DRYLAND ECOLOGY

Grazing and ecosystem service delivery in global drylands

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Grazing represents the most extensive use of land worldwide. Yet its impacts on ecosystem services remain uncertain because pervasive interactions between grazing pressure, climate, soil properties, and biodiversity may occur but have never been addressed simultaneously. Using a standardized survey at 98 sites across six continents, we show that interactions between grazing pressure, climate, soil, and biodiversity are critical to explain the delivery of fundamental ecosystem services across drylands worldwide. Increasing grazing pressure reduced ecosystem service delivery in warmer and species-poor drylands, whereas positive effects of grazing were observed in colder and species-rich areas. Considering interactions between grazing and local abiotic and biotic factors is key for understanding the fate of dryland ecosystems under climate change and increasing human pressure.

Grazing accounts for 77% of global agricultural land (*1*), sustains billions of people worldwide, and is closely linked to 10 of 17 United Nations (UN) Sustainable Development Goals (*2*). Despite its importance, there is no consensus on how grazing affects ecosystem services (*3*–*6*), which may depend on the coevolutionary history between vegetation and herbivores (*3*), grazing pressure (*4*), and local climatic, edaphic, and biodiversity conditions (*7*, *8*). Most field assessments have focused on local to regional scales (*3*, *4*, *6*, *8*), have studied a limited number of taxa—mostly plants—and single ecosystem services (*3*, *4*, *9*), and have not considered domestic and wild herbivores simultaneously. Another major source of uncertainty relates to interactions between grazing pressure and abiotic and biotic features, which results in strong context-dependent ecological impacts of grazing (*3*, *4*, *10*, *11*). Large-scale, standardized field surveys that explore how such impacts depend on above- and belowground biodiversity, soils, and climate to drive multiple ecosystem services across contrasting regions and environmental contexts are lacking at present but are sorely needed to evaluate whether general patterns emerge beyond these context dependencies (*12*).

Investigating the effects of grazing pressure across global abiotic and biotic gradients is particularly important in drylands [areas with an aridity index (precipitation divided by potential evapotranspiration) <0.65 (*13*)] because they constitute 78% of rangelands worldwide (*14*) and support ~1 billion people who rely on grazing by livestock as a critical source of protein and income (*15*). Although grazing may have beneficial effects by reducing fuel loads and enhancing primary production and plant diversity under certain conditions (*3*, *16*), increasing grazing pressure is also considered a major driver of rangeland degradation and desertification across drylands worldwide (*17*). These contrasting effects of grazing likely depend on local climate, soil conditions, and both plant and soil diversity, which largely influence dryland functioning (*18*, *19*). However, the interactions of these factors with grazing pressure have never, to our knowledge, been assessed. Identifying environmental conditions and biodiversity levels under which increasing grazing pressure will favor or detract ecosystem service delivery is a crucial step toward achieving multiple UN Sustainable Development Goals (*2*) and other international initiatives related to dryland desertification and restoration (*20*).

Here, we used a standardized field survey (*13*) carried out at 98 sites across 25 countries and six continents (Fig. 1 and movie S1) to assess how the effects of grazing pressure on nine essential ecosystem services depend on biodiversity, climate, and soil conditions across global drylands. Each site included a collection of three or four 45-m–by–45-m plots representing local gradients of grazing pressure [from ungrazed or low grazing pressure to high grazing pressure (*13*)], resulting in a total of 326 plots. These gradients were mostly driven by livestock (fig. S1), although wild herbivores were also present in each site and taken into account. In each plot, we assessed vascular plant, mammalian herbivore (accounting for domestic and wild herbivores), and belowground (soil bacteria, fungi, protists, and invertebrates) diversity as well as multiple regulating (water regulation, soil carbon storage, organic matter decomposition, and erosion control), supporting (soil fertility and aboveground plant biomass and its temporal stability), and provisioning (wood quantity, forage quantity, and quality) ecosystem services (table S1). Our survey captured most climatic conditions supporting livestock grazing in drylands, as well as a wide range of ecosystem types; soil properties; plant, soil, and mammalian diversities; and grazing pressure levels (figs. S2 to S9 and table S2). These distinctive features of our global study rendered grazing pressure largely independent of climate, soil, and biodiversity attributes [table S3 and (*13*)] and allowed us to (i) evaluate the main and interactive effects of grazing pressure, climate, soil properties, and biodiversity on ecosystem service delivery across global drylands; (ii) identify the environmental and biodiversity conditions under which the effects

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of grazing pressure on ecosystem services are positive or negative; and (iii) simultaneously assess relationships between plant, soil, and mammalian herbivore diversity and multiple ecosystem services.

We fitted linear mixed models to data from all sites and grazing pressure levels and applied a multimodel inference procedure based on Akaike information criterion (AIC) to select the set of best-fitting models [i.e., those with a ΔAIC <2 (*13*)]. We also considered potential indirect effects of grazing through the modification of local biodiversity and soil parameters using confirmatory path analyses (*13*). We found that increasing grazing pressure affects ecosystem services through direct effects (no significant indirect effects through changes in soil properties or biodiversity were found; figs. S10 and S11 and tables S4 to S12) and interactive effects (interactions between grazing and climate, grazing and soil properties, or grazing and biodiversity were selected in 86% of the best-fitting models; Fig. 2 and tables S13 to S28).

