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1 Vulnerability of mineral-associated soil organic carbon to climate across 2 global drylands

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4 Paloma Díaz-Martínez¹, Fernando T. Maestre², Eduardo Moreno-Jiménez^{3,4}, Manuel Delgado-
5 Baquerizo⁵, David J. Eldridge⁶, Hugo Saiz⁷, Nicolas Gross⁸, Yoann Le Bagousse-Pinguel⁹,
6 Beatriz Gozalo¹⁰, Victoria Ochoa¹⁰, Emilio Guirado¹⁰, Miguel García-Gómez¹¹, Enrique
7 Valencia¹², Sergio Asensio¹⁰, Miguel Berdugo¹², Jaime Martínez-Valderrama^{10,13}, Betty J.
8 Mendoza¹⁴, Juan C. García-Gil¹, Claudio Zaccone¹⁵, Marco Panettieri¹, Pablo García-
9 Palacios^{1,16}, Wei Fan¹⁷, Iria Benavente-Ferraces¹, Ana Rey¹⁸, Nico Eisenhauer^{19,20}, Simone
10 Cesarz^{19,20}, Mehdi Abedi²¹, Rodrigo J. Ahumada²², Julio M. Alcántara²³, Fateh Amghar²⁴,
11 Valeria Aramayo²⁵, Antonio I. Arroyo²⁶, Khadijeh Bahalkeh²¹, Farah Ben Salem²⁷, Niels
12 Blaum²⁸, Bazartseren Boldgiv²⁹, Matthew A. Bowker^{30,31}, Donaldo Bran²⁵, Cristina
13 Branquinho³², Chongfeng Bu³³, Yonatan Cáceres³⁴, Rafaella Canessa³⁵, Andrea P. Castillo-
14 Monroy³⁶, Ignacio Castro³⁷, Patricio Castro-Quezada³⁸, Roukaya Chibani³⁹, Abel A.
15 Conceição⁴⁰, Courtney M. Currier^{41,42}, Anthony Darrouzet-Nardi⁴³, Balázs Deák⁴⁴, Christopher
16 R. Dickman⁴⁵, David A. Donoso³⁶, Andrew J. Dougill⁴⁶, Jorge Durán⁴⁷, Hamid Ejtehadi⁴⁸, Carlos
17 Espinosa⁴⁹, Alex Fajardo⁵⁰, Mohammad Farzam^{51,52}, Daniela Ferrante⁵³, Lauchlan H. Fraser⁵⁴,
18 Juan J. Gaitán^{55,56}, Elizabeth Gusman Montalván⁴⁹, Rosa M. Hernández-Hernández³⁷, Andreas
19 von Hessberg⁵⁷, Norbert Hölzel⁵⁸, Elisabeth Huber-Sannwald⁵⁹, Frederic M. Hughes^{60,40,61},
20 Oswaldo Jadán-Maza³⁸, Katja Geissler²⁸, Anke Jentsch⁵⁷, Mengchen Ju^{33,62}, Kudzai F. Kaseke⁶³,
21 Liana Kindermann⁶⁴, Jessica E. Koopman⁶⁵, Peter C. Le Roux⁶⁶, Pierre Liancourt^{67,68}, Anja
22 Linstädter^{64,69}, Jushan Liu⁷⁰, Michelle A. Louw⁶⁶, Gillian Maggs-Kölling⁷¹, Thulani P.
23 Makhalanyane⁷², Oumarou Malam Issa⁷³, Eugene Marais⁷¹, Pierre Margerie⁷⁴, Antonio J.
24 Mazaneda⁷⁵, Mitchel P. McClaran⁷⁶, João Vitor S. Messeder⁷⁷, Juan P. Mora⁵⁰, Gerardo
25 Moreno³⁴, Seth M. Munson⁷⁸, Alice Nunes³², Gabriel Oliva^{53,69}, Gastón R. Oñatibia⁷⁹, Brooke
26 Osborne⁸⁰, Guadalupe Peter^{55,81}, Yolanda Pueyo²⁶, R. Emiliano Quiroga^{22,82}, Sasha C. Reed⁸³,
27 Victor M. Reyes⁸⁴, Alexandra Rodríguez⁴⁷, Jan C. Ruppert⁶⁸, Oswaldo Sala^{41,85,42}, Ayman
28 Salah⁸⁶, Julius Sebei⁸⁷, Michael Sloan³⁰, Shijirbaatar Solongo⁸⁸, Ilan Stavi⁸⁹, Colton R.A.
29 Stephens⁵⁴, Alberto L. Teixido¹², Andrew D. Thomas⁹⁰, Heather L. Throop^{91,41}, Katja
30 Tielbörger⁶⁸, Samantha Travers⁶, James Val⁹², Orsolya Valko⁴⁴, Liesbeth van den Brink^{68,93},
31 Frederike Velbert⁵⁸, Wanyoike Wamiti⁹⁴, Deli Wang⁷⁰, Lixin Wang⁹⁵, Glenda M. Wardle⁴⁵,
32 Laura Yahdjian⁷⁹, Eli Zaady^{96,97}, Juan M. Zeberio⁸¹, Yuanming Zhang⁹⁸, Xiaobing Zhou⁹⁸, César
33 Plaza¹

34
35 ¹Instituto de Ciencias Agrarias (ICA), CSIC, Madrid, Spain. ²Environmental Sciences and
36 Engineering, Biological and Environmental Science and Engineering Division, King Abdullah
37 University of Science and Technology, Thuwal, Kingdom of Saudi Arabia. ³Department of
38 Agricultural and Food Chemistry, Faculty of Sciences, Universidad Autónoma de Madrid,
39 Madrid, Spain. ⁴Institute for Advanced Research in Chemical Sciences, Madrid,
40 Spain. ⁵Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos
41 Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Sevilla, Spain. ⁶Centre for Ecosystem
42 Science, School of Biological, Earth and Environmental Sciences, University of New South
43 Wales, Sydney, New South Wales, Australia. ⁷Institut de Biología Evolutiva, UPF-CSIC,

