



**HAL**  
open science

## Upper boundary on tree cover at global drylands

Lucio Biancari, Martín Aguiar, Hugo Saiz, Nicolas Gross, Yoann Le Bagousse-Pinguet, David Eldridge, Fernando Maestre

► **To cite this version:**

Lucio Biancari, Martín Aguiar, Hugo Saiz, Nicolas Gross, Yoann Le Bagousse-Pinguet, et al.. Upper boundary on tree cover at global drylands. *New Phytologist*, 2024, 242 (3), pp.836-840. 10.1111/nph.19598 . hal-04495845

**HAL Id: hal-04495845**

**<https://amu.hal.science/hal-04495845v1>**

Submitted on 18 Sep 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Upper boundary on tree cover at global drylands: a comment on “Linking resource-**  
2 **and disturbance-based models to explain tree–grass coexistence in savannas”**

3 **Lucio Biancari<sup>1,2</sup>, Martín R. Aguiar<sup>1,2</sup>, Hugo Saiz<sup>3,4</sup>, Nicolas Gross<sup>5</sup>, Yoann Le Bagousse-Pinguet<sup>6</sup>, David J.**  
4 **Eldridge<sup>7</sup>, Fernando T. Maestre<sup>8,9</sup>**

5 <sup>1</sup>IFEVA, Facultad de Agronomía, Universidad de Buenos Aires, CONICET, Buenos Aires, C1417DSE,  
6 Argentina, <sup>2</sup>Cátedra de Ecología, Departamento de Recursos Naturales y Ambiente, Facultad de  
7 Agronomía, UBA, Buenos Aires, C1417DSE, Argentina, <sup>3</sup>Departamento de Ciencias Agrarias y Medio  
8 Natural, Escuela Politécnica Superior, Instituto Universitario de Investigación en Ciencias Ambientales de  
9 Aragón (IUCA), Universidad de Zaragoza, Huesca, 50009, Spain, <sup>4</sup>Institute of Plant Sciences, University of  
10 Bern, Bern, 3013, Switzerland, <sup>5</sup>Université Clermont Auvergne, l’Institut national de recherche pour  
11 l’agriculture, l’alimentation et l’environnement, VetAgro Sup, Unité Mixte de Recherche 212 Ecosystème  
12 Prairial, Clermont-Ferrand, F-63000, France, <sup>6</sup>Aix Marseille Univ, CNRS, Avignon Université, IRD, IMBE, Aix-  
13 en-Provence, F-13545, France, <sup>7</sup>Centre for Ecosystem Science, School of Biological, Earth and  
14 Environmental Sciences, University of New South Wales, Sydney, New South Wales, 2052,  
15 Australia, <sup>8</sup>Instituto Multidisciplinar para el Estudio del Medio “Ramon Margalef”, Universidad de  
16 Alicante, Carretera de San Vicente del Raspeig s/n, Alicante, 03690, Spain, <sup>9</sup>Departamento de Ecología,  
17 Universidad de Alicante, Carretera de San Vicente del Raspeig s/n, Alicante, 03690, Spain

18 **Author for correspondence:** Lucio Biancari. IFEVA, Facultad de Agronomía, Universidad de  
19 Buenos Aires, CONICET, Av. San Martín 4453. Buenos Aires (1417). Argentina. E-mail:  
20 [biancari@agro.uba.ar](mailto:biancari@agro.uba.ar)

21

22 **ORCID:**

23 Lucio Biancari: 0000-0002-6539-6267

24 Martín R. Aguiar: 0000-0002-1213-4028

25 Hugo Saiz: 0000-0002-7568-2996

26 Nicolas Gross: 0000-0001-9730-3240

27 David Eldridge: 0000-0002-2191-486X

28 Fernando T. Maestre: 0000-0002-7434-4856

29

30 **Brief Heading:** Testing the upper boundary on tree cover at global drylands

31 **Twitter:** @Maestrelab

32

33 **Key words:** coexistence, tree cover, drylands, rangelands, grazing, soil texture, aridity