Interactions between grazing and climate were selected in 48% of the best-fitting models (fig. S12), with grazing primarily interacting with mean annual temperature (40% of the best-fitting models) and rainfall seasonality (20% of the best-fitting models) and, to a lesser extent, with mean annual precipitation (9% of the best-fitting models). A negative relationship between mean annual temperature and soil carbon storage, organic matter decomposition, and erosion control was found under high, but not under low, grazing pressure (Fig. 3, A to C). Our results provide an empirical validation of the importance of interactions between climate change drivers, grazing, and soil carbon storage that are predicted by global modeling studies (*21*). They also indicate that considering grazing pressure can improve our capacity to assess soil carbon–temperature feedbacks, a key process involved in climate warming (*22*).

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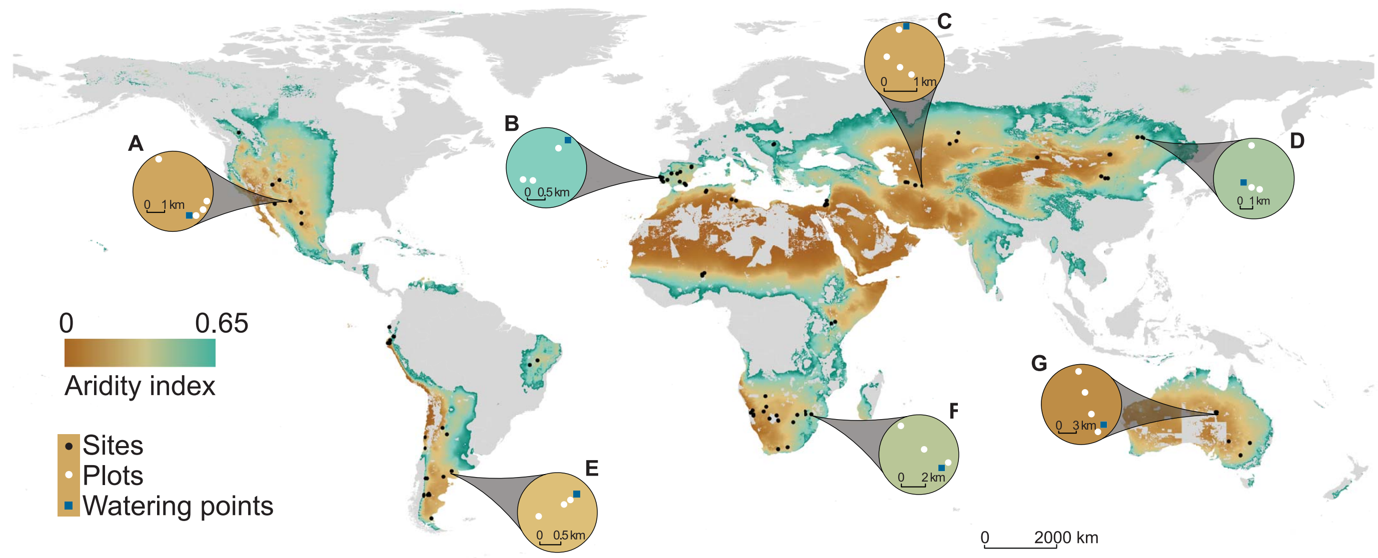

Fig. 1. Locations of the 98 study sites with examples of the local grazing gradients surveyed at each site. Each black dot represents a site with multiple 45-m–by–45-m plots (white dots) surveyed in situ; a total of 326 plots were surveyed across the 98 study sites. The inset graphics [(**A**) to (**G**)] highlight examples of the local gradients surveyed at each site. Watering points are ponds, impoundments, or drinking troughs that provide permanent sources of water for livestock in drylands; they were used in this study to create local grazing gradients (*13*). The background of the map indicates the extent of dryland rangeland areas. The aridity index is calculated as precipitation divided by potential evapotranspiration and is strongly related to mean annual precipitation in our dataset [coefficient of determination (R^2) = 0.82]. See (*13*) for the aridity index and rangeland area data sources that were used.

Soil texture also regulated grazing pressure effects on multiple ecosystem services, which include soil fertility, wood quantity, and forage quality (interactions between grazing and sand content were selected in 37% of the best-fitting models; fig. S12). As sand content increased, soil fertility declined more steeply under high grazing pressure (Fig. 3E), wood quantity increased under high but declined under low grazing pressure (Fig. 3G), and forage quality declined under high but increased under low grazing pressure (Fig. 3I). These findings illustrate how increases in grazing pressure interact with soil properties to either increase or reduce the delivery of multiple ecosystem services.