44 Barcelona, Spain.⁸Université Clermont Auvergne, INRAE, VetAgro Sup, Unité Mixte de
45 Recherche Ecosystème Prairial, Clermont-Ferrand, France.⁹Aix Marseille Univ, CNRS, Avignon
46 Université, IRD, IMBE, Aix-en-Provence, France.¹⁰Instituto Multidisciplinar para el Estudio del
47 Medio "Ramón Margalef", Universidad de Alicante, Alicante, Spain.¹¹Departamento de
48 Ingeniería y Morfología del Terreno, Escuela Técnica Superior de Ingenieros de Caminos,
49 Canales y Puertos, Universidad Politécnica de Madrid, Madrid, Spain.¹²Departamento de
50 Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad
51 Complutense de Madrid, Madrid, Spain.¹³Estación Experimental de Zonas Áridas (EEZA),
52 CSIC, Almería, Spain.¹⁴Departamento de Biología y Geología, Física y Química Inorgánica,
53 Universidad Rey Juan Carlos, Madrid, Spain.¹⁵Department of Biotechnology, University of
54 Verona, Verona, Italy.¹⁶Department of Plant and Microbial Biology, University of Zurich,
55 Zurich, Switzerland.¹⁷Institute of Agricultural Environment and Resources, Jilin Academy of
56 Agricultural Sciences, Changchun, China.¹⁸Museo Nacional de Ciencias Naturales (MNCN),
57 CSIC, Madrid, Spain.¹⁹German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-
58 Leipzig, Leipzig, Germany.²⁰Leipzig University, Institute of Biology, Leipzig,
59 Germany.²¹Department of Range Management, Faculty of Natural Resources and Marine
60 Sciences, Tarbiat Modares University, Noor, Mazandaran Province, Iran.²²Instituto Nacional de
61 Tecnología Agropecuaria, Estación Experimental Agropecuaria Catamarca, Catamarca,
62 Argentina.²³Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía,
63 Universidad de Jaén, Jaén, Spain.²⁴Laboratoire de Recherche: Biodiversité, Biotechnologie,
64 Environnement et Développement Durable (BioDev), Faculté des Sciences, Université M'hamed
65 Bougara de Boumerdès, Boumerdès, Algérie.²⁵Instituto Nacional de Tecnología Agropecuaria
66 (INTA), Estación Experimental Agropecuaria Bariloche. Bariloche, Río Negro,
67 Argentina.²⁶Instituto Pirenaico de Ecología (IPE), CSIC, Zaragoza, Spain.²⁷Laboratory of
68 Pastoral Ecosystems and Promotion of Spontaneous plants and Associated Microorganisms,
69 Institut des Régions Arides (IRA) Médenine, Tunisia.²⁸University of Potsdam, Plant Ecology and
70 Nature Conservation, Potsdam, Germany.²⁹Laboratory of Ecological and Evolutionary Synthesis,
71 Department of Biology, School of Arts and Sciences, National University of Mongolia,
72 Ulaanbaatar, Mongolia.³⁰School of Forestry, Northern Arizona University, Flagstaff, AZ,
73 USA.³¹Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ,
74 USA.³²Center for Ecology, Evolution and Environmental Changes (cE3c) & CHANGE - Global
75 Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Campo
76 Grande, Lisboa, Portugal.³³Institute of Soil and Water Conservation, Northwest Agriculture and
77 Forestry University, Yangling, Shaanxi, China.³⁴Forestry School, INDEHESA, Universidad de
78 Extremadura, Plasencia, Spain.³⁵Ecological Plant Geography, Faculty of Geography, University
79 of Marburg, Marburg, Germany.³⁶Grupo de Investigación en Ecología y Evolución en los
80 Trópicos-EETrop-Universidad de las Américas, Campus Udlapark, Quito,
81 Ecuador.³⁷Universidad Nacional Experimental Simón Rodríguez (UNESR), Instituto de Estudios
82 Científicos y Tecnológicos (IDECYT), Centro de Estudios de Agroecología Tropical (CEDAT),
83 Laboratorio de Biogeoquímica, Miranda, Venezuela.³⁸Universidad de Cuenca, Facultad de
84 Ciencias Agropecuarias, Carrera de Ingeniería Agronómica, Grupo de Agroforestería, Manejo y
85 Conservación del paisaje, Ecuador.³⁹Laboratory of Eremology and Combating Desertification;
86 Institut des Régions Arides (IRA), Médenine, Tunisia.⁴⁰Universidade Estadual de Feira de
87 Santana, Departamento de Ciências Biológicas, Feira de Santana, Bahia, Brazil.⁴¹School of Life
88 Sciences, Arizona State University, Tempe, AZ, USA.⁴²Global Drylands Center, Arizona State
89 University, Tempe, AZ, USA.⁴³Department of Biological Sciences, University of Texas at El

90 Paso, El Paso, TX, USA.⁴⁴Lendület Seed Ecology Research Group, Institute of Ecology and
91 Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary.⁴⁵Desert Ecology
92 Research Group, School of Life and Environmental Sciences, The University of Sydney, Sydney,
93 New South Wales, Australia.⁴⁶School of Earth and Environment, University of Leeds, Leeds,
94 UK.⁴⁷Misión Biológica de Galicia (MBG), CSIC, Pontevedra, Spain.⁴⁸Quantitative Plant
95 Ecology and Biodiversity Research Lab., Department of Biology, Faculty of Science, Ferdowsi
96 University of Mashhad, Mashhad, Iran.⁴⁹Departamento de Ciencias Biológicas, Universidad
97 Técnica Particular de Loja, Loja, Ecuador.⁵⁰Instituto de Investigación Interdisciplinaria (I3),
98 Universidad de Talca, Talca, Chile.⁵¹Department of Range and Watershed Management,
99 Ferdowsi University of Mashhad, Mashhad, Iran.⁵²Department of Molecular and Life Sciences,
100 Curtin University, Australia.⁵³Universidad Nacional de la Patagonia Austral, Río Gallegos, Santa
101 Cruz, Argentina.⁵⁴Department of Natural Resource Science, Thompson Rivers University,
102 British Columbia, Canada.⁵⁵Consejo Nacional de Investigaciones Científicas y Técnicas de
103 Argentina (CONICET), Buenos Aires, Argentina.⁵⁶Departamento de Tecnología, Universidad
104 Nacional de Luján, Buenos Aires, Argentina.⁵⁷Department of Disturbance Ecology, Bayreuth
105 Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Bayreuth,
106 Germany.⁵⁸Institute of Landscape Ecology, University of Münster, Münster, Germany.⁵⁹Instituto
107 Potosino de Investigación Científica y Tecnológica, A.C., SLP, Mexico.⁶⁰Universidade Estadual
108 de Santa Cruz, Conselho de Curadores das Coleções Científicas and Zoologia, Ilhéus, Bahia,
109 Brazil.⁶¹Universidade Federal de Minas Gerais, Bioinformática, Belo Horizonte, Minas Gerais,
110 Brazil.⁶²Yangling Vocational & Technical College, Yangling, Shaanxi, China.⁶³Earth Research
111 Institute, University of California Santa Barbara, CA, USA.⁶⁴University of Potsdam, Institute of
112 Biochemistry and Biology, Biodiversity Research / Systematic Botany, Potsdam,
113 Germany.⁶⁵Centre for Microbial Ecology and Genomics, Department of Biochemistry, Genetics
114 and Microbiology, University of Pretoria, Pretoria, South Africa.⁶⁶Department of Plant and Soil
115 Sciences, University of Pretoria, Pretoria, South Africa.⁶⁷Institute Botany Department, State
116 Museum of Natural History Stuttgart, Stuttgart, Germany.⁶⁸Plant Ecology Group, University of
117 Tübingen, Tübingen, Germany.⁶⁹Institute of Crop Science and Resource Conservation,
118 University of Bonn, Bonn, Germany.⁷⁰Key Laboratory of Vegetation Ecology of the Ministry of
119 Education, Jilin Songnen Grassland Ecosystem National Observation and Research Station,
120 Institute of Grassland Science, Northeast Normal University, Changchun, China.⁷¹Gobabeb-
121 Namib Research Institute, Walvis Bay, Namibia.⁷²Department of Microbiology and the School
122 of Data Science and Computational Thinking, Faculty of Science, Stellenbosch University,
123 Stellenbosch, South Africa.⁷³Institut d'Écologie et des Sciences de l'Environnement de Paris
124 (iEES-Paris), Sorbonne Université, IRD, CNRS, INRAE, Université Paris Est Creteil, Université
125 de Paris, France.⁷⁴Normandie Univ, UNIROUEN, INRAE, ECODIV, Rouen,
126 France.⁷⁵Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén,
127 Jaén, Spain.⁷⁶School of Natural Resources and the Environment, University of Arizona, Tucson,
128 AZ, USA.⁷⁷Biology Department & Ecology Program, The Pennsylvania State University,
129 University Park, PA, USA.⁷⁸US Geological Survey, Southwest Biological Science Center,
130 Flagstaff, AZ, USA.⁷⁹Cátedra de Ecología, Facultad de Agronomía, Universidad de Buenos
131 Aires, Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura
132 (IFEVA-CONICET), Buenos Aires, Argentina.⁸⁰Department of Environment and Society, Utah
133 State University, Moab, UT, USA.⁸¹Universidad Nacional de Río Negro, Sede Atlántica,
134 CEANPa, Río Negro, Argentina.⁸²Cátedra de Manejo de Pastizales Naturales, Facultad de
135 Ciencias Agrarias, Universidad Nacional de Catamarca, Catamarca, Argentina.⁸³US Geological

