

DRYLAND ECOLOGY

Grazing and ecosystem service delivery in global drylands

Fernando T. Maestre^{1,2*}, Yoann Le Bagousse-Pinguet³, Manuel Delgado-Baquerizo^{4,5}, David J. Eldridge⁶, Hugo Saiz^{7,8}, Miguel Berdugo^{9,10}, Beatriz Gozalo¹, Victoria Ochoa¹¹, Emilio Guirado¹, Miguel García-Gómez¹², Enrique Valencia^{13,14}, Juan J. Gaitán^{15,16,17}, Sergio Asensio¹, Betty J. Mendoza¹³, César Plaza¹¹, Paloma Díaz-Martínez¹¹, Ana Rey¹⁸, Hang-Wei Hu^{19,20}, Ji-Zheng He^{19,20}, Jun-Tao Wang^{21,22,23}, Anika Lehmann^{24,25}, Matthias C. Rillig^{24,25}, Simone Cesarz^{26,27}, Nico Eisenhauer^{26,27}, Jaime Martínez-Valderrama¹, Eduardo Moreno-Jiménez²⁸, Osvaldo Sala^{29,30,31}, Mehdi Abedi³², Negar Ahmadian³², Concepción L. Alados³³, Valeria Aramayo³⁴, Fateh Amghar³⁵, Tulio Arredondo³⁶, Rodrigo J. Ahumada³⁷, Khadijeh Bahalkeh³², Farah Ben Salem³⁸, Niels Blaum³⁹, Bazartseren Boldgiv⁴⁰, Matthew A. Bowker^{41,42}, Donald Bran³⁴, Chongfeng Bu^{43,44}, Raffaella Canessa^{45,46}, Andrea P. Castillo-Monroy⁴⁷, Helena Castro⁴⁸, Ignacio Castro⁴⁹, Patricio Castro-Quezada⁵⁰, Roukaya Chibani³⁸, Abel A. Conceição⁵¹, Courtney M. Currier^{29,31}, Anthony Darrouzet-Nardi⁵², Balázs Deák⁵³, David A. Donoso^{47,54}, Andrew J. Dougill⁵⁵, Jorge Durán^{48,56}, Batdelger Erdenetsetseg⁴⁰, Carlos I. Espinosa⁵⁷, Alex Fajardo⁵⁸, Mohammad Farzam⁵⁹, Daniela Ferrante^{60,61}, Anke S. K. Frank^{62,63,64}, Lauchlan H. Fraser⁶⁵, Laureano A. Gherardi⁶⁶, Aaron C. Greenville⁶³, Carlos A. Guerra^{26,67}, Elizabeth Gusmán-Montalvan⁵⁷, Rosa M. Hernández-Hernández⁴⁹, Norbert Hölze⁶⁸, Elisabeth Huber-Sannwald³⁶, Frederic M. Hughes^{51,69}, Oswaldo Jadán-Maza⁵⁰, Florian Jeltsch^{25,39}, Anke Jentsch⁷⁰, Kudzai F. Kaseke⁷¹, Melanie Köbel⁷², Jessica E. Koopman⁷³, Cintia V. Leder^{17,74}, Anja Linstädter^{64,75}, Peter C. le Roux⁷⁶, Xinkai Li^{43,44}, Pierre Liancourt^{46,77,78}, Jushan Liu⁷⁹, Michelle A. Louw⁷⁶, Gillian Maggs-Kölling⁸⁰, Thulani P. Makhalanyane⁷³, Oumarou Malam Issa⁸¹, Antonio J. Manzaneda^{82,83}, Eugene Marais⁸⁰, Juan P. Mora⁵⁸, Gerardo Moreno⁸⁴, Seth M. Munson⁸⁵, Alice Nunes⁷², Gabriel Oliva^{60,61}, Gastón R. Oñativia⁸⁶, Guadalupe Peter^{17,74}, Marco O. D. Pivari⁸⁷, Yolanda Pueyo³³, R. Emiliano Quiroga^{37,88}, Soroor Rahmanian^{59,89}, Sasha C. Reed⁹⁰, Pedro J. Rey^{82,83}, Benoit Richard⁹¹, Alexandra Rodríguez⁴⁸, Victor Rolo⁸⁴, Juan G. Rubalcaba⁹², Jan C. Ruppert⁴⁶, Ayman Salah⁹³, Max A. Schuchardt⁷⁰, Sedona Spann⁴¹, Ilan Stavi⁹⁴, Colton R. A. Stephens⁶⁵, Anthony M. Swemmer⁹⁵, Alberto L. Teixeira⁹⁶, Andrew D. Thomas⁹⁷, Heather L. Throop^{98,99}, Katja Tielbörger⁴⁶, Samantha Travers¹⁰⁰, James Val¹⁰¹, Orsolya Valkó⁵³, Liesbeth van den Brink⁴⁶, Sergio Velasco Ayuso⁸⁶, Frederike Velbert⁶⁸, Wanyoike Wamiti¹⁰², Deli Wang⁷⁹, Lixin Wang¹⁰³, Glenda M. Wardle⁶³, Laura Yahdjian⁸⁶, Eli Zaady¹⁰⁴, Yuanming Zhang¹⁰⁵, Xiaobing Zhou¹⁰⁵, Brajesh K. Singh^{21,22}, Nicolas Gross¹⁰⁶