Biodiversity impacts on ecosystem functioning and services are typically examined in isolation from other drivers in experimental and observational studies (*23*). However, we found interactions between grazing and biodiversity in 44% of the best-fitting models (fig. S12). For instance, increasing grazing pressure shifted the relationships between plant species richness and water regulation from positive to negative (Fig. 3D) and those between plant species richness and both wood quantity and aboveground plant biomass and its temporal stability from negative to positive (Fig. 3, F and G). We also found positive relationships between plant species richness and soil carbon storage, organic matter decomposition, erosion control, and both forage quality and quantity (Fig. 3, A to C, H, and I) and between belowground diversity and organic

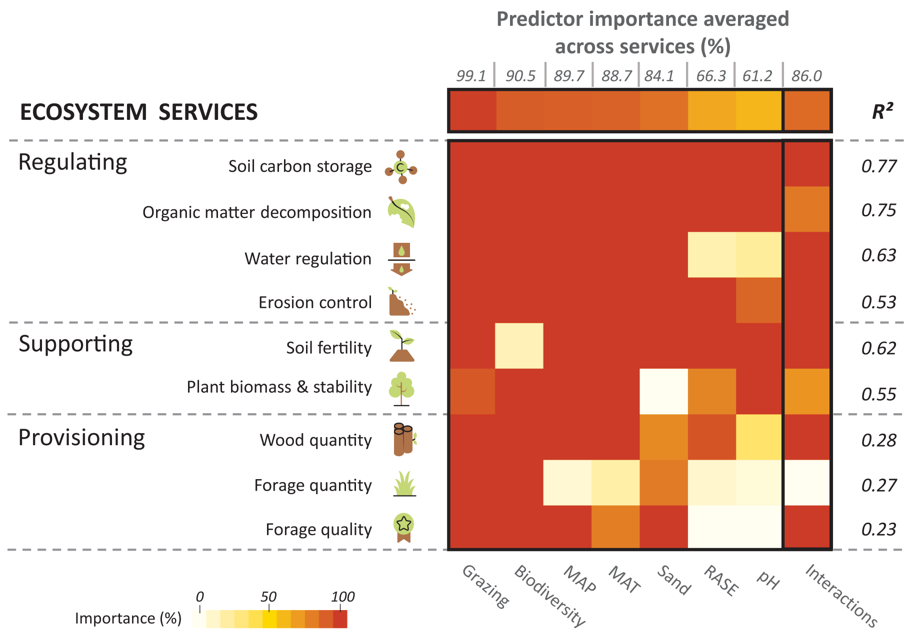

Fig. 2. Relative importance of predictors of ecosystem services selected in the best-fitting models. Importance is quantified as the sum of the Akaike weights of all models that included the predictor (grazing pressure, climate, biodiversity, and soil variables, and their interactions) of interest, considering the number of models in which each predictor appears. It is proportional to the number of times that a given predictor (and its interactions with other predictors) was selected in the final set of best-fitting models (*13*). Interactions include all interactions between grazing pressure and climate, biodiversity, and soil variables; the importance of each interaction type is shown in fig. S12. In the case of biodiversity, predictor importance considers the number of models that include at least one biodiversity proxy (plant species richness, mammalian herbivore richness, or belowground diversity). Separate results for each biodiversity proxy are shown in fig. S12. Full details on model results, including the number of best-fitting models, are available in tables S13 to S15. "Plant biomass and stability" represents aboveground plant biomass and its temporal stability, and "grazing" represents grazing pressure. MAT, mean annual temperature; RASE, rainfall seasonality; MAP, mean annual precipitation.

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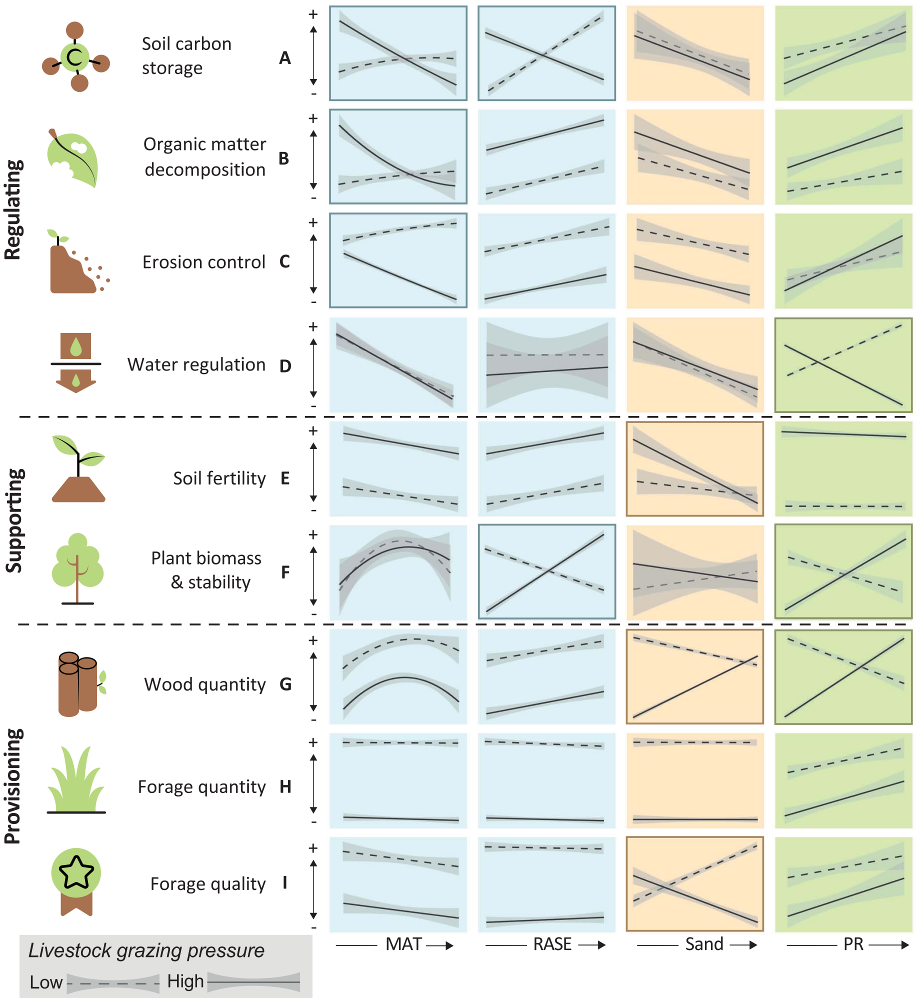

