 University of Sydney, Sydney, New South Wales 2006, Australia

191 <sup>84</sup>Cátedra de Ecología, Facultad de Agronomía, Universidad de Buenos Aires.  
192 Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura  
193 (IFEVA-CONICET); Ciudad Autónoma de Buenos Aires, Argentina

194 <sup>85</sup>Department of Natural Resources, Agricultural Research Organization, Institute of  
195 Plant Sciences, Gilat Research Center, Israel, and Kaye College of Education, Be'er  
196 Sheva, Israel

197 <sup>86</sup>State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology  
198 and Geography, Chinese Academy of Sciences, Urumqi 830011, China.

199 <sup>87</sup>Environmental Sciences and Engineering, Biological and Environmental Science  
200 and Engineering Division, King Abdullah University of Science and Technology,  
201 Thuwal, 23955-6900, Kingdom of Saudi Arabia.

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,  
275 a factor that operates at the local scale, on fertile islands (Hypothesis 2a). More  
276 specifically, irrespective of grazing pressure, we would expect that plants would make  
277 a greater contribution to fertile islands in arid and hyper-arid ecosystems where soils  
278 are extremely bare and infertile compared with less arid ecosystems where the  
279 influence of plants would be relatively lower. For example, reduced rainfall and/or  
280 increased temperature would increase the harshness of the interspaces compared with  
281 the vegetated and more protected islands, thereby strengthening the fertile island  
282 effect. Plant effects might also be expected to vary among broad functional groups  
283 (tree vs shrub vs grass; Hypothesis 2b). These broad groups could have varying  
284 effects on soil biogeochemistry because of marked differences in shape, size, and  
285 structural complexity. Quantifying the contribution of grazing by different herbivores  
286 at different pressures, plant traits, climate, and soil properties on fertile islands  
287 allowed us to assess current and future impacts of grazing on ecosystem structure and  
288 functioning across global drylands, where woody vegetation is a predominant plant  
289 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  
385 with larger values of the Conservation function (more stable, with greater water  
386 holding capacity) tended to be associated with taller island plants, potentially through  
387 mechanisms involving hydraulic 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  
405<sup>40</sup>, 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  
419 provides refugia for plants and animals. Our results dispel the long-term assumption  
420 that increasing grazing pressure, either recent or longer term, or differences in  
421 herbivore type, can explain the magnitude of fertile island effects in drylands. Plant  
422 size, with taller and wider shrubs and grasses, supported stronger island effects. Stable  
423 and functional soils were also linked to species-rich sites with taller plants. The  
424 overwhelming importance of aridity and plant traits suggests that fertile islands may  
425 represent an autogenic response to drying and warming climates. These  
426 biogeochemical hotspots are likely to be more important as Earth's climate becomes  
427 hotter and drier.

428

## 429 **Methods**

### 430 **Study area**

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

436 sufficient trait data (see below). Site selection aimed to capture as much as possible of  
437 the wide variety of abiotic (climate, soil type, slope) and biotic (vegetation type, cover  
438 and species richness) features characterizing dryland ecosystems (e.g., grasslands,  
439 shrublands, savannas, open woodlands) found in drylands worldwide <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.  
460 To measure dung, we collected the dung of different herbivores from within two 25  
461 m<sup>2</sup> (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  
570 P, Mn, K, Zn, Mg, Fe, Cu and soil C, hereafter ‘Fertility’), and 3) resource  
571 conservation (water regulation, using measures of soil water holding capacity, soil  
572 porosity, stability of macro-aggregates  $>250 \mu\text{m}$  and mean weight diameter of soil  
573 aggregates (hereafter ‘Conservation’). Detailed measurements on these 24 soil  
574 ecological attributes are described in Table S1 in Supplementary Information.

### 575 **Data compilation and statistical analysis**

576 Rainfall seasonality (coefficient of variation of 12 monthly rainfall totals) data were  
577 extracted from the WorldClim Version 2.0 (<http://www.worldclim.org/>) <sup>60</sup> database,  
578 which provides global climate data ( $0^{\circ}30'' \times 0^{\circ}30''$ ) for the 1970-2000 period. Aridity  
579 was identified as precipitation/potential evapotranspiration and was derived from the  
580 Global Aridity Index and Potential Evapotranspiration Climate Database v2 aridity  
581 database ([https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-  
582 evapotranspiration-climate-database-v2/](https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/)) <sup>61</sup>, which includes global aridity data ( $0^{\circ}30''$   
583  $\times 0^{\circ}30''$ ) for the 1970-2000 period. Soil texture is a major determinant of water  
584 holding capacity and pH is a major driver of plant and soil function in drylands <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],  
632 resprouting [RESP], deciduousness [DECID], and allelopathy [ALLELO]), and  
633 grazing (standardised grazing pressure) on the fertile island effect (RII) after  
634 accounting for the effects of location (latitude, cosine longitude, sine longitude)  
635 across the globe. All explanatory variables were standardized (z-transformed) in the  
636 SEM analyses. The nine plant traits used in these analyses were selected from a  
637 potential pool of 15 potential traits using the significance of percentage increase in  
638 mean square error using Random Forest analyses (Fig. S3 in Supplementary  
639 Information). With these analyses we aimed to determine which traits are the most  
640 influential in describing the relative difference between islands and their interspaces  
641 (as measured with the RII) for each of the three synthetic functions (Decomposition,  
642 Fertility, Conservation). Random Forest is a robust approach when working with  
643 continuous and categorical variables. The 15 traits considered, which relate to plant  
644 size and structure, leaf characteristics, and ability to respond to environmental stimuli  
645 (palatability, resprouting, deciduousness, allelopathy) potentially influence: 1) how