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

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 $\Delta\text{AIC} < 2$ (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 eco-

system 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).

¹Instituto Multidisciplinar para el Estudio del Medio “Ramón Margalef,” Universidad de Alicante, Alicante, Spain. ²Departamento de Ecología, Universidad de Alicante, Alicante, Spain. ³Aix Marseille Univ, CNRS, Avignon Université, IRD, IMBE, Aix-en-Provence, France. ⁴Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Sevilla, Spain. ⁵Unidad Asociada CSIC-UPO (BioFun), Universidad Pablo de Olavide, Sevilla, Spain. ⁶Department of Planning and Environment, c/o Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia. ⁷Departamento de Ciencias Agrarias y Medio Natural, Escuela Politécnica Superior, Instituto Universitario de Investigación en Ciencias Ambientales de Aragón (IUCA), Universidad de Zaragoza, Huesca, Spain. ⁸Institute of Plant Sciences, University of Bern, Bern, Switzerland. ⁹Institut de Biologia Evolutiva (UPF-CSIC), Barcelona, Spain. ¹⁰Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland. ¹¹Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, Madrid, Spain. ¹²Departamento de Ingeniería y Morfología del Terreno, Escuela Técnica Superior de Ingenieros de Caminos, Canales y Puertos, Universidad Politécnica de Madrid, Madrid, Spain. ¹³Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain. ¹⁴Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Madrid, Spain. ¹⁵Instituto Nacional de Tecnología Agropecuaria (INTA), Instituto de Suelos-CNIA, Buenos Aires, Argentina. ¹⁶Universidad Nacional de Luján, Departamento de Tecnología, Luján, Argentina. ¹⁷Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET), Buenos Aires, Argentina. ¹⁸Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, Spain. ¹⁹Key Laboratory for Humid Subtropical Ecogeographical Processes of the Ministry of Education, School of Geographical Science, Fujian Normal University, Fuzhou, China. ²⁰Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, Melbourne, Victoria, Australia. ²¹Global Centre for Land-Based Innovation, Western Sydney University, Sydney, New South Wales, Australia. ²²Hawkesbury Institute for the Environment, Western Sydney University, Sydney, New South Wales, Australia. ²³State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China. ²⁴Freie Universität Berlin, Institute of Biology, Berlin, Germany. ²⁵Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany. ²⁶German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. ²⁷Leipzig University, Institute of Biology, Leipzig, Germany. ²⁸Department of Agricultural and Food Chemistry, Faculty of Sciences, Universidad Autónoma de Madrid, Madrid, Spain. ²⁹School of Life Sciences, Arizona State University, Tempe, AZ, USA. ³⁰School of Sustainability, Arizona State University, Tempe, AZ, USA. ³¹Global Drylands Center, Arizona State University, Tempe, AZ, USA. ³²Department of Range Management, Faculty of Natural Resources and Marine Sciences, Tarbiat Modares University, Noor, Mazandaran Province, Iran. ³³Instituto Pirenaico de Ecología (IPE, CSIC), Zaragoza, Spain. ³⁴Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Agropecuaria Bariloche, Bariloche, Río Negro, Argentina. ³⁵Laboratoire de Recherche: Biodiversité, Biotechnologie, Environnement et Développement Durable (BioDev), Faculté des Sciences, Université M'hamed Bougara de