136 Survey, Southwest Biological Science Center, Moab, UT, USA.⁸⁴Instituto de Ecologia,
137 INECOL, Chihuahua, Chihuahua, Mexico.⁸⁵School of Sustainability, Arizona State University,
138 Tempe, AZ, USA.⁸⁶Al-Quds University, Palestine.⁸⁷Department of Agriculture, Makhado,
139 Limpopo, South Africa.⁸⁸Sustainable Fibre Alliance, Grand Office, Ulaanbaatar, Mongolia.⁸⁹The
140 Dead-Sea and Arava Science Center, Yotvata, Israel.⁹⁰Department of Geography and Earth
141 Sciences. Aberystwyth University, Wales, UK.⁹¹School of Earth & Space Exploration, Arizona
142 State University, Tempe, AZ, USA.⁹²Science Division, Department of Planning, and
143 Environment, New South Wales Government, Buronga, New South Wales,
144 Australia.⁹³ECOBIOSIS, Departement of Botany, University of Concepcion, Concepcion,
145 Chile.⁹⁴Zoology Department, National Museums of Kenya, Nairobi, Kenya.⁹⁵Department of
146 Earth and Environmental Sciences, Indiana University Indianapolis, Indianapolis, IN,
147 USA.⁹⁶Department of Natural Resources, Agricultural Research Organization, Institute of Plant
148 Sciences, Gilat Research Center, Mobile Post Negev, Israel.⁹⁷Kaye Academic College of
149 Education, Beer Sheva, Israel.⁹⁸State Key Laboratory of Desert and Oasis Ecology, Xinjiang
150 Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China.

151

152

153 email: cesar.plaza@csic.es; eduardo.moreno@uam.es; fernando.maestregil@kaust.edu.sa

154 **Mineral-associated organic carbon (MAOC) constitutes a major fraction of global soil**
155 **carbon (C), and is assumed less sensitive to climate than particulate organic C (POC) due**
156 **to protection by minerals. Despite its importance for long-term C storage, the response of**
157 **MAOC to changing climates in drylands, which cover more than 40% of the global land**
158 **area, remains unexplored. Here we assess topsoil organic C fractions across global**
159 **drylands using a standardized field survey in 326 plots from 25 countries and six**
160 **continents. We find that soil biogeochemistry explained the majority of variation in both**
161 **MAOC and POC. Both C fractions decreased with increases in mean annual temperature**
162 **and reductions in precipitation, with MAOC responding similarly to POC. Therefore, our**
163 **results suggest that ongoing climate warming and aridification may result in unforeseen C**
164 **losses across global drylands, and that the protective role of minerals may not dampen**
165 **these effects.**

166
167 Soils in drylands—the largest set of biomes of the planet —store 646 Pg of organic C, more than
168 all living vegetation on Earth ^{1,2}. This vast soil organic C pool supports essential ecosystem
169 services, including food provision and water and climate regulation for more than 2.5 billion
170 people ^{3,4}. Yet, temperature increases and precipitation reductions forecasted for many dryland
171 regions are expected to disrupt the balance of soil organic C, accelerating microbial
172 decomposition, reducing plant C inputs into the soil, and resulting in more CO₂ emissions to the
173 atmosphere ^{5,6}.

174 The sensitivity of organic C in soils (sensu ref. ⁷) to temperature and precipitation at
175 timescales relevant to climate change mitigation is thought to be controlled largely by
176 interactions with soil minerals, which restrict the accessibility of microbial decomposers by

177 encapsulating and adsorbing organic matter^{8–10}. Plant-derived materials at early stages of
178 decomposition are the main constituents of the mineral-unprotected, particulate organic C (POC)
179 fraction of soil organic matter⁹. The POC fraction is thus directly affected by changes in plant C
180 inputs into the soil and is more exposed to microbial decomposition than the organic component
181 of the mineral-associated organic C (MAOC) fraction, which has, therefore, a lower turnover rate
182^{11,12}. As a result, large scale meta-analyses and observational studies suggest that POC is more
183 sensitive to changes in climate, and particularly to warming, than MAOC^{7,13–16}. Because of the
184 typically large ratio of soil minerals to organic matter in drylands, MAOC is expected to
185 dominate over POC, potentially driving a high persistence of soil organic C in these ecosystems
186^{7,10,17}. However, no studies to date have examined the relationship of POC and MAOC with
187 climate across the diverse environmental gradients that characterize global drylands.

188 Investigating this relationship is particularly timely and relevant, as it would significantly reduce
189 the uncertainty surrounding the land carbon-climate feedback. Additionally, it would provide
190 valuable insights for adapting soil carbon-related ecosystem services to ongoing climate change.

191 Here we evaluated how mean annual temperature and precipitation relates to POC and
192 MAOC contents across global drylands after accounting for major biotic (net primary
193 productivity, vegetation type, woody cover, plant and herbivore richness, and grazing pressure)
194 and soil biogeochemistry (clay and silt contents, pH, chemical index of alteration, exchangeable
195 Ca, non-crystalline Al and Fe, available N and P, and microbial biomass C) factors known to
196 potentially affect soil organic C content by regulating C inputs and stabilization processes^{5,18}. To
197 do so, we surveyed *in situ* 326 plots from 98 dryland ecosystems located in 25 countries from six
198 continents (Extended Data Fig. 1). Our survey spans the broad gradients of temperature,
199 precipitation, aridity, soil properties, vegetation types, and grazing pressures that can be found

200 across drylands worldwide (Extended Data Tables 1 and 2)^{19,20}. At each site, we collected
201 topsoil samples (0-7.5 cm) from areas both covered (322) and not covered (326) by perennial
202 vegetation from two to four plots located across a local gradient of extensive grazing pressure
203 (648 samples in total, see Methods). We subjected all samples to a size fractionation procedure
204 to separate and quantify C content in POC and MAOC pools^{9,21}. Using these data, we tested the
205 hypothesis that MAOC, being protected by minerals, is less sensitive than POC to increases in
206 temperature and decreases in precipitation^{7,10,16,22}. We also hypothesize that the presence of
207 vegetation mitigates declines in soil C, particularly POC, by increasing soil C inputs.

208

209 **MAOC dominates soil organic C and is sensitive to climate**

210 Our results show that MAOC was the dominant soil organic C fraction in drylands globally (Fig.
211 1a). In particular, median MAOC content was 5.2 g C kg⁻¹ soil, equivalent to 66% of the total
212 soil organic C content, whereas median POC content was 2.3 g C kg⁻¹ soil. This quantification
213 falls within the range of soil organic C content (MAOC and POC) commonly found in drylands,
214 and is relevant to improve the performance of emerging models of soil organic C formation and
215 persistence using POC and MAOC frameworks^{2, 23-25}.

216 Contrary to our hypothesis, we found that MAOC and POC were equally sensitive to
217 differences in climate across global drylands. In particular, both MAOC and POC were
218 negatively associated with increasing temperature and decreasing precipitation to a similar
219 extent, as indicated by the similar slopes of the associations (Fig. 1bc). These results were
220 supported by the lack of a significant interaction between the effects of temperature and
221 precipitation and the type of fraction (MAOC versus POC) tested by a linear mixed-effects
222 model (Fig. 1d, see Methods). Based on the results from this model, we estimated that POC and

223 MAOC contents significantly declined with temperature at an average rate of 3.2% per °C (95%
224 confidence interval (CI): 1.8, 4.6) and increased with precipitation at an average rate of 6.6% per
225 100 mm (95% CI: 0.6, 12.6).