646 nutrients are mineralized and made available to plants (Decomposition), 2) contribute  
647 to soil nutrient (including carbon) pools (Fertility) and 3) how soil and water are  
648 conserved (Conservation). Random forest analyses were conducted with the  
649 rfPermute package <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.,  
712 A.R., P.D.M., C.P., N.E., M.R., S.C. and M.D-B. The remaining authors collected and  
713 managed field data collection. D.J.E. and J.DING wrote the draft manuscript in  
714 collaboration with F.T.M. and O.S., and with contributions from all authors.

#### 715 **Competing interests**

716 The authors declare no competing interests.

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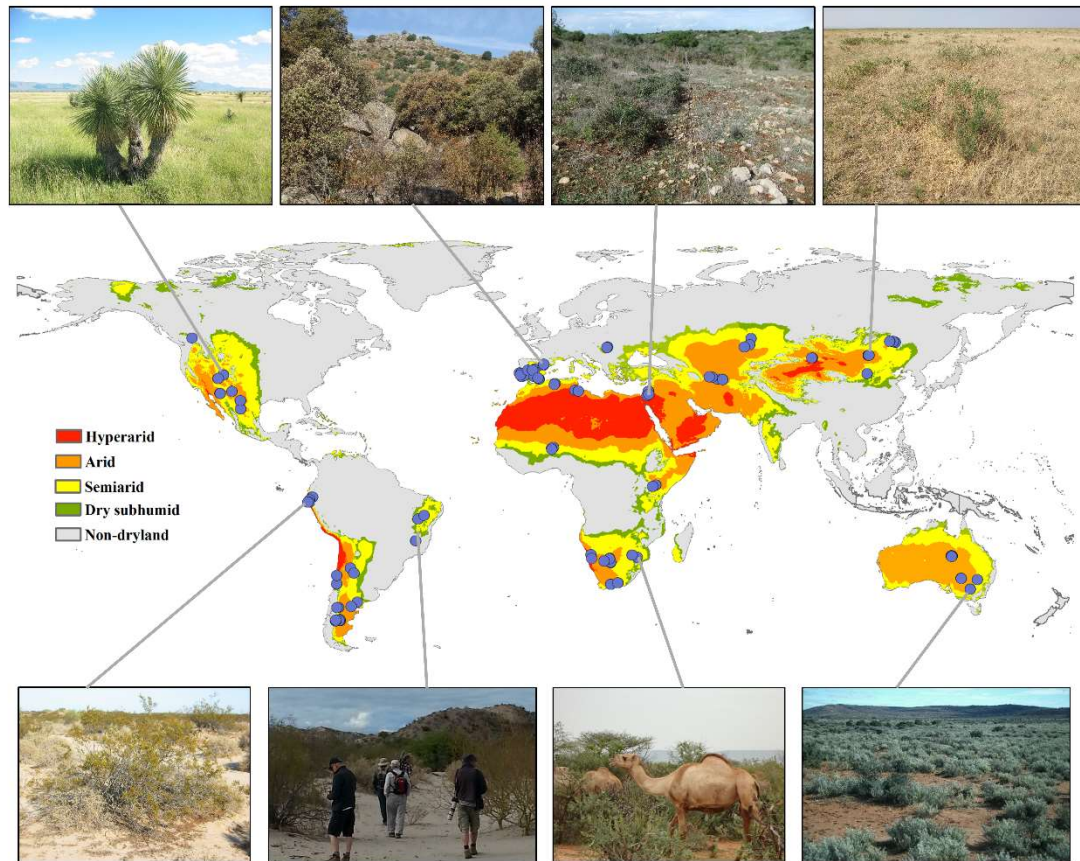
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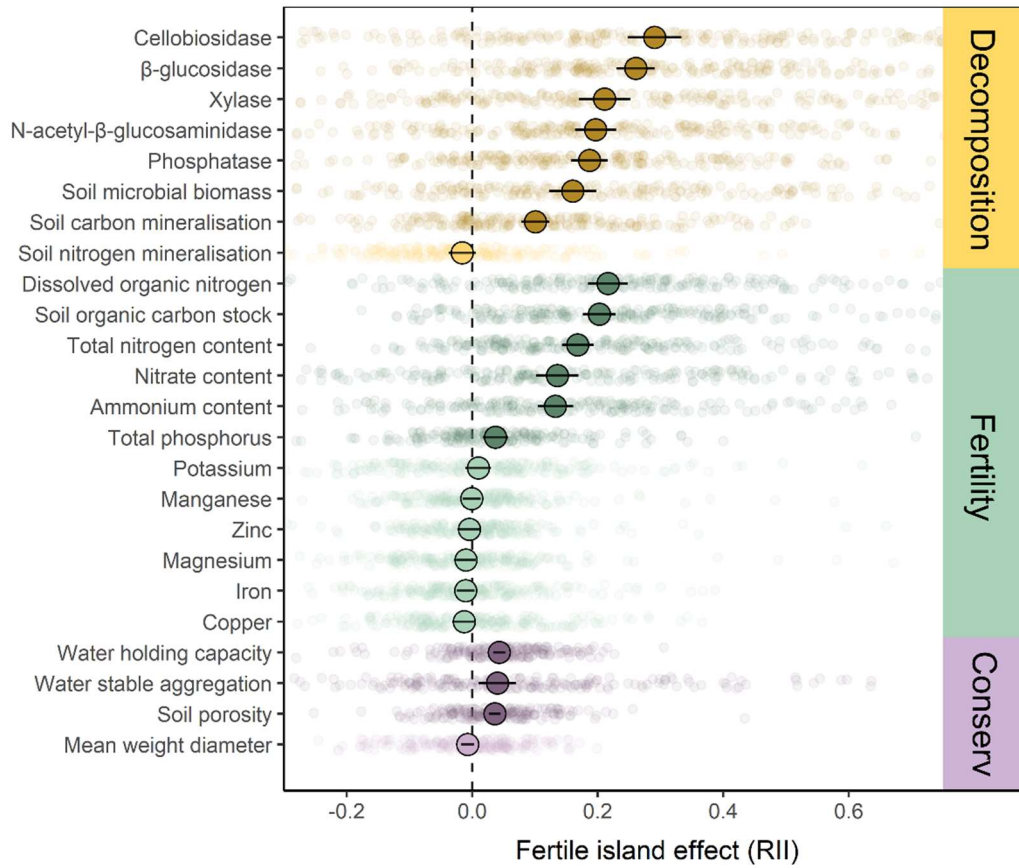