34 In their recent Tansley Review, Holdo and Nippert (2023) provide a comprehensive  
35 analysis of existing models that explain tree-grass coexistence along precipitation  
36 gradients in savannas. They highlight the diverse assumptions of the different models  
37 proposed in the literature and conclude that none can fully explain tree-grass  
38 coexistence along a rainfall gradient. Consequently, they propose essential elements  
39 that a synthetic model should incorporate to solve the '*treeness conundrum*' (*sensu*  
40 House *et al.* 2003). Holdo and Nippert assert that tree dominance is mainly limited by  
41 ecohydrological mechanisms in dry savannas and by disturbances in wet savannas.  
42 These concepts and mechanisms are summarized in their Figure 1, where they modify  
43 the '*Sankaran curve*' estimated for Africa (Sankaran *et al.*, 2005) to account for the effect  
44 of soil texture along rainfall gradients (upper boundary on tree cover is achieved with  
45 lower precipitation in coarser than in fine soils).

46 Here we aimed to test the upper boundary of tree cover predicted by Holdo and  
47 Nippert using data from BIODESERT (Maestre *et al.*, 2022a,b), a global field survey  
48 comprising mixed rangelands (*i.e.*, grazed areas composed of herbaceous and woody  
49 species) and accounting for the wide rainfall gradients that can be found across global  
50 drylands (Figure S1). While Holdo and Nippert propose that grass competition and  
51 disturbance are the mechanisms that determine the upper boundary of tree cover in  
52 arid- and humid-savannas, respectively, we expect similar mechanisms to operate in  
53 other grasslands with trees (see reviews by Scholes & Archer, 1997; Jeltsch *et al.*, 2000;  
54 House *et al.*, 2003; Sankaran *et al.*, 2004). If our global data support this pattern, they  
55 would provide evidence for the relevance and accuracy of the mechanisms proposed by  
56 Holdo and Nippert. Also, testing this pattern in rangelands with varying grazing  
57 pressures, which are largely driven by domestic livestock (Maestre *et al.*, 2022a), allows  
58 us to infer the presence and importance of disturbance-based mechanisms.

59 The BIODESERT survey combines comprehensive global plant type coverages of  
60 various mixed dryland rangelands with highly detailed local information on grazing  
61 management and multiple ecosystem structural and functional attributes. As in  
62 Sankaran *et al.* (2005), we focused our analysis exclusively on the highest tree cover  
63 values, specifically the 99th percentile, omitting shrubs from consideration. Following

64 Holdo and Nippert (2023), we denote this as the upper boundary for tree cover. Details  
65 of the methodology and statistical analysis conducted are presented in Methods S1.

66 We found that the upper boundary on tree cover in dryland rangelands increased  
67 with mean annual precipitation (MAP) before reaching a threshold of 453 mm (Figure 1,  
68 Table S1; the threshold corresponds to the vertex of the quadratic functions fitted to  
69 the data). These results suggest that the general pattern proposed by Holdo and Nippert  
70 (i.e., increase, threshold, and no-increase phases) also hold for global drylands.  
71 However, we found some specific differences to this pattern: a lower precipitation  
72 threshold and a declining tree cover beyond the threshold.

73 The differences in the precipitation threshold (453 mm here vs. 650 mm in Holdo &  
74 Nippert, 2023) can be explained because the rainfall gradient evaluated in our study  
75 differs from that of Sankaran *et al.* (2005) and is skewed -intentionally, as the BIODESERT  
76 survey is restricted to drylands- towards drier systems (132 to 1185 mm in Sankaran vs.  
77 29 to 891 mm in our dataset). Interestingly, the MAP threshold found here also matches  
78 a previously proposed global ecosystem threshold driven by aridity (1-  
79 [Precipitation/Evapotranspiration]) that implies systemic and abrupt changes in multiple  
80 functional and structural ecosystem attributes (Berdugo *et al.*, 2020, 2022). Specifically,  
81 the 0.7 aridity threshold is related to drastic changes in plant-soil feedbacks, including  
82 reductions in vegetation cover and soil fertility and changes in the composition of soil  
83 microbial communities (Berdugo *et al.*, 2020, 2022).