Boumerdes, Boumerdes, Algérie. ³⁶Instituto Potosino de Investigación Científica y Tecnológica, A.C., San Luis Potosí, Mexico. ³⁷Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Catamarca, Catamarca, Argentina. ³⁸Laboratory of Range Ecology, Institut des Régions Arides (IRA), Médenine, Tunisia. ³⁹University of Potsdam, Plant Ecology and Conservation Biology, Potsdam, Germany. ⁴⁰Laboratory of Ecological and Evolutionary Synthesis, Department of Biology, School of Arts and Sciences, National University of Mongolia, Ulaanbaatar, Mongolia. ⁴¹School of Forestry, Northern Arizona University, Flagstaff, AZ, USA. ⁴²Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA. ⁴³Institute of Soil and Water Conservation, Northwest A&F University, Yangling, Shaanxi, China. ⁴⁴Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, Shaanxi, China. ⁴⁵Ecological Plant Geography, Faculty of Geography, University of Marburg, Marburg, Germany. ⁴⁶Plant Ecology Group, University of Tübingen, Tübingen, Germany. ⁴⁷Departamento de Biología, Escuela Politécnica Nacional, Quito, Ecuador. ⁴⁸Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal. ⁴⁹Universidad Nacional Experimental Simón Rodríguez (UNESR), Instituto de Estudios Científicos y Tecnológicos (IDECYT), Centro de Estudios de Agroecología Tropical (CEDAT), Miranda, Venezuela. ⁵⁰Universidad de Cuenca, Facultad de Ciencias Agropecuarias, Carrera de Ingeniería Agronómica, Grupo de Agroforestería, Manejo y Conservación del paisaje, Cuenca, Ecuador. ⁵¹Universidade Estadual de Feira de Santana (UEFS), Departamento de Ciências Biológicas, Bahia, Brazil. ⁵²Department of Biological Sciences, University of Texas at El Paso, El Paso, TX, USA. ⁵³Landület Seed Ecology Research Group, Institute of Ecology and Botany, Centre for Ecological Research, Vácrátót, Hungary. ⁵⁴Centro de Investigación de la Biodiversidad y Cambio Climático, Universidad Tecnológica Indoamérica, Quito, Ecuador. ⁵⁵Department of Environment and Geography, University of York, York, UK. ⁵⁶Misión Biológica de Galicia, CSIC, Pontevedra, Spain. ⁵⁷Departamento de Ciencias Biológicas, Universidad Técnica Particular de Loja, Loja, Ecuador. ⁵⁸Instituto de Investigación Interdisciplinaria (I³), Vicerrectoría Académica, Universidad de Talca, Talca, Chile. ⁵⁹Department of Range and Watershed Management, Ferdowsi University of Mashhad, Mashhad, Iran. ⁶⁰Instituto Nacional de Tecnología Agropecuaria EEA Santa Cruz, Río Gallegos, Santa Cruz, Argentina. ⁶¹Universidad Nacional de la Patagonia Austral, Río Gallegos, Santa Cruz, Argentina. ⁶²School of Agriculture, Environmental and Veterinary Sciences, Charles Sturt University, Port Macquarie, New South Wales, Australia. ⁶³Desert Ecology Research Group, School of Life and Environmental Sciences, The University of Sydney, Sydney, New South Wales, Australia. ⁶⁴Institute of Crop Science and Resource Conservation, University of Bonn, Bonn, Germany. ⁶⁵Department of Natural Resource Science, Thompson Rivers University, Kamloops, British Columbia, Canada. ⁶⁶Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA, USA. ⁶⁷Institute of Biology, Martin-Luther University Halle Wittenberg, Halle (Saale), Germany. ⁶⁸Institute of Landscape Ecology, University of Münster, Münster, Germany. ⁶⁹Instituto Nacional da Mata Atlântica (INMA), Espírito Santo, Brazil. ⁷⁰Department of Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Bayreuth, Germany. ⁷¹Earth Research Institute, University of California, Santa Barbara, Santa