Fig. 3. Predicted responses of ecosystem services to changes in climate, sand content, and plant species richness at low and high grazing pressure levels. (**A** to **I**) Predicted responses of regulating [(A) to (D)], supporting [(E) and (F)], and provisioning [(G) to (I)] ecosystem services. The lines in each panel show model fits (using partial residuals) for each predictor selected in the final best-fitting models at low (dashed lines) and high (solid lines) grazing pressures for each service. Shading around each line represents the 95% confidence interval. Panels surrounded by a border denote significant interactions between grazing and other predictors. Predicted responses of ecosystem services to all grazing pressure levels (ungrazed, low, medium, and high) and to other model predictors are presented in figs. S13 to S15. The complete set of statistical results and model fits are available in tables S13 to S15. "Sand" represents sand content. PR, plant species richness.

matter decomposition (fig. S13), irrespective of grazing pressure. These results broaden and validate previous findings on the relationship between biodiversity and ecosystem functioning (*18*, *19*) and support arguments for conserving and restoring diverse plant communities to prevent land degradation, increase forage production, and mitigate climate change in grazed drylands (*20*).

Mammalian herbivore richness, which was selected in 33% of the best-fitting models (fig. S12), was positively related to multiple ecosystem services. Greater herbivore richness positively correlated with soil carbon storage regardless of grazing pressure (fig. S13), with aboveground plant biomass and its temporal stability under high grazing pressure (fig. S14), and with forage quality under low grazing pressure (fig. S15). Both domestic and wild herbivore species can exhibit strong feeding niche differences (*24*, *25*); thus, increasing their diversity can enhance ecosystem functioning (*25*). Despite a renewed interest in mixed-species grazing, studies have been conducted at only a handful of sites or with a limited suite of herbivores (*25*–*27*). Our findings provide empirical evidence of the potential benefits of increasing herbivore richness to enhance the delivery of key ecosystem services across contrasting environmental and biodiversity conditions. They also suggest that efforts to promote diverse grazing systems may enhance soil carbon storage and reduce negative impacts of increased grazing pressure. To date, such results have only been modeled or observed locally (*26*, *27*).

The multiple interactions we observed highlight that the effect of grazing pressure on ecosystem services can be positive or negative depending on local climate, soil, and biodiversity conditions (Fig. 4). On average, increasing grazing pressure had positive effects on ecosystem services in colder sites with high plant species richness but negative effects in warmer sites with high rainfall seasonality and low plant species richness (Fig. 4, E and I). When sets of ecosystem services were considered separately, responses to grazing pressure ranged from mostly neutral to positive (regulating and supporting services; Fig. 4, B and C) and from negative to neutral (provisioning services; Fig. 4D). These results allow us to identify ecological conditions under which ecosystem services are positively or negatively associated with changes in grazing pressure (Fig. 4 and figs. S16 to S18) and to frame new hypotheses that explore the local context dependencies of grazing impacts. For instance, we observed negative effects of increasing grazing pressure on ecosystem services in plant species–poor drylands, as reported in recent local-scale studies [e.g., (*11*)], whereas positive effects of grazing were mostly observed in species-rich drylands. Thus, protecting biodiversity in species-rich areas or restoring it in species-poor areas could minimize some of the negative effects of increasing grazing pressure on ecosystem service delivery (fig. S19).

The effects of increasing grazing pressure on ecosystem services were mostly negative in warmer drylands (Fig. 4 and fig. S17), where a large proportion of the human population relies heavily on livestock for subsistence (*15*). Limiting grazing pressure through livestock removal is neither socially nor economically feasible in these areas (*2*), yet they are expected to experience high warming rates and water shortages under most climate change scenarios (*17*). Our results thus suggest that grazing pressure may interact with climate change to reduce ecosystem service delivery in warmer drylands, with potentially devastating implications for the fate of these ecosystems [e.g., increased land degradation and desertification (*17*)] and their inhabitants [e.g., greater poverty, migration, and/or social unrest (*28*)]. Although dryland pastoralists have historically adopted strategies to cope with environmental uncertainty (e.g., nomadism, transhumance), benefits of these strategies will wane if livestock concentrates in particular areas as a result of resource scarcity or droughts (*29*).