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884 **Figure 1.** Average function (mean relative interaction effect value across 24 soil  
 885 attributes, see Methods) for the 288 plots at 88 sites across global drylands and  
 886 examples of fertile islands at selected sites. The background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

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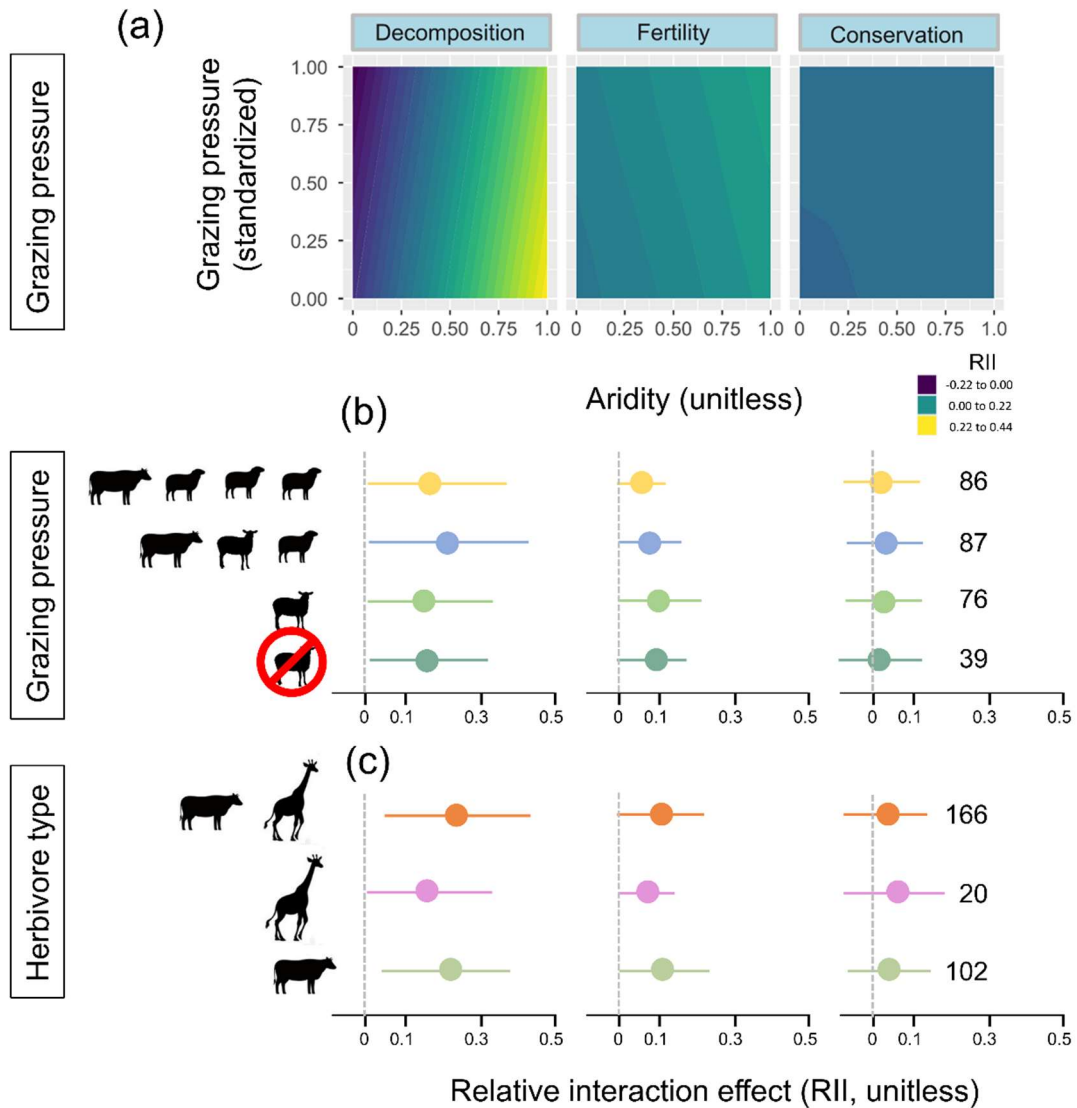
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893 **Figure 2.** The fertile island effect, as measured with the relative interaction effect  
 894 (RII), beneath perennial dryland plants for the 24 soil attributes measured across three  