Barbara, CA, USA. ⁷²Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal. ⁷³Microbiome@UP, Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria, South Africa. ⁷⁴Universidad Nacional de Río Negro, Sede Atlántica, CEANPa, Río Negro, Argentina. ⁷⁵Biodiversity Research/Systematic Botany Group, Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany. ⁷⁶Department of Plant and Soil Sciences, University of Pretoria, Pretoria, South Africa. ⁷⁷Institute of Botany, Czech Academy of Sciences, Pruhonice, Czech Republic. ⁷⁸Botany Department, State Museum of Natural History Stuttgart, Stuttgart, Germany. ⁷⁹Key Laboratory of Vegetation Ecology of the Ministry of Education, Jilin Songnen Grassland Ecosystem National Observation and Research Station, Institute of Grassland Science, Northeast Normal University, Changchun, China. ⁸⁰Gobabeb-Namib Research Institute, Walvis Bay, Namibia. ⁸¹Institut d'Ecologie et des Sciences de l'Environnement de Paris (iEES-Paris), Sorbonne Université, IRD, CNRS, INRAE, Université Paris Est Creteil, Université de Paris, Centre IRD de France Nord, Bondy, France. ⁸²Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía, Universidad de Jaén, Jaén, Spain. ⁸³Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, Jaén, Spain. ⁸⁴Forestry School, INDEHESA, Universidad de Extremadura, Plasencia, Spain. ⁸⁵US Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, USA. ⁸⁶Cátedra de Ecología, Facultad de Agronomía, Universidad de Buenos Aires, Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA-CONICET), Ciudad Autónoma de Buenos Aires, Argentina. ⁸⁷Departamento de Botánica, Universidade Federal de Minas Gerais, Minas Gerais, Brazil. ⁸⁸Cátedra de Manejo de Pastizales Naturales, Facultad de Ciencias Agrarias, Universidad Nacional de Catamarca, Catamarca, Argentina. ⁸⁹Department of Forest Engineering, Forest Management Planning and Terrestrial Measurements, Faculty of Silviculture and Forest Engineering, Transilvania University of Brasov, Brasov, Romania. ⁹⁰US Geological Survey, Southwest Biological Science Center, Moab, UT, USA. ⁹¹Normandie Univ, UNIROUEN, INRAE, ECODIV, Rouen, France. ⁹²Department of Biology, McGill University, Montreal, Quebec, Canada. ⁹³Al Quds University, Abu Dis, Palestine. ⁹⁴Dead Sea and Arava Science Center, Yotvata, Israel. ⁹⁵South African Environmental Observation Network (SAEON), Phalaborwa, Kruger National Park, South Africa. ⁹⁶Departamento de Botánica e Ecología, Instituto de Biociências, Universidade Federal de Mato Grosso, Mato Grosso, Brazil. ⁹⁷Department of Geography and Earth Sciences, Aberystwyth University, Wales, UK. ⁹⁸School of Earth and Space Exploration, Arizona State University, Tempe, AZ, USA. ⁹⁹School of Life Sciences, Arizona State University, Tempe, AZ, USA. ¹⁰⁰Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia. ¹⁰¹Science Division, Department of Planning, Industry and Environment, New South Wales Government, Buronga, New South Wales, Australia. ¹⁰²Zoology Department, National Museums of Kenya, Nairobi, Kenya. ¹⁰³Department of Earth Sciences, Indiana University–Purdue University Indianapolis (IUPUI), Indianapolis, IN, USA. ¹⁰⁴Department of Natural Resources, Agricultural Research Organization, Institute of Plant Sciences, Gilat Research Center, Mobile Post Negev, Israel. ¹⁰⁵State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China. ¹⁰⁶Université Clermont Auvergne, INRAE, VetAgro Sup, Unité Mixte de Recherche Ecosystème Prairial, Clermont-Ferrand, France.