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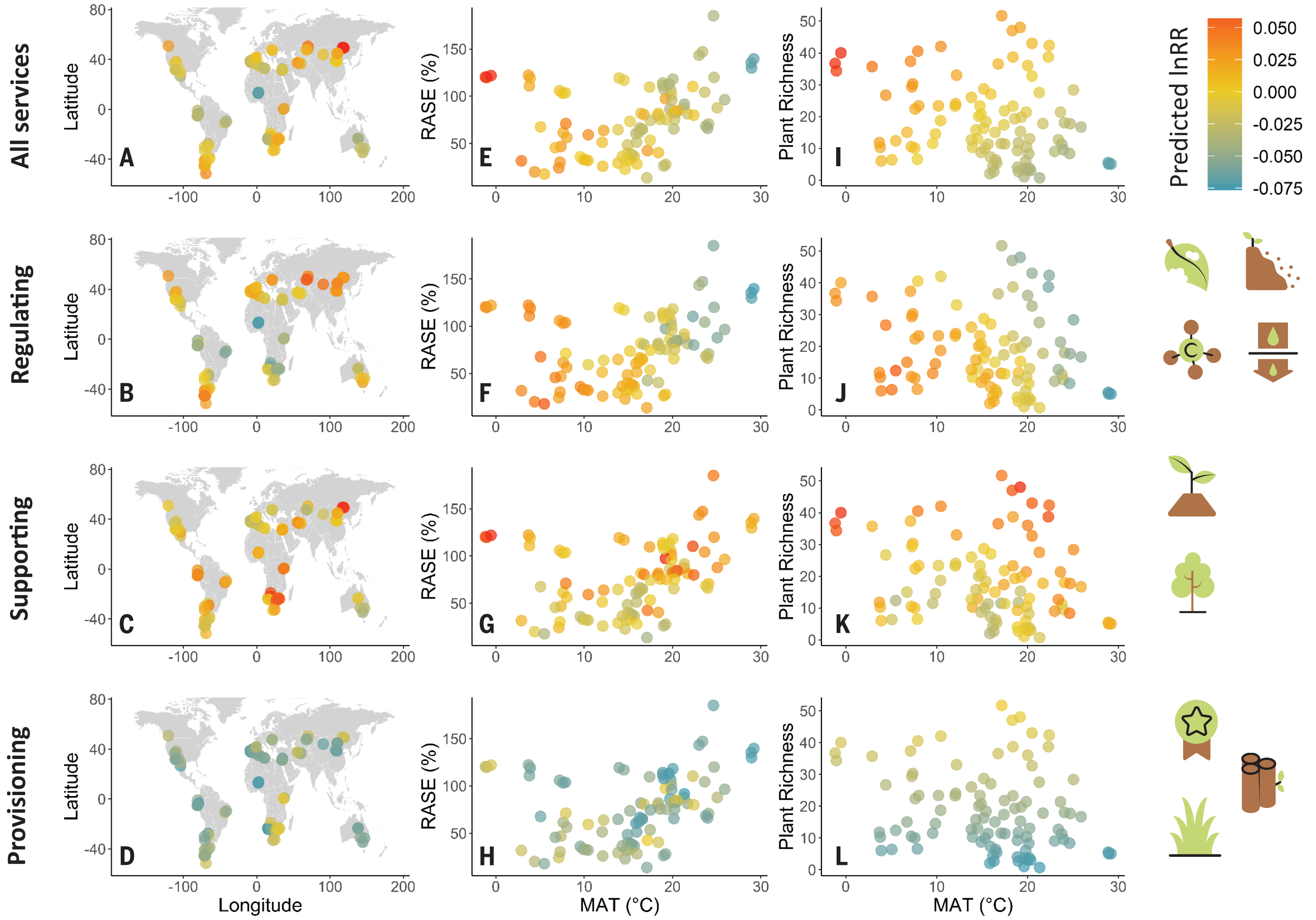

Fig. 4. Geographical variation in the effect of grazing pressure on ecosystem services across global drylands. (**A** to **L**) For each of the 98 sites surveyed, the effect of grazing pressure on ecosystem services predicted by model parameters is plotted along the wide climatic and plant species richness gradients that were evaluated. To do this, each ecosystem service at low and high grazing pressures was first predicted using predictor estimates of the best-fitting models (see tables S13 to S15). Then, the predicted effect of grazing at each site was calculated as the difference between high and low grazing pressure levels using a log response ratio (lnRR) (*13*). Predictions were made using plant species richness, mean annual temperature, and rainfall seasonality; all other parameters were fixed at their mean value (*13*). For simplicity, grazing effects were averaged across all ecosystem services [(A), (E), and (I)] and across regulating [(B), (F), and (J)], supporting [(C), (G), and (K)], and provisioning [(D), (H), and (L)] services. Blue and red dots indicate the most-negative and most-positive effects of grazing, respectively. See figs. S16 and S17 for detailed results on each service and Fig. 2 for the meaning of the symbols depicting each ecosystem service.