84 We observed that the upper boundary on tree cover declined beyond the  
85 precipitation threshold in our global dataset, rather than stabilizing as expected  
86 according to the 'Sankaran curve' (see table S2 for an AIC comparison of different models  
87 fitted to the data, including quadratic functions and functions that include a plateau).  
88 The patterns observed may be driven by several mechanisms. First, the differences  
89 between our results and the 'Sankaran curve' can be explained by a greater intensity of  
90 water competition relative to light competition within the BIODESERT survey. Water is  
91 the most important limiting resource for organisms in dryland ecosystems (Noy-Meir,  
92 1973). Consequently, a reduction in tree cover is expected if grasses outcompete trees  
93 for water, but trees are unable to exclude grasses through light limitation (Donaldson *et*  
94 *al.*, 2022). Second, at the global scale, biogeographical drivers may gain importance

95 compared to single continent data. For example, in the Neotropical region, the species  
96 pool lacks tree species capable of effectively using excess water in high precipitation  
97 areas (Wiens & Graham, 2005; Chaneton *et al.*, 2012). These two mechanisms may act  
98 simultaneously to explain lower values of the upper boundary on tree cover observed in  
99 sites where we would expect the opposite based on global patterns of aridity and tree  
100 cover (Whittaker, 1975). A third possible explanation may involve fire limiting tree cover  
101 in the wetter extreme of the gradient, because its occurrence and intensity increase in  
102 wetter and productive regions (Pausas & Paula, 2012; Devine *et al.*, 2015). However,  
103 Figure S2 shows that even though the probability of fire increases along the precipitation  
104 gradient, most of the plots in our survey did not experience fire during the last 20 years.  
105 Finally, a potential methodological explanation for the declining upper boundary on tree  
106 cover observed may be the low number of sites with MAP greater than 600 mm  
107 surveyed, limiting the ability to detect sites with higher tree cover values. However, a  
108 similar pattern to that reported here has also been observed in South African savannas  
109 (see Figure 5 in Stevens *et al.* (2016), ranging from 302 mm to 1134 mm) which casts  
110 doubt on whether a higher “sampling effort” would yield a different pattern.

111 Even if our data do not conform exactly to the ‘Sankaran curve’, they support the  
112 three mechanisms that comprise the building blocks of the model proposed by Holdo  
113 and Nippert. The first mechanism suggests that trees persist and grow due to excess  
114 water infiltrating below the grass functional rooting layer, even though grasses may  
115 consistently outcompete trees for water in the upper soil layers. Our results support this  
116 mechanism based on Walter's two-layer hypothesis and functional rooting separation  
117 (Walter, 1971). We found that as MAP increases, the upper boundary in fine soils  
118 consistently lies beneath that of coarse soils ( $p < 0.05$ , Table S1). In other words, a greater  
119 amount of precipitation is required to increase tree cover in finer soils, where there is  
120 greater water retention in the surface layers and less percolation to the subsoil  
121 (Fensham *et al.*, 2015). After the threshold was crossed, we found that the upper  
122 boundary on tree species cover declined with MAP more rapidly in finer than coarser  
123 soils. Since grasses may consistently outcompete trees for water in the upper soil layers  
124 (Holdo & Nippert, 2023), coarser soils, which retain less water and allow more water  
125 infiltration to deeper layers, can sustain greater tree cover at higher precipitation values.

126 However, it is also interesting to note that the maximum tree cover achieved in our  
127 study (ca. 45%) is similar for finer and coarser textures at the middle of the rainfall  
128 gradient evaluated. This feature of equal maximum tree cover for both soil textures is  
129 also represented in Figure 1 of Holdo and Nippert (2023), and our data suggest that  
130 along this precipitation window tree cover is no longer constrained by water availability.  
131 We did not find support for the inverse texture hypothesis in relation to the upper  
132 boundary on tree cover (Noy-Meir, 1973), similar to previous studies on African  
133 savannas (Bucini & Hanan, 2007).