 895 functions. Conserv = Conservation. Error bars are 95%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

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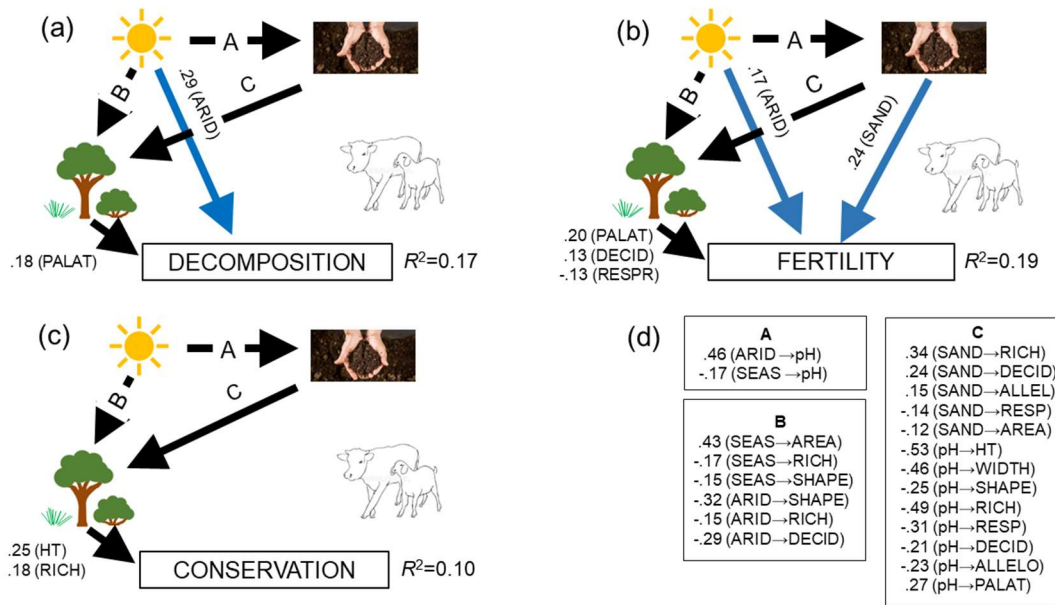
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901 **Figure 3.** Impacts of recent grazing and climate on the fertile island effect. (a)  
 902 Relative interaction effect (RII) value surfaces for the three measures of ecosystem  
 903 function (Decomposition, Fertility, Conservation) in relation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



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