226 Warming accelerates the microbial decomposition of soil organic matter, and precipitation
227 reduction constrains plant production and organic matter inputs into the soil ^{5,26}. Our results are,
228 therefore, consistent with previously reported reductions in soil organic C content with
229 increasing temperature and reducing precipitation across terrestrial ecosystems ²⁷⁻²⁹. However,
230 and contrary to expectations of smaller sensitivity of MAOC versus POC to changes in climate
231 observed in more mesic systems ^{14,15}, our findings based on a space-for-time substitution
232 highlight that the MAOC and POC fractions may decrease at similar rates in response to climate
233 warming and precipitation reduction across global drylands. Therefore, they suggest that the
234 current paradigm of mineral protection may not determine soil C persistence in dryland
235 ecosystems ^{8,30-32}. The apparent lack of protection by minerals, which contrasts with what was
236 observed in mesic systems richer in organic matter, was consistent across the range of soil
237 organic C content found in drylands (Extended Data Fig. 2). There is recent evidence that
238 MAOC is controlled not only by C stabilization in soil organo-mineral complexes, but also by
239 changes in C inputs driven by climate ¹⁵. In drylands, not only precipitation reduction but also
240 warming may increase water deficit, which may decrease plant productivity ⁵, C inputs into the
241 soil and C accumulation into the MAOC fraction. There is also evidence that dryland soils
242 maintain a high oxidative potential during dry periods, mainly through the stabilization of
243 enzymes, which result in a rapid organic matter decomposition in wet periods ^{28,29} and may
244 further limit C inputs to the MAOC fraction.

245

246 **Vegetation buffers soil C declines with warming**

247 Both POC and MAOC contents were higher in soil beneath perennial vegetation (Fig. 2). We
248 further observed that as mean annual temperature increased, POC and MAOC contents
249 decreased, but to a lesser extent, beneath vegetation. Conversely, as mean annual precipitation
250 increased, both contents increased in a similar manner in open areas and in areas under the
251 canopy of perennial vegetation (Fig. 2). These results are important because they suggest that the
252 presence of vegetation buffers, but does not fully compensate for, the negative effects of higher
253 temperature on soil C fractions. While the buffering effect of vegetation did not completely
254 counteract the vulnerability of organic C pools to increasing temperatures, our findings indicate
255 that management practices aimed at protecting vegetation in drylands may help to maintain soil
256 organic C stocks in global drylands and reducing their losses in response to a changing climate.

257

258 **Coupling of POC and MAOC in drylands**

259 We found that POC and MAOC contents were strongly correlated across global drylands ($r =$
260 0.83 , $n = 326$, $P < 0.001$; Fig. 3a). These results strongly suggest that both fractions remain
261 highly coupled in drylands despite their different levels of putative protection against
262 decomposition by microorganisms.

263 Variance partitioning of linear mixed-effects models and random forest analysis showed that
264 the order of importance of the group of factors that explained most of the variation of POC and
265 MAOC across global drylands was essentially the same for both organic C fractions (Fig. 3b,
266 Extended Data Fig. 3). Soil biogeochemistry, above climate and biotic factors, was the most
267 important predictor of both POC and MAOC contents. Both C fractions were negatively
268 associated with soil pH and positively associated to exchangeable Ca, available N and P, and

269 microbial biomass C contents; additionally, MAOC was associated positively with clay and silt
270 and non-crystalline Al and Fe contents (Extended Data Fig. 4). Slightly-acidic-to-neutral soils
271 generally feature higher nutrient availability and more fertility than alkaline soils³³, which may
272 thus favor soil organic C accumulation in drylands through increased plant-derived C inputs and
273 microbial activity. The prevalent role of soil fine texture and non-crystalline Al and Fe in MAOC
274 formation has been widely documented in the literature³¹. Sorption of organic matter to mineral
275 surfaces is known to be promoted by the relatively high specific surface area and charge of clay
276 and silt, while non-crystalline Fe and Al phases are also known to form strong associations with
277 organic matter³¹.

278 The coupling of POC and MAOC observed here for drylands may be, however, disrupted in
279 more productive terrestrial ecosystems, where higher plant inputs may result in larger POC
280 contents^{13–15}. In contrast to experimental manipulation studies¹⁴, our work addresses the
281 vulnerability of soil C fractions using a space-for-time substitution. Further research into the
282 pace of the climate-induced changes and the causality of the associations found in our study is
283 thus warranted.

284

285 **Concluding remarks**

286 By using a global standardized field study and by focusing exclusively on dryland ecosystems,
287 our work expands previous efforts to understand abiotic and biotic drivers of POC and MAOC
288 along large geographical gradients, which have either been based on literature syntheses, which
289 use datasets that are inherently heterogenous, or have focused on ecosystems other than drylands
290¹⁶. Our study generated highly standardized field data on the POC and MAOC fractions of

291 dryland soils worldwide, along with their major predictors. These data significantly expand
292 existing global databases and can be used to refine current soil organic C models.

293 Our findings suggest that ongoing changes in climate, particularly warming, may adversely
294 affect both unprotected and mineral-protected soil C content in drylands to a similar extent. The
295 results obtained also indicate that maintaining vegetation cover can mitigate, but not fully
296 counteract, the negative impacts of rising temperatures on soil organic C fractions. Our study
297 enhances our understanding of how POC and MAOC contents in soil respond to key abiotic and
298 biotic drivers, revealing that mineral protection has limited potential to sustain organic C storage
299 in dryland soils in the face of ongoing global warming. The novel insights about dryland soil C
300 pools and their sensitivity provided here could facilitate much-needed advances in our model
301 representation of dryland ecosystems and their response to climate change.

302

303

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330

331 **Author contributions**

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341 W.W., D.W., L.W., G.M.W., L.Y., E.Z., J.M.Z., Y.Z., and X.Z. performed field research.
342 P.D.M., V.O., B.G., B.J.M., S.C., N.E., J.C.G.G., C.Z., M.P., W.F., I.B.F., A.Re., E.M.J., and
343 C.P. conducted laboratory research and analysis. P.D.M., E.G., and C.P. carried out data
344 analysis, after discussion, suggestions, and contributions from F.T.M., E.M.J., M.D.B., N.G.,
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347 results and contributed to editing the manuscript.

348

349 **Competing interests**

350 The authors declare no competing interests.

351

352 **Figure captions**

353

354 **Fig. 1 | Distribution of soil organic carbon (C) contents in particulate organic C (POC) and**
355 **mineral-associated organic C (MAOC) fractions and their relationships with climate in**
356 **global drylands. a**, Boxplot of POC and MAOC contents. Box, 1st, and 3rd quartiles; central
357 horizontal line, median; upper vertical line end, largest value smaller than 1.5 times the
358 interquartile range; lower vertical line, smallest value larger than 1.5 times the interquartile range
359 (n = 326 plots). **b-c**, Relationships between POC and MAOC contents and mean annual
360 temperature (MAT, **b**) and precipitation (MAP, **c**). Lines and shading represent linear regressions
361 and 95% confidence intervals. **d**, Summary of a linear mixed-effects model, controlling for biotic
362 factors and soil biogeochemistry (see Methods). The panel shows coefficients (circles) and 95%

363 confidence intervals (CI, bars) for main and interaction effects of C fraction type (binary
364 variable, either POC or MAOC) and climate (MAT and MAP) on POC and MAOC contents.
365 The variance explained (R^2) by the fixed and random effects relative to the total variance was
366 77% and 12%, respectively (n = 634 POC and MAOC observations). Carbon fraction contents
367 were natural-logarithm transformed, and all the predictors were standardized. The positive
368 coefficient of C fraction type (MAOC vs. POC) indicate that MAOC contents are significantly
369 greater than POC contents ($P < 0.001$). For the observed negative association of MAT and
370 positive association of MAP with C content ($P < 0.001$ and $P = 0.039$ respectively), negative
371 coefficients for the interaction of C fraction type with MAT and MAP indicate that increasing
372 MAT has a stronger negative effect on MAOC than on POC contents ($P = 0.053$), while
373 decreasing MAP has a stronger negative effect on POC than on MAOC ($P = 0.181$).