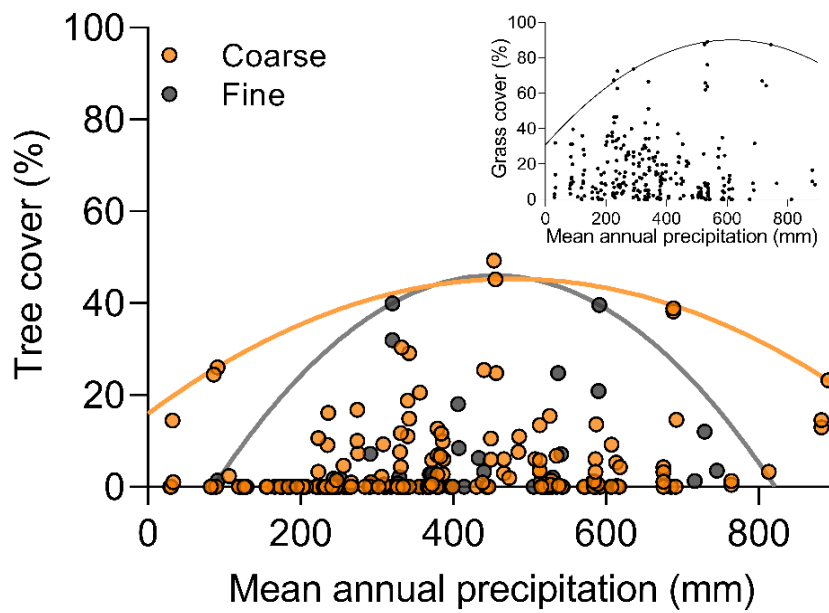
134 The second mechanism proposed by Holdo and Nippert hypothesizes that trees are  
135 unable to exclude grasses at drier sites through light limitation due to water availability  
136 constraining leaf area. Our data accords with this assertion because the upper boundary  
137 on tree species cover is lower in drier sites. Furthermore, the upper limit of leaf area in  
138 woody species along the rainfall gradient exhibits a similar trend to that of woody cover  
139 (Figure S3). In addition, there is an increase in the upper boundary on grass cover with  
140 higher mean annual precipitation, indicating that interactions among trees and grasses  
141 at the drier side of the rainfall gradient (<453 mm) may be neutral or positive (*i.e.*,  
142 facilitation), rather than negative (see inset of Figure 1).

143 The third mechanism proposed by Holdo and Nippert posits that grass competition  
144 allows for demographic bottlenecks in trees, leading to a decline in their cover. In our  
145 dataset, demographic bottlenecks may primarily occur due to grazing because fire is  
146 almost absent in our sampled sites (Figure S2). Our results show that increasing grazing  
147 pressure is associated with a lower upper boundary on tree cover (Figure 2). This  
148 deleterious effect of grazing may result from multiple mechanisms, including indirect  
149 effects on vital rates of tree species due to increases in the cover of non-palatable  
150 grasses and direct effects due to browsing, trampling, and a lower consumption  
151 selectivity of grazers at higher grazing pressures (Augustine & McNaughton, 1998;  
152 Sankey, 2012; Lezama & Paruelo, 2016; Oñatibia & Aguiar, 2019). Distinct variations in  
153 the upper boundary on tree cover between low and medium grazing pressure levels  
154 become apparent at intermediate levels of mean annual precipitation (MAP) and  
155 beyond. This suggests that water availability is a stronger constraint than disturbance  
156 under low precipitation values. Rather, when grazing pressure is high, the upper

157 boundary on tree cover is lower across the entire rainfall gradient. Hence, we observed  
158 an interplay between resource-based and disturbance-based mechanisms of  
159 coexistence, as their relative importance depends on water availability and grazing  
160 pressure.