*Corresponding author. Email: ft.maestre@ua.es

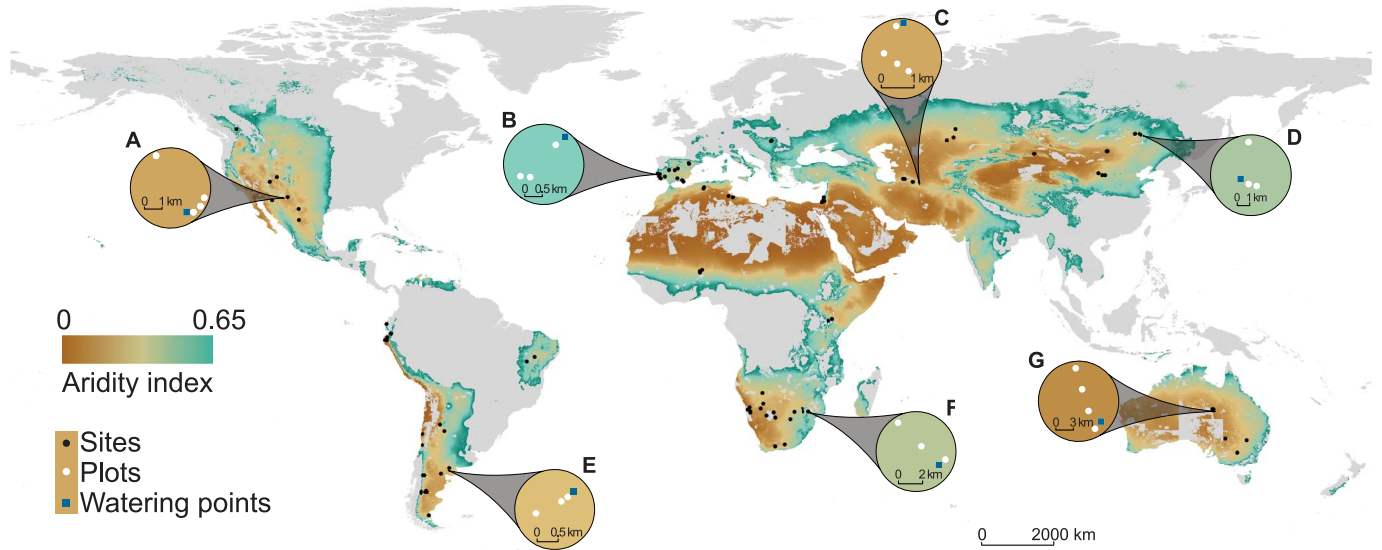


Fig. 1. Locations of the 98 study sites with examples of the local grazing gradients surveyed at each site. Each black dot represents a site with multiple 45-m-by-45-m plots (white dots) surveyed in situ; a total of 326 plots were surveyed across the 98 study sites. The inset graphics [(A) to (G)] highlight 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