374 **Fig. 2 | Relationships between climate and particulate organic C (POC) and mineral-**
375 **associated organic C (MAOC) contents in soils under the canopy of the dominant perennial**
376 **vegetation (V) and in open areas (O) across global drylands. a-d**, Relationships between POC
377 and mean annual temperature (MAT, **a**) and precipitation (MAP, **c**), and between MAOC and
378 MAT (**b**) and MAP (**d**) in both O and V microsites. Lines and shading represent linear
379 regressions and 95% confidence intervals (n = 326 and 322 for O and V, respectively). **e**,
380 Coefficients (dots) and 95% confidence intervals (bars) of linear mixed-effects model illustrating
381 the fixed main and interaction effects of MAT, MAP, and the presence of vegetation cover (V vs.
382 O) on POC and MAOC contents (n = 648 V and O areas). The variance explained (R^2) by the
383 fixed and random effects relative to the total variance was 30% and 55%, respectively, for POC,
384 and 32% and 61%, respectively, for MAOC.

385 **Fig. 3 | Coupling and drivers of particulate organic C (POC) and mineral-associated**
386 **organic C (MAOC) in global drylands. a**, Relationship between POC and MAOC contents.
387 Dots represent individual dryland plots, with the colors of the dots illustrating their aridity (1 –
388 annual precipitation/potential evapotranspiration) values. The line and shading represent the
389 fitted linear regression and 95% confidence interval, respectively. **b**, Variance explained (R^2) by
390 linear mixed-effects models for POC and MAOC contents partitioned into the fraction
391 attributable to unique and shared among groups of drivers (climate: mean annual temperature
392 and mean annual precipitation; biotic factors: net primary productivity, type of vegetation,
393 woody cover, plant richness, grazing pressure, and herbivore richness; and soil biogeochemistry:

394 clay and silt, pH, chemical index of alteration, exchangeable Ca, non-crystalline Al and Fe,
395 available N and P, and microbial biomass carbon). The variance explained (R^2) by the fixed and
396 random effects relative to the total variance was 69% and 20% for POC (n = 317) and 84% and
397 11% for MAOC (n = 317), respectively.

398

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478 **Methods**

479 **Global field survey and soil sampling.** Fieldwork was conducted from January 2016 to
480 September 2019. A total of 326 plots distributed across 98 study sites in 25 countries from all
481 continents except Antarctica (Algeria, Argentina, Australia, Botswana, Brazil, Canada, Chile,
482 China, Ecuador, Hungary, Iran, Israel, Kazakhstan, Kenya, Mexico, Mongolia, Namibia, Niger,
483 Palestine, Peru, Portugal, South Africa, Spain, Tunisia, and USA) and encompassing the wide
484 range of vegetation, soil, climate, and grazing pressure levels found in drylands worldwide were
485 surveyed using a common and standardized protocol ^{19,20}.

486 At each site, we gathered field data within multiple 45 m x 45 m plots situated along a
487 gradient of grazing pressure, encompassing high (n = 98), medium (n = 97), and low (n = 88)
488 pressure levels, as well as ungrazed areas (n = 43). To establish the grazing gradients, in 90 out
489 of the 98 sites surveyed, we strategically positioned these plots at varying distances from
490 artificial watering points, which are usually created in drylands to supply introduced livestock
491 with permanent water sources ³⁴. The closer the plot to the permanent water source, the more
492 intense the grazing ^{34,35}. In the remaining eight sites, local variations in grazing pressure
493 gradients were ascertained by observing different paddocks featuring varying grazing intensities.
494 See ref. ²⁰ for additional details on the characterization and validation of the local grazing
495 pressure gradients established.

496 A portable Global Positioning System was used to record the coordinates and elevation of
497 each plot, which were standardized to the WGS84 ellipsoid for visualization and analyses.
498 During the dry season at each site, four soil cores (145 cm³) from 0 to 7.5-cm depth (topsoil)
499 were collected from five 50 × 50-cm quadrats randomly placed in areas under the canopy of the
500 dominant perennial vegetation and five placed in open areas not covered by perennial vegetation.

501 The soil cores were homogenized and composited to form a sample representative of the soil
502 under the dominant vegetation and a sample representative of the soil in open areas within each
503 plot. The soil samples were passed through a 2-mm sieve. A portion of each soil sample was air-
504 dried and used for organic matter fractionation and texture and pH analysis, and another portion
505 was stored at -20 °C and used for microbial biomass C analysis. A portion of the air-dried soil
506 samples was ground with a ball mill for additional chemical analysis.

507 **Soil organic carbon fractionation and quantification.** All the soil samples, a total of 648 (326
508 from open areas and 322 from under the canopy of the dominant vegetation), were subjected to a
509 size fractionation method ^{21,36} to separate the POC (not protected by minerals from microbial
510 decomposition) and MAOC (protected by minerals) fractions. Aggregates were dispersed by
511 adding 30 mL of sodium hexametaphosphate (5 g L⁻¹) to 10 g of soil and shaking with an
512 overhead shaker for 18 h. After dispersion, the mixture was thoroughly rinsed through a 53- μ m
513 sieve, to separate the POC (> 53 μ m) and MAOC (< 53 μ m) fractions using an automated wet
514 sieving system. The isolated fractions were oven-dried at 60 °C, weighed, and ground with a ball
515 mill. The whole soil samples and the POC and MAOC fractions were analyzed for organic C
516 contents by dry combustion and gas chromatography using a ThermoFlash 2000 NC Soil
517 Analyzer (Thermo Fisher Scientific, MA) after removing carbonates by acid fumigation ³⁷.

518 **Climate data.** Mean annual temperature and mean annual precipitation data were obtained from
519 WorldClim 2.0 ³⁸ a high resolution (30 arc seconds or ~ 1 km at the equator) database based on a
520 large number of climate observations and topographical data for the 1970-2000 period. Aridity
521 index (ratio of average annual precipitation to potential evapotranspiration) data were obtained
522 from the Global Aridity Index and Potential Evapotranspiration Climate Database v3 ³⁹. Aridity
523 was calculated as 1 – aridity index.

524 **Vegetation and herbivore richness survey.** Each plot was classified as grassland, shrubland, or
525 forest by identifying the dominant type of vegetation. Net primary productivity (NPP) was
526 estimated using the mean annual Normalized Difference Vegetation Index (NDVI) averaged
527 monthly values between 1999 and 2019 at a resolution of 30 m from Landsat 7 Enhanced
528 Thematic Mapper Plus (ETM+) ⁴⁰. The cover of perennial vascular plants (plant cover) was
529 measured along four parallel 45-m transects separated by 10 m and oriented downslope during
530 the peak of the growing season using the line-intercept method ^{19,41,42}. Woody cover was
531 measured in 25 contiguous quadrats (1.5 m × 1.5 m) placed in each transect (100 quadrats per
532 plot). Plant richness was the total number of unique perennial species found along the quadrats
533 and transects surveyed. The richness of herbivores was quantified at each plot using dung data
534 collected systematically in situ along the four 45-m transects established as described in ref. ²⁰.