Our findings underscore the importance of accounting for interactions between grazing and local abiotic and biotic factors when assessing ecosystem service delivery in drylands. They also illustrate those climate change and biodiversity loss drivers that are the most likely to interact with increases in grazing pressure. Understanding these drivers is critical to predict the fate of dryland ecosystems under increasing temperature, biodiversity loss, and demand for animal products. Our study also allowed us to overcome uncertainties in grazing assessments that arise from the use of unstandardized data (*30*) and provides abundant ground data to validate remote-sensing products that are used when mapping and modeling grazing impacts at the global scale (*5*). Finally, we deliver empirical evidence of the positive links between mammalian herbivore richness and the provision of multiple ecosystem services across contrasting environmental conditions, plant and soil diversities, and grazing pressure levels. Our work addresses a key knowledge gap that can lead to better management of drylands, the largest rangeland area on Earth.

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ACKNOWLEDGMENTS

We acknowledge S. Undrakhbold, M. Uuganbayar, B. Byambatsogt, S. Khaliun, S. Solongo, B. Batchuluun, M. Sloan, J. Spence, E. Geiger, I. Souza, R. Onoo, T. Araújo, M. Mabaso, P. M. Lunga, L. Eloff, P. Eloff, J. Sebei, J. Joordan, E. Mudongo, V. Mokoka, B. Mokhou, T. Maphanga, F. Hoffmann, R. Peters, A. Lozada, E. Vidal, F. Perrona, R. Ledezma, R. Matjea, L. Kindermann, C. Goebel, B. Semple, and B. Tamayo for assistance with field work. We thank Bush Heritage Australia; the University of Limpopo; the Ministry of Environment and Tourism (Namibia); the Ministry of Agriculture, Water and Land Reform (Namibia); Corporación Nacional Forestal (CONAF) and the agricultural community Quebrada de Talca (Chile); and the South African military for granting research permissions and/or granting access to their research farms and properties. We also thank B. Benito for his revisions to the R code, and C. Abel for her comments on the manuscript. Any use of trade, product, or firm names in this paper is for descriptive purposes only and does not imply endorsement by the US government. **Funding:** This research was funded by the European Research Council [ERC grant agreement 647038 (BIODESERT)] and Generalitat Valenciana (CIDEGENT/2018/041). F.T.M. acknowledges support from a Rei Jaume I Award, the Alexander von Humboldt Foundation, and the Synthesis Center (sDiv) of the German Centre for Integrative Biodiversity Research Halle–Jena–Leipzig (iDiv). C.A.G., S.C., and N.E. acknowledge support from iDiv and the Deutsche Forschungsgemeinschaft (DFG– FZT 118, 202548816; Flexpool proposal 34600850). Y.L.B.-P. was supported by a Marie Sklodowska-Curie Actions Individual Fellowship (MSCA-IF) within the European Program Horizon 2020 (DRYFUN Project 656035). N.G. was supported by CAP 20-25 (16-IDEX-0001) and the AgreenSkills+ fellowship program, which has received funding from the EU's Seventh Framework Programme under grant agreement N° FP7-609398 (AgreenSkills+ contract). B.B. and B.E. were supported by the Taylor Family–Asia Foundation Endowed Chair in Ecology and Conservation Biology. J.D., A.Ro., and H.C. acknowledge support from the Fundação para a Ciência e a Tecnologia (IF/00950/2014 and 2020.03670.CEECIND, SFRH/BDP/108913/2015, and in the scope of the framework contract foreseen in the numbers 4-6 of the article 23, of the Decree-Law 57/2016, August 29, changed by Law 57/2017, July 19, respectively), as well as from the MCTES, FSE, UE, and the CFE (UIDB/04004/2020) research unit financed by Fundação para a Ciência e a Tecnologia/MCTES through national funds (PIDDAC). C.P. acknowledges support from the Spanish Ministry of Science and Innovation (ref. AGL201675762-R, AEI/FEDER, UE, and PID2020-116578RB-I00, MCIN/AEI/10.13039/501100011033) and the European Union's Horizon 2020 Research and Innovation Programme under grant agreement no. 101000224. E.V. was funded by the 2017 program for attracting and retaining talent of Comunidad de Madrid (no. 2017-T2/ AMB-5406). M.A.B. acknowledges support from the School of Forestry and College of the Environment, Forestry and Natural Sciences of Northern Arizona University. E.H.