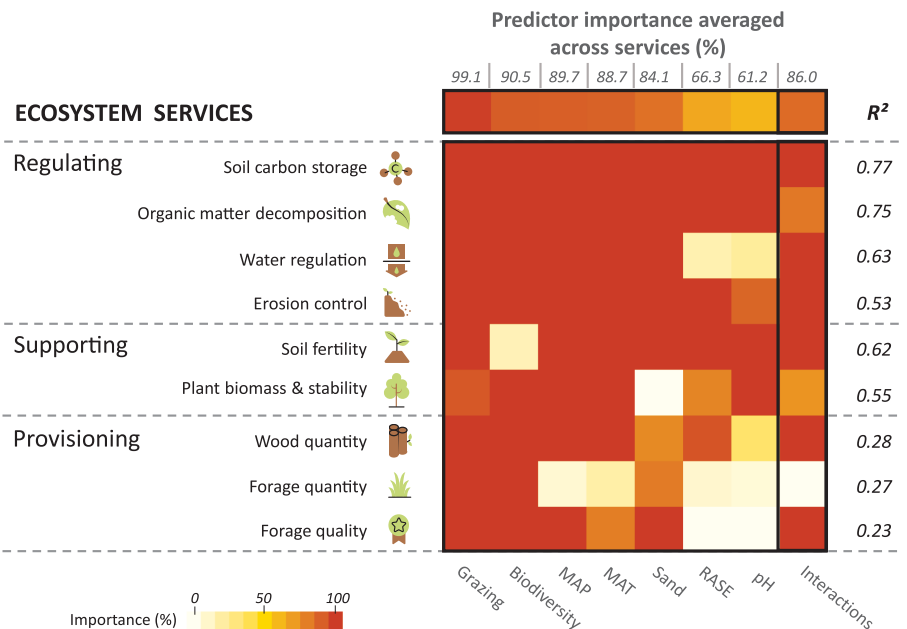


Fig. 2. Relative importance of predictors of ecosystem services selected in the best-fitting models. Importance is quantified as the sum of the Akaike weights of all models that included the predictor (grazing pressure, climate, biodiversity, and soil variables, and their interactions) of interest, considering 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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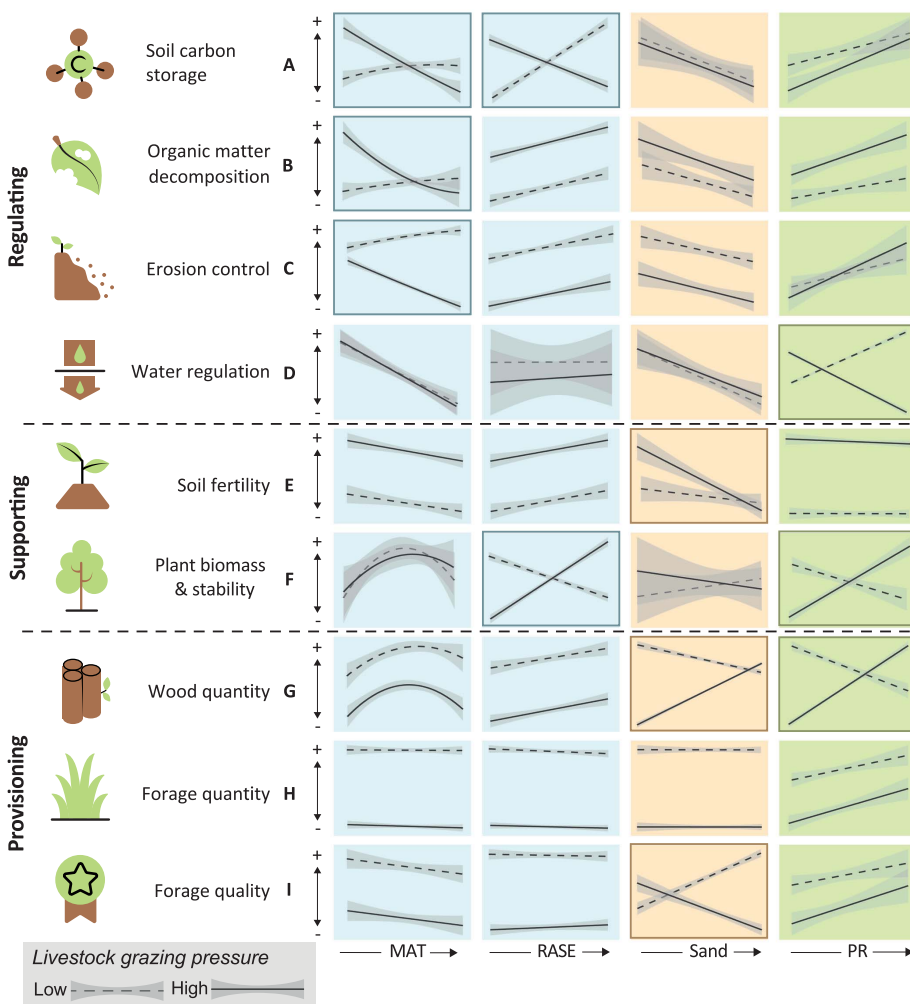


Fig. 3. Predicted responses of ecosystem services to changes in climate, sand content, and plant species richness at low and high grazing pressure levels. (A to I) Predicted responses of regulating [(A) to (D)], supporting [(E) and (F)], and provisioning [(G) to (I)] ecosystem services. The lines in 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 service delivery 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).