161 While we found evidence for the key elements of a definitive savanna model  
162 proposed by Holdo and Nippert, we believe that these elements may differ or vary in  
163 importance under future global change scenarios. Global change drivers have the  
164 potential to modify tree cover patterns and the importance of the three coexistence  
165 mechanisms proposed by Holdo and Nippert (Venter *et al.*, 2018). For instance, changes  
166 in features beyond mean annual precipitation, such as its variability, seasonality or  
167 frequency of extreme events, may influence tree-grass interactions (Kulmatiski & Beard,  
168 2013; Wang *et al.*, 2022). Also, land-use change may have an important role, as the  
169 effect of grazing pressure on the upper boundary on tree cover may differ between  
170 herbivore species: browsers often exert a negative impact on tree species, while grazers  
171 exert a positive effect because of reductions in grass biomass (Manier & Hobbs, 2007;  
172 Donaldson *et al.*, 2022). Furthermore, drivers currently considered less important in  
173 explaining coexistence in savannas, such as temperature regime or nutrient dynamics  
174 (*e.g.*, nitrogen deposition), may become more significant in a more human-dominated  
175 world (Yahdjian *et al.*, 2011; Brandt *et al.*, 2017). And finally, changes in community  
176 composition due to biological invasions can alter the general patterns observed in our  
177 results. For example, the invasion of tree species with traits that effectively use water  
178 surplus in high precipitation sites and exclude grasses through light limitation could  
179 modify currently observed patterns (Mazia *et al.*, 2001; Chaneton *et al.*, 2012).

180 Overall, our findings validate several patterns proposed by Holdo and Nippert (2023)  
181 to explain the upper boundary pattern of tree cover in savannas. They also highlight  
182 some features that may be specific for water-limited rangelands, including a lower  
183 precipitation threshold, a declining tree cover beyond the threshold, and an interplay  
184 between resource- and disturbance-based mechanisms. By doing so, our study sets the  
185 stage for building a more comprehensive and definitive tree-grass coexistence model  
186 that fully accounts for the characteristics of drylands, the largest rangeland area on our  
187 planet (Asner *et al.*, 2004).