535 **Soil analyses.** All the bulk soil samples were analyzed as follows. Clay and silt contents were
536 determined by sieving and sedimentation ⁴³. Soil pH was measured in a water suspension at a
537 soil-to-water ratio of 1:2.5 ⁴⁴. The chemical index of alteration, which is an indicator of the
538 degree of weathering, was calculated as the molecular proportion of Al₂O₃ versus Al₂O₃ + CaO +
539 Na₂O + K₂O ⁴⁵, using total Al, Ca, Na, and K contents and after correcting Ca for soils with
540 carbonates ¹⁸; total Al, Ca, Na and K contents were determined by inductively coupled plasma
541 atomic emission spectroscopy (ICP-AES) after digestion in nitric and perchloric acids ^{44,46}.
542 Exchangeable Ca content was determined by ICP-AES after extraction with ammonium acetate
543 at pH 7.0 ^{44,47}. Non-crystalline Fe and Al contents were determined by ICP-AES after extraction
544 with acid ammonium oxalate ⁴⁸. Available N (ammonium and nitrate) content was determined by
545 extraction with 0.5 M K₂SO₄ and the indophenol blue method using a microplate reader ⁴⁹.

546 Available P content was determined by the Olsen method⁵⁰. Microbial biomass C was
547 determined by substrate-induced respiration⁵¹ using an automated microrespirometer⁵².

548 **Statistical analyses.** We compared the content of MAOC with that of POC in global dryland
549 soils controlling for confounding factors, and tested the hypothesis that the effects of climate
550 (mean annual temperature and precipitation) on POC and MAOC contents depends on (interacts
551 with) the C fraction type. For these analyses, we aggregated soil data for open and vegetation
552 covered areas by plot using plant cover area as a weighting factor, and fitted a linear mixed-
553 effects model on the response of C content with C fraction type as a binary categorical predictor
554 (either MAOC or POC). In the fixed-effects term of the model, we also included mean annual
555 temperature, mean annual precipitation, and the interactions of mean annual temperature and
556 mean annual precipitation with C fraction type, as well as key biotic (net primary productivity,
557 type of vegetation, woody cover, plant richness, grazing pressure, and herbivore richness) and
558 soil biogeochemical (clay and silt, pH, chemical index of alteration, exchangeable Ca, non-
559 crystalline Al and Fe, available N and P, and microbial biomass C) covariates to control for
560 confounding factors. In the random term of the model, we incorporated an intercept structure
561 with plot nested within site as a categorical variable to account for the lack of independence in
562 the residuals due to the paired POC and MAOC separation and the plot sampling design. We
563 checked whether the fit of this linear mixed-effects model improved by including quadratic terms
564 of mean annual temperature, mean annual precipitation, and both mean annual temperature and
565 precipitation, using the Akaike information criterion (AIC) and likelihood ratio tests. None of the
566 quadratic models tested was a significantly better fit to the data ($\chi^2 (1) < 1.0$, $P > 0.3$) than the
567 linear model (lowest AIC).

568 To examine separately the variance of POC and MAOC contents explained by the groups of
569 predictors (climate: mean annual temperature and mean annual precipitation; biotic factors: net
570 primary productivity, type of vegetation, woody cover, plant richness, grazing pressure, and
571 herbivore richness; soil biogeochemistry: clay and silt, pH, chemical index of alteration,
572 exchangeable Ca, non-crystalline Al and Fe, available N and P, and microbial biomass C), we
573 built two linear mixed-effects models (one for POC and another one for MAOC) with site as a
574 random categorical variable. These two separate models were used to assess the importance of
575 the different groups of predictors in explaining either POC or MAOC, and not to test statistically
576 for differences in the size of the effects of the predictors between POC and MAOC. To support
577 the linear mixed-effects models, we tested the importance of the same groups of predictors of
578 POC and MAOC using random forest regression modeling⁵³. In particular, we built two random
579 forest models, one for POC and one for MAOC, combining 500 trees, and quantified the
580 importance of each predictor by computing the increase in mean squared error across trees when
581 the predictor was permuted.

582 We tested whether the presence of vegetation cover interacted with the effects of temperature
583 and precipitation also by linear mixed-effects modeling. For this purpose, we built two linear
584 mixed-effects models, one for POC content and another one for MAOC content in areas under
585 the canopy of the dominant perennial vegetation and open areas, with vegetation cover as a
586 binary predictor and plot nested within site in the random term.

587 For all the linear mixed-effects models, POC, MAOC, exchangeable Ca, non-crystalline Al
588 and Fe, available N and P, and microbial biomass C were natural-logarithm transformed to
589 reduce the skewness of the data. To compare effect sizes, all the numeric predictors were
590 standardized by subtracting the mean and dividing by two standard deviations, and the binary

591 variables (C fraction type and vegetated vs. open areas) were rescaled to -0.5 and 0.5 ⁵⁴. The
592 coefficients of the models were estimated by the restricted maximum likelihood approach, 95%
593 confidence intervals were calculated, and P-values were computed based on Satterthwaite
594 approximation ⁵⁵. The validity of the assumptions of normality, homoscedasticity and linearity
595 were examined using residual plots. The generalized variance inflation factors (GVIFs) were
596 computed to check for multicollinearity among predictors (GVIF values were less than 3 in all
597 cases, suggesting that multicollinearity was low ⁵⁶). All statistical analyses were performed using
598 R ⁵⁷ and the R packages arm ⁵⁸, ggplot2 ⁵⁹, lme4 ⁶⁰, lmerTest ⁵⁵, partR2 ⁶¹, patchwork ⁶²,
599 rnatualearth ⁶³, randomForest ⁶⁴, sf ⁶⁵, terra ⁶⁶, and viridis ⁶⁷.

600

601 **Data availability**

602 The data associated with this study are publicly available in

603 <https://figshare.com/s/8aeac2300650181f2c86> (<https://doi.org/10.6084/m9.figshare.24678891>) ⁶⁸.