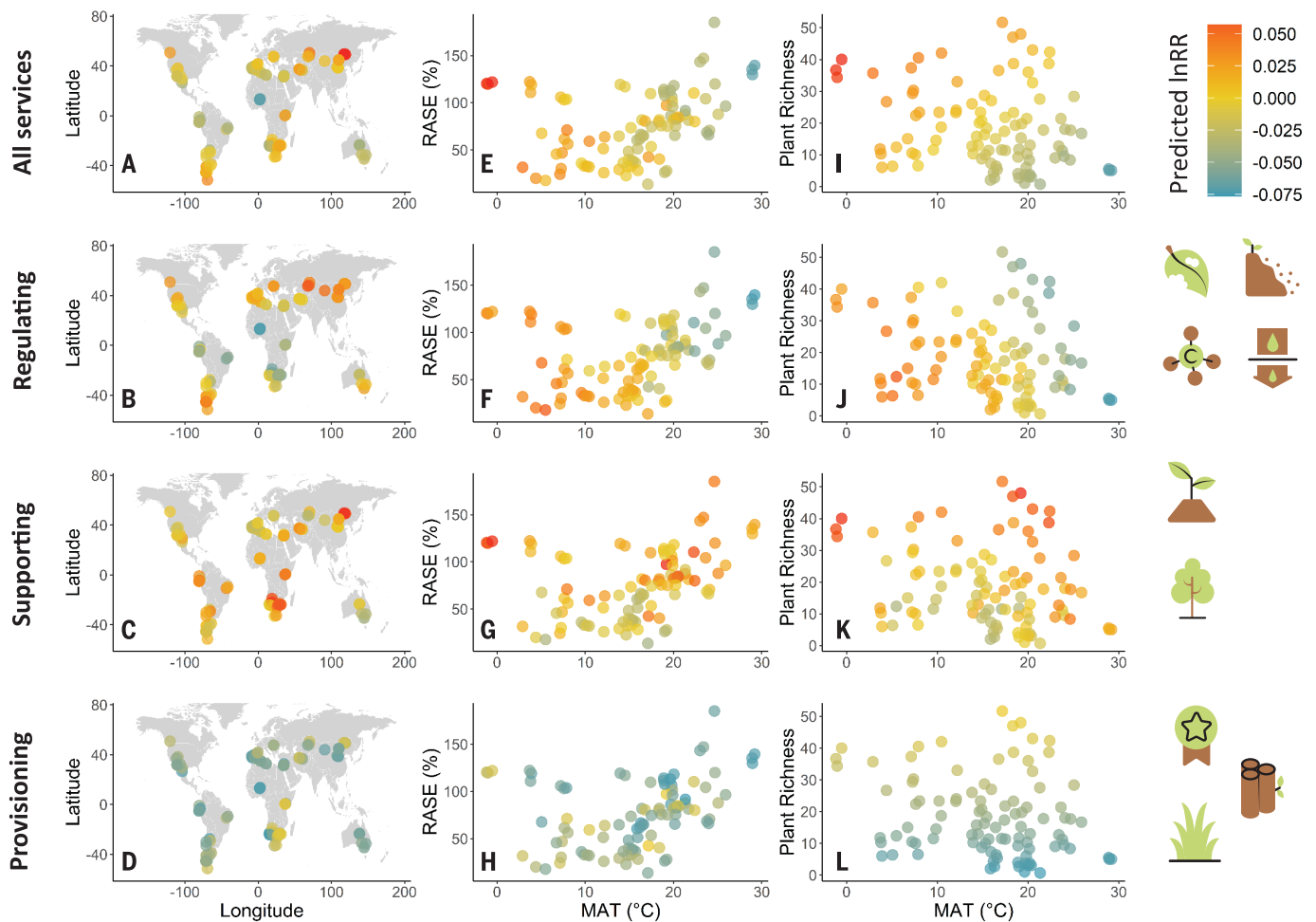


Fig. 4. Geographical variation in the effect of grazing pressure on ecosystem services across global drylands. (A to L) For each of the 98 sites surveyed, the effect of grazing pressure on ecosystem services predicted by model parameters is plotted along the wide climatic and plant species richness gradients 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 her-

bivore 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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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., 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., 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., M.D.-B.; 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., 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., 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). **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.abq4062](https://doi.org/10.1126/science.abq4062)
Materials and Methods
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Movie S1

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Grazing and ecosystem service delivery in global drylands

Fernando T. Maestre Yoann Le Bagousse-Pinguet Manuel Delgado-Baquerizo David J. Eldridge Hugo Saiz Miguel Berdugo Beatriz Gozalo Victoria Ochoa Emilio Guirado Miguel García-Gómez Enrique Valencia Juan J. Gaitán Sergio Asensio Betty J. Mendoza César Plaza Paloma Díaz-Martínez Ana Rey Hang-Wei Hu Ji-Zheng He Jun-Tao Wang Anika Lehmann Matthias C. Rillig Simone Cesarz Nico Eisenhauer Jaime Martínez-Valderrama Eduardo Moreno-Jiménez Osvaldo Sala Mehdi Abedi Negar Ahmadian Concepción L. Alados Valeria Aramayo Fateh Amghar Tulio Arredondo Rodrigo J. Ahumada Khadijeh Bahalkeh Farah Ben