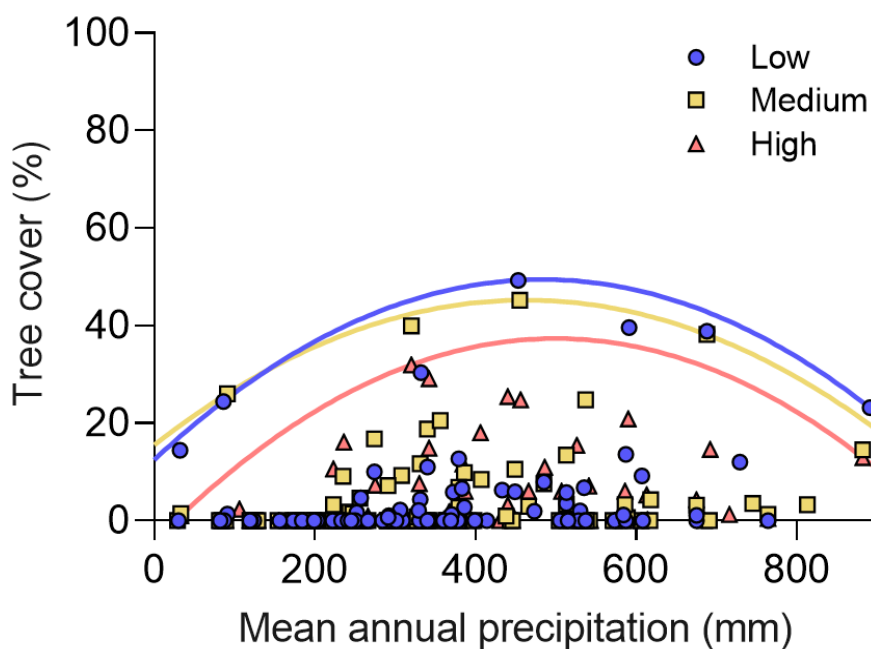
188

189 **Figure 1.** Tree species cover (%) along the mean annual precipitation (mm) gradient  
 190 captured by the BIODESERT global survey. Orange and grey full lines represent 99<sup>th</sup>  
 191 quadratic quantile regression adjustment for coarse- and fine-soil textures, respectively  
 192 (n = 283: coarse-textured soils n = 213, fine-textured soils, n = 70). **Inset:** Grass cover (%)  
 193 along a mean annual precipitation (mm) gradient until the 453 mm threshold. The fitted  
 194 line represents the 99<sup>th</sup> quadratic quantile regression adjustment.

195

196





197

198 **Figure 2.** Tree species cover (%) under different grazing pressure along the mean annual  
 199 precipitation (mm) gradient described by the BIODESERT global survey. The curves fitted  
 200 represent 99<sup>th</sup> quadratic quantile regression adjustment for low (n=88, blue line),  
 201 medium (n=97, yellow line), and high (n=98, pink line) grazing pressure levels.

202

## 203 Acknowledgments

204

205 We would like to express our gratitude to Editor Dr. Sasha C. Reed, two anonymous  
 206 reviewers and Dr. Amy T. Austin for their valuable comments and feedback that  
 207 contributed to improve the overall quality and clarity of this manuscript. We also thank  
 208 all the participants in the BIODESERT global survey, which was supported by the  
 209 European Research Council (BIODESERT project, Grant Agreement number 647038) and  
 210 Generalitat Valenciana (BIOMORES project, CIDEAGENT/2018/041). LB is sponsored by a  
 211 postdoctoral fellowship of Agencia Nacional de Promoción de la Investigación, el  
 212 Desarrollo Tecnológico y la Innovación (Agencia I+D+i, PICT 2019-2645) and a grant for  
 213 a short-term research stay by the Universidad de Buenos Aires (UBACYT  
 214 20020170100687BA). MRA is supported by grants from Agencia I+D+i (PICT-2020-  
 215 SERIEA-I-A-03336) and CONICET (PIP 2019-11220200103016CO). FTM is supported by  
 216 Universidad de Alicante (UADIF22-74 and VIGROB22-350) and the Spanish Ministerio de  
 217 Ciencia e Innovación (PID2020-116578RB-I00). HS is supported by a María Zambrano  
 218 fellowship funded by the Spanish Ministerio de Universidades and the European Union-  
 219 Next Generation plan. DJE is supported by the Hermon Slade Foundation.

220

221 **Author contributions**

222 LB, MRA and FTM conceived the original idea. FTM, HS, DJE, NG, YLBP coordinated and  
223 conducted fieldwork and data acquisition. LB analyzed data. MRA, HS, YLBP, NG, DJE and  
224 FTM contributed to data interpretation and additional ideas. LB and FTM wrote the  
225 manuscript. MRA, DJE, YLBP, NG, HS reviewed and improved the first version of the  
226 manuscript. All authors contributed equally to the final revision of the article based on  
227 reviewers' comments.

228 **Data availability**

229 The data that supports the findings of this study is available as a supplementary material  
230 of this article (Dataset S1).

231 **Competing interests**

232 None declared.

233 **References**

234 **Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT. 2004.** Grazing systems,  
235 ecosystem responses and global change. *Annual Review of Environment and Resources*  
236 **29**: 261–299.

237 **Bucini G, Hanan NP. 2007.** A continental-scale analysis of tree cover in African  
238 savannas. *Global Ecology and Biogeography* **16**: 593–605.

239 **Noy-Meir I. 1973.** Desert Ecosystems: environment and producers. *Annual Review of*  
240 *Ecology and Systematics* **4**: 25–51.

241 **Augustine DJ, McNaughton SJ. 1998.** Ungulate Effects on the Functional Species  
242 Composition of Plant Communities : Herbivore Selectivity and Plant Tolerance. *The*  
243 *Journal of Wildlife Management* **62**: 1165–1183.