-S. acknowledges support from the Consejo Nacional de Ciencia y Tecnología (SEP-CB-2015-01-251388, PN 2017-5036 and PRONAII 319059). F.M.H. acknowledges support from the National Council for Scientific and Technological Development (CNPq - PCI/INMA) of the Brazilian Ministry of Science, Technology and Innovation (MCTI, processes number 302381/2020-1). H.L.T. acknowledges support from the US National Science Foundation (NSF) (DEB 0953864). A.N. and M.K. acknowledge support from the Fundação para a Ciência e a Tecnologia (SFRH/BD/130274/2017, CEECIND/02453/2018/CP1534/CT0001, PTDC/ASP-SIL/7743/2020 and UIDB/00329/2020). A.A.C. acknowledges support from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. J.E.K. and T.P.M. acknowledge the National Research Foundation of South Africa (grant no. 114412). F.J. and N.B. acknowledge support from the German Federal Ministry of Education and Research (BMBF) in the framework of the SPACES projects OPTIMASS (FKZ: 01LL1302A) and ORYCS (FKZ: 01LL1804A). A.Li. and A.S.K.F. acknowledge support from the German Federal Ministry of Education and Research (BMBF) in the framework of the SPACES projects Limpopo Living Landscapes (FKZ: 01LL1304D) and SALLnet (FKZ: 01LL1802C). L.W. acknowledges support from the US NSF (EAR 1554894). L.H.F. acknowledges support from the Natural Sciences and Engineering Research Council of Canada Industrial Research Chair Program in Ecosystem Reclamation. S.C.R. acknowledges support from the US Geological Survey Ecosystems Mission Area and the US Bureau of Land Management. G.M.W. acknowledges support from the Australian Research Council. L.v.d.B. and K.T. acknowledge support from the German Research Foundation (DFG) priority research program SPP-1803 "EarthShape: Earth Surface Shaping by Biota" (TI 338/14-1). M.D.-B. acknowledges support from the Spanish Ministry of Science and Innovation for the I+D+i project PID2020-115813RA-I00 funded by MCIN/AEI/10.13039/501100011033. M.D.-B. is also supported by a project of the Fondo Europeo de Desarrollo Regional (FEDER) and the Consejería de Transformación Económica, Industria, Conocimiento y Universidades of the Junta de Andalucía (FEDER Andalucía 2014-2020 Objetivo temático "01 - Refuerzo de la investigación, el desarrollo tecnológico y la innovación") associated with the research project P20_00879 (ANDABIOMA). P.J.R. and A.J.M. acknowledge support from Fondo Europeo de Desarrollo Regional through the FEDER Andalucía operative program, FEDER-UJA 1261180 project. A.F. thanks ANID PIA/BASAL FB210006 and Millennium Science Initiative Program NCN2021-050. A.J. acknowledges support from the Bavarian Research Alliance Germany (BayIntAn_UBT_2017_61). C.B. acknowledges the National Natural Science Foundation of China (grant no. 41971131). Biodiversity and ecosystem function research in the B.K.S. laboratory is funded by the Australian Research Council (DP210102081). Any use of trade, product, or firm names in this paper is for descriptive purposes only and does not imply endorsement by the US government. H.S. is supported by a María Zambrano fellowship funded by the Ministry of Universities and European Union-Next Generation plan. G.P. and C.V.L. acknowledge support from Universidad Nacional de Río Negro (PI 40-C-873 and 654). V.R. acknowledges support from the Regional Government of Extremadura (Spain) through a "Talento" fellowship (TA18022). M.F. acknowledges support from the Department of Range and Watershed Management, Ferdowsi University of Mashhad, Mashhad, Iran. Participation of recent graduates in collecting field data at four sites in Namibia was supported by a capacity building grant to Gobabeb–Namib Research Institute by the Environmental Investment Fund in Namibia. **Author contributions:** Conceptualization: F.T.M., N.G., Y.L.B.-P.; Methodology: F.T.M., N.G., Y.L.B.-P., D.J.E., H.S.; Investigation: Y.L.B.-P., D.J.E., H.S., M.B., B.G., V.O., M.G.-G., E.V., J.J.G., S.A., B.J.M., C.P., P.D.-M., A.Re., A.Le., M.C.R., S.C., N.E., E.M.-J., O.S., M.A., N.A., C.L.A., V.A., F.A., T.A., R.J.A., K.B., F.B.S., N.B., B.B., M.A.B., D.B., C.B., R.Ca., A.P.C.-M., H.C., I.C., P.C.-Q., R.Ch., A.A.C., C.M.C., A.D.-N., B.D., D.A.D., A.J.D., J.D., B.E., C.I.E., A.F., M.F., D.F., A.S.K.F., L.H.F., L.A.G., A.C.G., E.G.-M., R.M.H.-H., N.H., E.H.-S., F.M.H., O.J.-M., F.J., A.J., K.F.K., M.K., J.E.K., C.V.L., A.Li., P.C.I.R., X.L., P.L., J.L., M.A.L., G.M.