Salem Niels Blaum Bazartseren Boldgiv Matthew A. Bowker Donald Bran Chongfeng Bu Rafaella Canessa Andrea P. Castillo-Monroy Helena Castro Ignacio Castro Patricio Castro-Quezada Roukaya Chibani Abel A. Conceição Courtney M. Currier Anthony Darrouzet-Nardi Balázs Deák David A. Donoso Andrew J. Dougill Jorge Durán Batdelger Erdenetsetseg Carlos I. Espinosa Alex Fajardo Mohammad Farzam Daniela Ferrante Anke S. K. Frank Lauchlan H. Fraser Laureano A. Gherardi Aaron C. Greenville Carlos A. Guerra Elizabeth Guzmán-Montalvan Rosa M. Hernández-Hernández Norbert Hölzel Elisabeth Huber-Sannwald Frederic M. Hughes Oswaldo Jadán-Maza Florian Jeltsch Anke Jentsch Kudzai F. Kaseke Melanie Köbel Jessica E. Koopman Cintia V. Leder Anja Linstädter Peter C. le Roux Xinkai Li Pierre Liancourt Jushan Liu Michelle A. Louw Gillian Maggs-Kölling Thulani P. Makhalanyane Oumarou Malam Issa Antonio J. Manzaneda Eugene Marais Juan P. Mora Gerardo Moreno Seth M. Munson Alice Nunes Gabriel Oliva Gastón R. Oñatibia Guadalupe Peter Marco O. D. Pivari Yolanda Pueyo R. Emiliano Quiroga Soroor Rahmanian Sasha C. Reed Pedro J. Rey Benoît Richard Alexandra Rodríguez Víctor Rolo Juan G. Rubalcaba Jan C. Ruppert Ayman Salah Max A. Schuchardt Sedona Spann Ian Stavi Colton R. A. Stephens Anthony M. Swemmer Alberto L. Teixeira Andrew D. Thomas Heather L. Throop Katja Tielbörger Samantha Travers James Val Orsolya Valkó Liesbeth van den Brink Sergio Velasco Ayuso Frederike Velbert Wanyoike Wamiti Deli Wang Lixin Wang Glenda M. Wardle Laura Yahdjian Eli Zaady Yuanming Zhang Xiaobing Zhou Brajesh K. Singh Nicolas Gross

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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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