244 **Berdugo M, Delgado-Baquerizo M, Soliveres S, Hernández-Clemente R, Zhao Y,**  
245 **Gaitán JJ, Gross N, Saiz H, Maire V, Lehmann A, et al. 2020.** Global ecosystem  
246 thresholds driven by aridity. *Science* **367**: 787–790.

247 **Berdugo M, Vidiella B, Solé R V., Maestre FT. 2022.** Ecological mechanisms underlying  
248 aridity thresholds in global drylands. *Functional Ecology* **36**: 4–23.

249 **Brandt M, Rasmussen K, Peñuelas J, Tian F, Schurgers G, Verger A, Mertz O, Palmer**  
250 **JRB, Fensholt R. 2017.** Human population growth offsets climate-driven increase in  
251 woody vegetation in sub-Saharan Africa. *Nature Ecology and Evolution* **1**: 4–9.

252 **Bucini G, Hanan NP. 2007.** A continental-scale analysis of tree cover in African  
253 savannas. *Global Ecology and Biogeography* **16**: 593–605.

254 **Chaneton EJ, Mazía N, Batista WB, Rolhauser AG, Ghera CM. 2012.** Woody Plant  
255 Invasions in Pampa Grasslands: A Biogeographical and Community Assembly  
256 Perspective. In: Myster RW, ed. *Ecotones Between Forest and Grassland*. New York,  
257 NY: Springer New York, 115–144.

- 258 **Devine AP, Stott I, McDonald RA, Maclean IMD. 2015.** Woody cover in wet and dry  
259 African savannas after six decades of experimental fires. *Journal of Ecology* **103**: 473–  
260 478.
- 261 **Donaldson JE, Holdo R, Sarakikya J, Anderson TM. 2022.** Fire, grazers, and browsers  
262 interact with grass competition to determine tree establishment in an African savanna.  
263 *Ecology* **103**: e3715.
- 264 **Fensham RJ, Butler DW, Foley J. 2015.** How does clay constrain woody biomass in  
265 drylands? *Global Ecology and Biogeography* **24**: 950–958.
- 266 **Holdo RM, Nippert JB. 2023.** Linking resource- and disturbance-based models to  
267 explain tree–grass coexistence in savannas. *New Phytologist* **237**: 1966–1979.
- 268 **House JI, Archer S, Breshears DD, Scholes RJ, Coughenour MB, Dodd MB, Gignoux J,  
269 Hall DO, Hanan NP, Joffre R, et al. 2003.** Conundrums in mixed woody-herbaceous  
270 plant systems. *Journal of Biogeography* **30**: 1763–1777.
- 271 **Jeltsch F, Weber GE, Grimm V. 2000.** Ecological buffering mechanisms in savannas: A  
272 unifying theory of long-term tree-grass coexistence. *Plant Ecology* **150**: 161–171.
- 273 **Kulmatiski A, Beard KH. 2013.** Woody plant encroachment facilitated by increased  
274 precipitation intensity. *Nature Climate Change* **3**: 833–837.
- 275 **Lezama F, Paruelo JM. 2016.** Disentangling grazing effects: trampling, defoliation and  
276 urine deposition. *Applied Vegetation Science* **19**: 557–566.
- 277 **Maestre FT, Le Bagousse-Pinguet Y, Delgado-Baquerizo M, Eldridge DJ, Saiz H,  
278 Berdugo M, Gozalo B, Ochoa V, Guirado E, García-Gómez M, et al. 2022a.** Grazing and  
279 ecosystem service delivery in global drylands. *Science* **378**: 915–920.
- 280 **Maestre FT, Eldridge DJ, Gross N, Le Bagousse-Pinguet Y, Saiz H, Gozalo B, Ochoa V,  
281 Gaitán JJ. 2022b.** The BIODESERT survey: assessing the impacts of grazing on the  
282 structure and functioning of global drylands. *Web Ecol.* **22**: 75–96.
- 283 **Manier DJ, Hobbs NT. 2007.** Large herbivores in sagebrush steppe ecosystems:  
284 livestock and wild ungulates influence structure and function. *Oecologia* **152**: 739–  
285 750.
- 286 **Mazia CN, Chaneton EJ, Ghera CM, León RJC. 2001.** Limits to Tree Species Invasion in  
287 Pampean Grassland and Forest Plant Communities. *Oecologia* **128**: 594–602.
- 288 **Noy-Meir I. 1973.** Desert Ecosystems: environment and producers. *Annual Review of  
289 Ecology and Systematics* **4**: 25–51.
- 290 **Oñatibia GR, Aguiar MR. 2019.** Grasses and grazers in arid rangelands: Impact of sheep  
291 management on forage and non-forage grass populations. *Journal of Environmental  
292 Management* **235**: 42–50.
- 293 **Pausas JG, Paula S. 2012.** Fuel shapes the fire–climate relationship: evidence from  
294 Mediterranean ecosystems. *Global Ecology and Biogeography* **21**: 1074–1082.
- 295 **Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J,  
296 Higgins SI, Le Roux X, Ludwig F, et al. 2005.** Determinants of woody cover in African