-K., T.P.M., O.M.I., A.J.M., E.M., J.P.M., G.M., S.M.M., A.N., G.O., G.R.O., G.P., M.O.D.P., Y.P., R.E.Q., S.R., S.C.R., P.J.R., B.R., A.Ro., V.R., J.G.R., J.C.R., A.S., M.A.S., S.S., I.S., C.R.A.S., A.M.S., A.L.T., A.D.T., H.L.T., K.T., S.T., J.V., O.V., L.v.d.B., S.V.A., F.V., W.W., D.W., L.W., G.M.W., L.Y., E.Z., Y.Z., X.Z., N.G.; Formal analysis: N.G., Y.L.B.-P., M.B., D.J.E., E.V., C.A.G., J.-T.W., H.-W.H., J.-Z.H.; Resources: F.T.M., Y.L.B.-P., D.J.E., H.S., M.B., B.G., V.O., M.G.-G., E.V., J.J.G., S.A., B.J.M., C.P., P.D.-M., A.Re., H.-W.H., J.-Z.H., J.-T.W., A.Le., M.C.R., S.C., N.E., E.M.-J., O.S., M.A., N.A., C.L.A., V.A., F.A., T.A., R.J.A., K.B., F.B.S., N.B., B.B., M.A.B., D.B., C.B., R.Ca., A.P.C.-M., H.C., I.C., P.C.-Q., R.Ch., A.A.C., C.M.C., A.D.-N., B.D., D.A.D., A.J.D., J.D., B.E., C.I.E., A.F., M.F., D.F., A.S.K.F., L.H.F., L.A.G., A.C.G., E.G.-M., R.M.H.-H., N.H., E.H.-S., F.M.H., O.J.-M., F.J., A.J., K.F.K., M.K., J.E.K., C.V.L., A.Li., P.C.I.R., X.L., P.L., J.L., M.A.L., G.M.-K., T.P.M., O.M.I., A.J.M., E.M., J.P.M., G.M., S.M.M., A.N., G.O., G.R.O., G.P., M.O.D.P., Y.P., R.E.Q., S.R., S.C.R., P.J.R., B.R., A.Ro., V.R., J.G.R., J.C.R., A.S., M.A.S., S.S., I.S., C.R.A.S., A.M.S., A.L.T., A.D.T., H.L.T., K.T., S.T., J.V., O.V., L.v.d.B., S.V.A., F.V., W.W., D.W., L.W., G.M.W., L.Y., E.Z., Y.Z., X.Z., B.K.S., N.G., M.D.-B. ; Funding acquisition: F.T.M., N.G., N.E., Y.L.B.-P., B.B., B.E., J.D., A.Ro., C.P., M.A.B., E.H.-S., F.M.H., H.L.T., A.N., M.K., J.E.K., T.P.M., F.J., N.B., A.Li., A.S.K.F., L.W., L.H.F., S.C.R., G.M.W., K.T., A.F., C.B., A.J.; Project administration: F.T.M., N.G., Y.L.B.-P., H.S., E.V., J.M.-V., V.O., B.G.; Software: N.G., Y.L.B.-P.; Supervision: F.T.M.; Validation: M.B., C.P.; Visualization: N.G., Y.L.B.-P., D.J.E., E.G., M.B., E.V.; Writing – original draft: F.T.M., N.G., Y.L.B.-P., D.J.E., H.S., M.D.-B.; Writing – review and editing: F.T.M., N.G., Y.L.B.-P., D.J.E., M.D.-B., H.S., M.B., B.G., V.O., E.G., J.M.-V., M.G.-G., E.V., E.G., J.J.G., S.A., B.J.M., C.P., P.D.-M., A.Re., H.-W.H., J.-Z.H., J.-T.W., A.Le., M.C.R., S.C., N.E., E.M.-J., O.S., M.A., N.A., C.L.A., V.A., F.A., T.A., R.J.A., K.B., F.B.S., N.B., B.B., M.A.B., D.B., C.B., R.Ca., A.P.C.-M., H.C., I.C., P.C.-Q., R.Ch., A.A.C., C.M.C., A.D.-N., B.D., D.A.D., A.J.D., J.D., B.E., C.I.E., A.F., M.F., D.F., A.S.K.F., L.H.F., L.A.G., A.C.G., E.G.-M., R.M.H.-H., N.H., E.H.-S., F.M.H., O.J.-M., F.J., A.J., K.F.K., M.K., J.E.K., C.V.L., A.Li., P.C.I.R., X.L., P.L., J.L., M.A.L., G.M.-K., T.P.M., O.M.I., A.J.M., E.M., J.P.M., G.M., S.M.M., A.N., G.O., G.R.O., G.P., M.O.D.P., Y.P., R.E.Q., S.R., S.C.R., P.J.R., B.R., A.Ro., V.R., J.G.R., J.C.R., A.S., M.A.S., S.S., I.S., C.R.A.S., A.M.S., A.L.T., A.D.T., H.L.T., K.T., S.T., J.V., O.V., L.v.d.B., S.V.A., F.V., W.W., D.W., L.W., G.M.W., L.Y., E.Z., Y.Z., X.Z., B.K.S. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All the data used in this article and the R scripts used to generate the main results of the study are available through figshare (*31*). The raw sequence data generated in this study are also available through figshare (*32*).

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SUPPLEMENTARY MATERIALS

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Submitted 6 April 2022; accepted 6 October 2022
10.1126/science.abq4062

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Grazing and ecosystem service delivery in global drylands

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Science, 378 (6622), • DOI: 10.1126/science.abq4062

Complex effects of livestock

Livestock grazing provides food and livelihoods for billions of people but at the cost of ecosystem degradation in many places. Maestre *et al*. investigated how grazing by livestock and native herbivores affects ecosystem functions and services and how these effects vary with climate, soil properties, and biodiversity (see the Perspective by Ganguli and O'Rourke). Using a replicated survey at 98 dryland sites spanning six continents, the authors found that grazing effects on ecosystem services often depend on other factors. Interactions between grazing and climate were especially important; warmer sites had lower rates of carbon storage, organic matter deposition, and erosion control under high (but not low) grazing pressure. —BEL

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