604

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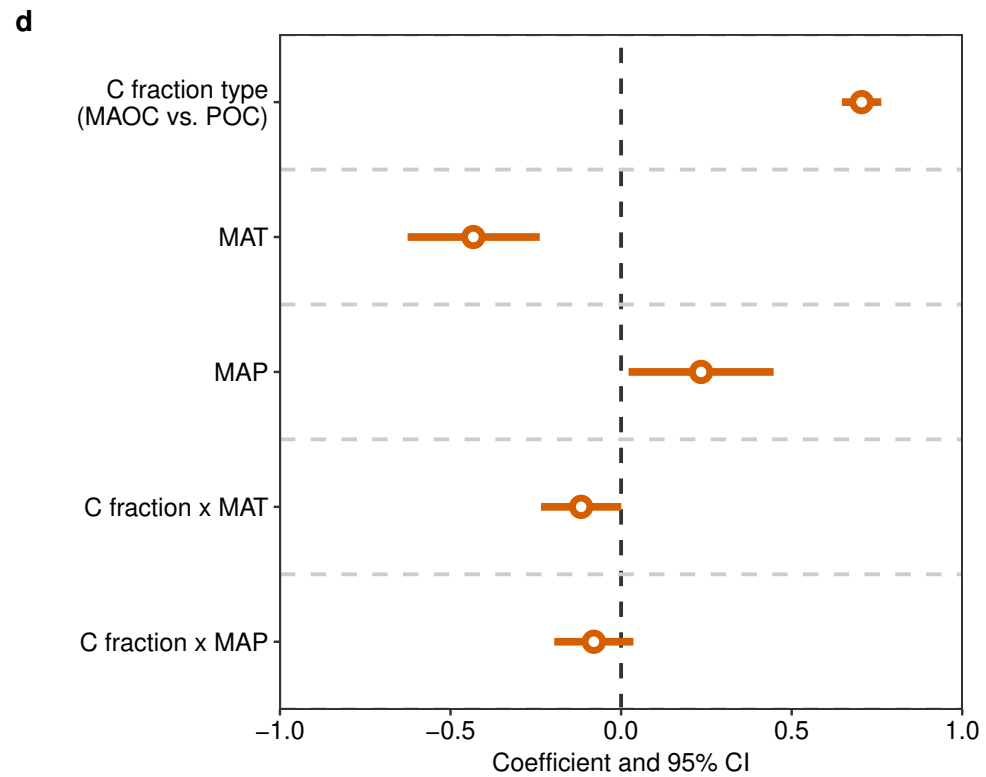
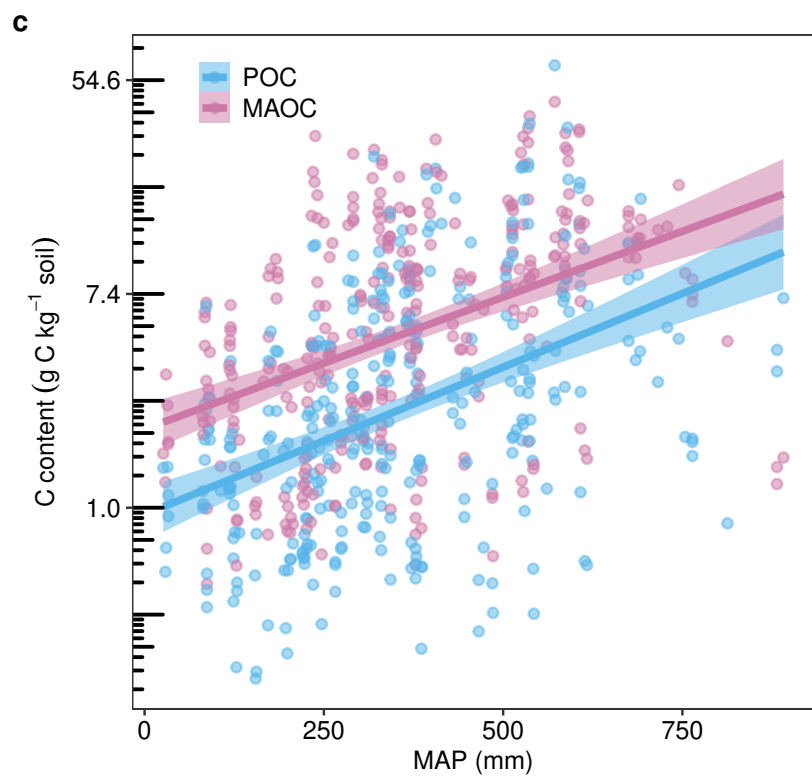
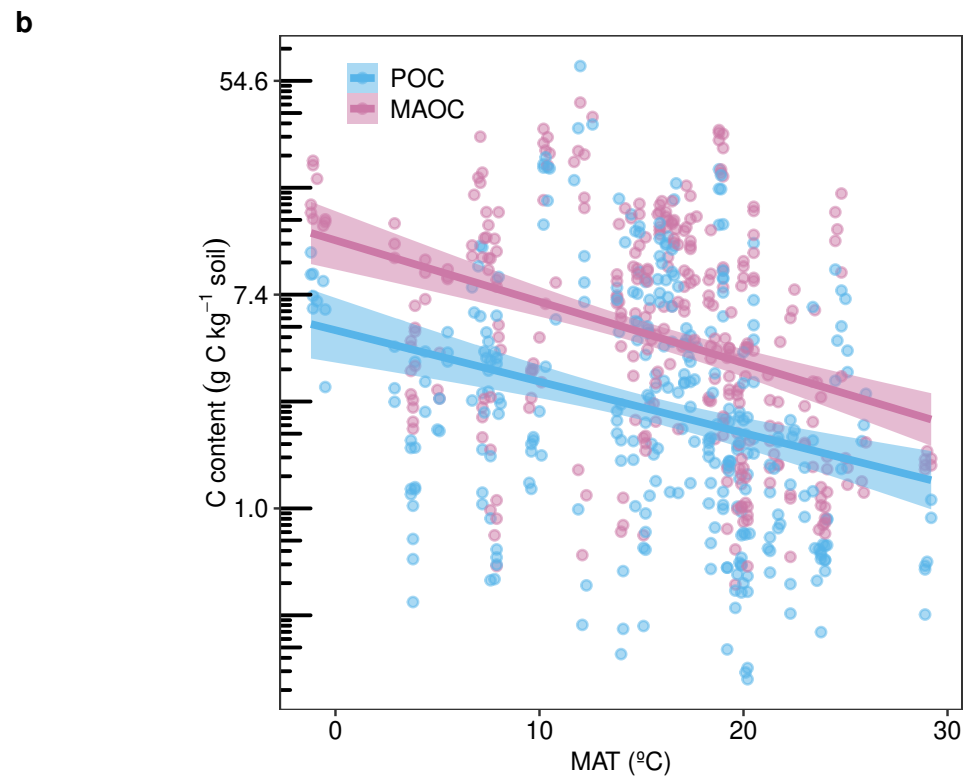
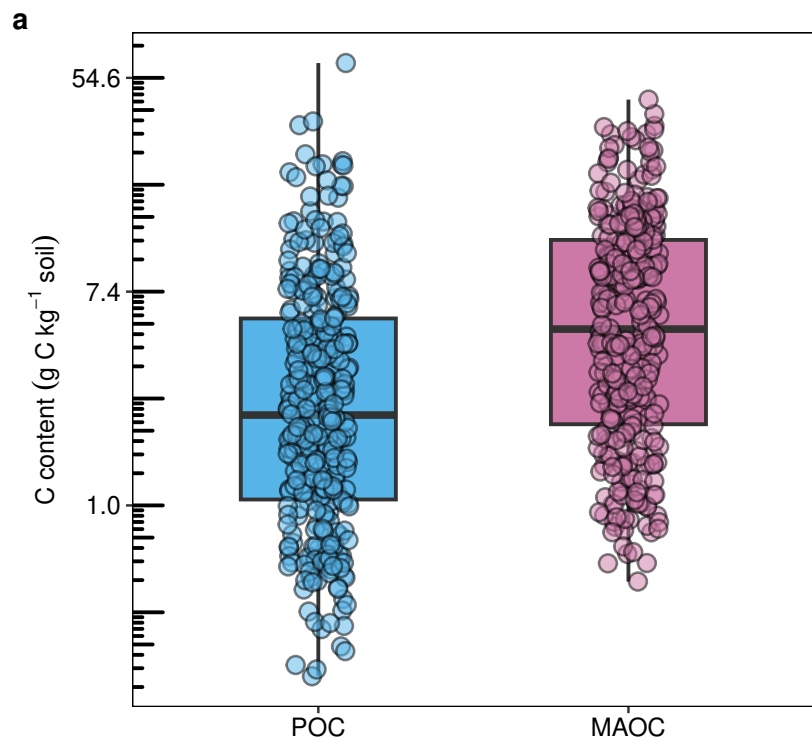
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