- 297 savannas. *Nature* **438**: 846–849.
- 298 **Sankaran M, Ratnam J, Hanan NP. 2004.** Tree-grass coexistence in savannas revisited -  
 299 Insights from an examination of assumptions and mechanisms invoked in existing  
 300 models. *Ecology Letters* **7**: 480–490.
- 301 **Sankey TT. 2012.** Woody–Herbaceous–Livestock Species Interaction. In: Myster RW,  
 302 ed. *Ecotones Between Forest and Grassland*. New York, NY: Springer New York, 89–  
 303 114.
- 304 **Scholes RJ, Archer SR. 1997.** Tree-Grass Interactions in Savannas. *Annual Review of*  
 305 *Ecology and Systematics* **28**: 517–544.
- 306 **Stevens N, Erasmus BFN, Archibald S, Bond WJ. 2016.** Woody encroachment over 70  
 307 years in South African savannas: Overgrazing, global change or extinction aftershock?  
 308 *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**.
- 309 **Venter ZS, Cramer MD, Hawkins HJ. 2018.** Drivers of woody plant encroachment over  
 310 Africa. *Nature Communications* **9**: 1–7.
- 311 **Walter H. 1971.** *Ecology of Tropical and Subtropical Vegetation* (Oliver & Boyd, Ed.).  
 312 Edinburgh, UK.
- 313 **Wang L, Jiao W, MacBean N, Rulli MC, Manzoni S, Vico G, D’Odorico P. 2022.** Dryland  
 314 productivity under a changing climate. *Nature Climate Change* **12**: 981–994.
- 315 **Westoby M, Wright IJ. 2006.** Land-plant ecology on the basis of functional traits.  
 316 *Trends in Ecology and Evolution* **21**: 261–268.
- 317 **Whittaker RH. 1975.** *Communities and Ecosystems*. Macmillan.
- 318 **Wiens JJ, Graham CH. 2005.** Niche Conservatism: Integrating Evolution, Ecology, and  
 319 Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics* **36**: 519–  
 320 539.
- 321 **Yahdjian L, Gherardi L, Sala OE. 2011.** Nitrogen limitation in arid-subhumid  
 322 ecosystems: A meta-analysis of fertilization studies. *Journal of Arid Environments* **75**:  
 323 675–680.
- 324 **Supporting information.**
- 325 Additional Supporting Information may be found online in the Methods S1 section.
- 326 Fig. S1. Location of the 98 sites surveyed for this study.
- 327 Fig. S2. Predicted probabilities of fire occurrence along the precipitation gradient for  
 328 the 326 plots surveyed.
- 329 Fig. S3. Community weighted mean for leaf area of woody species at each plot across  
 330 the precipitation gradient surveyed.
- 331 Table S1. Coefficients of the quadratic quantile regression models.
- 332
- 333 Table S2. Comparison of the different quantile regression models used.
- 334