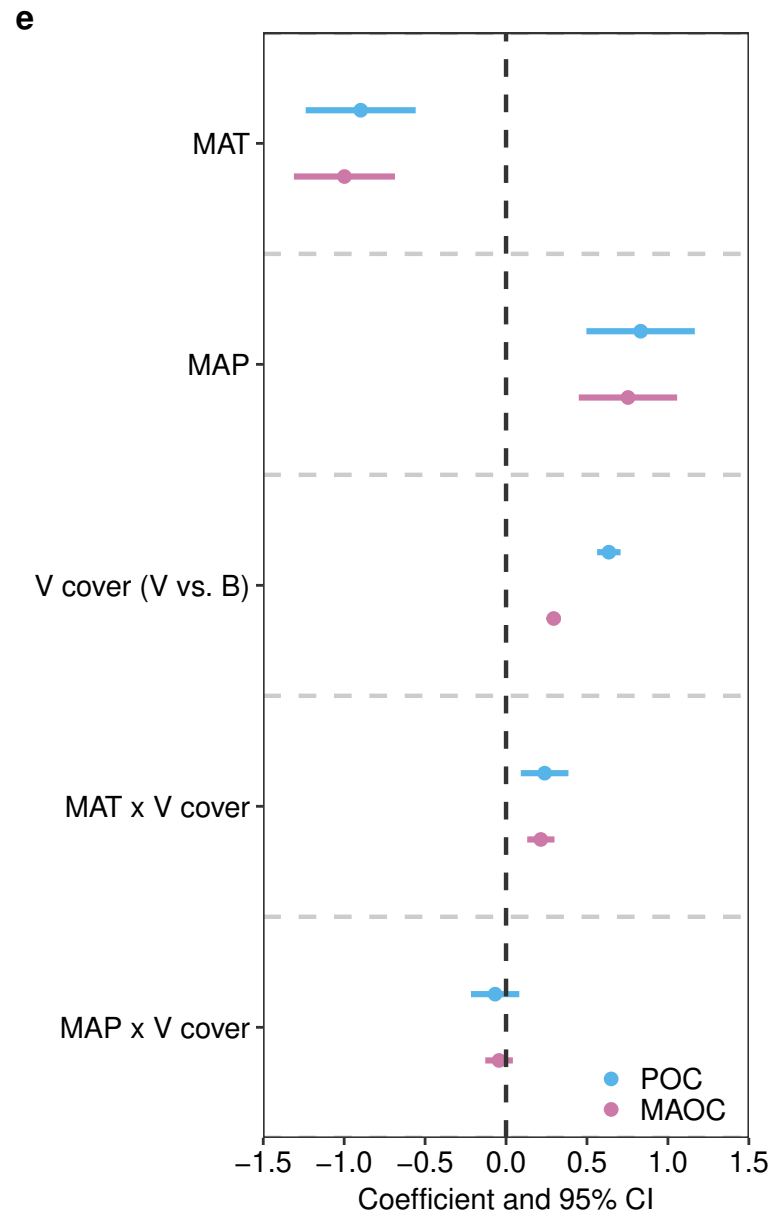
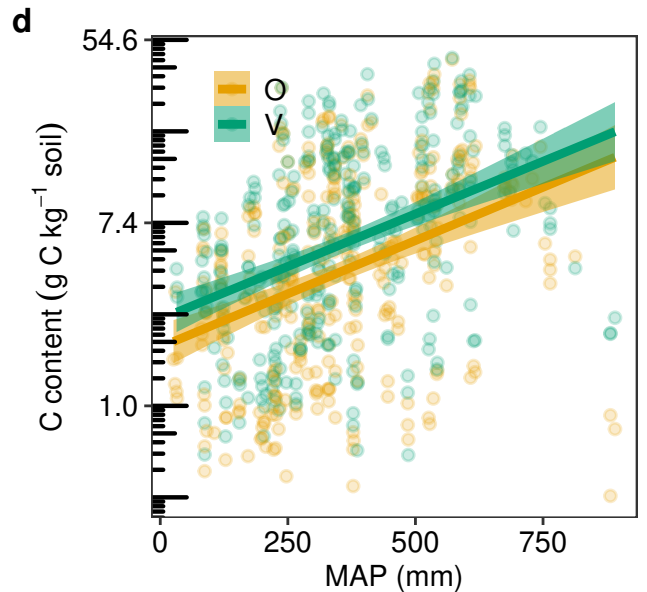
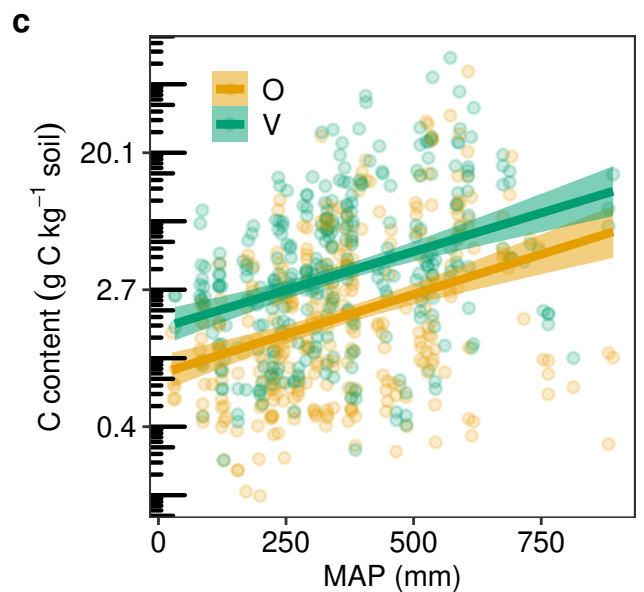
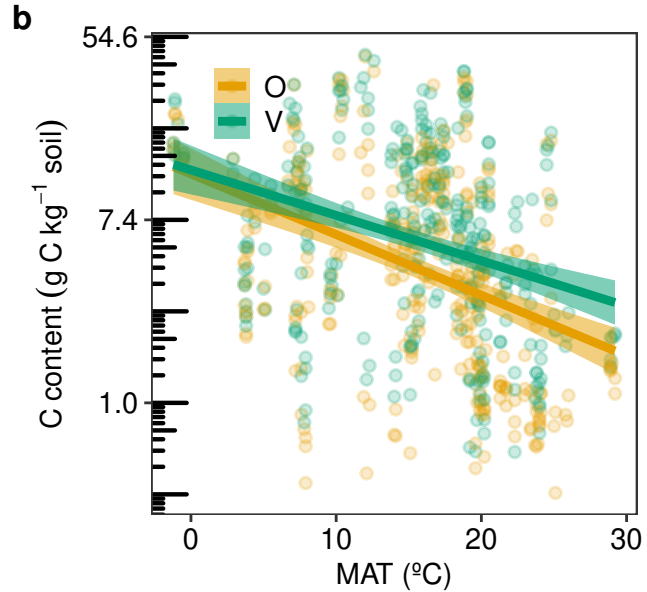
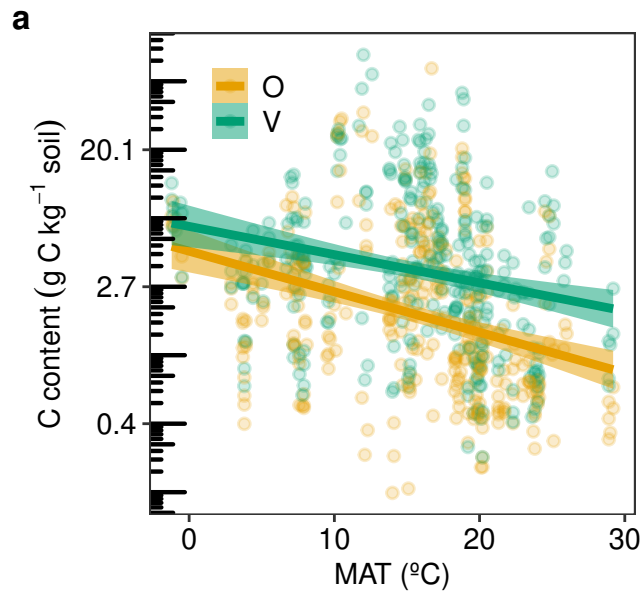
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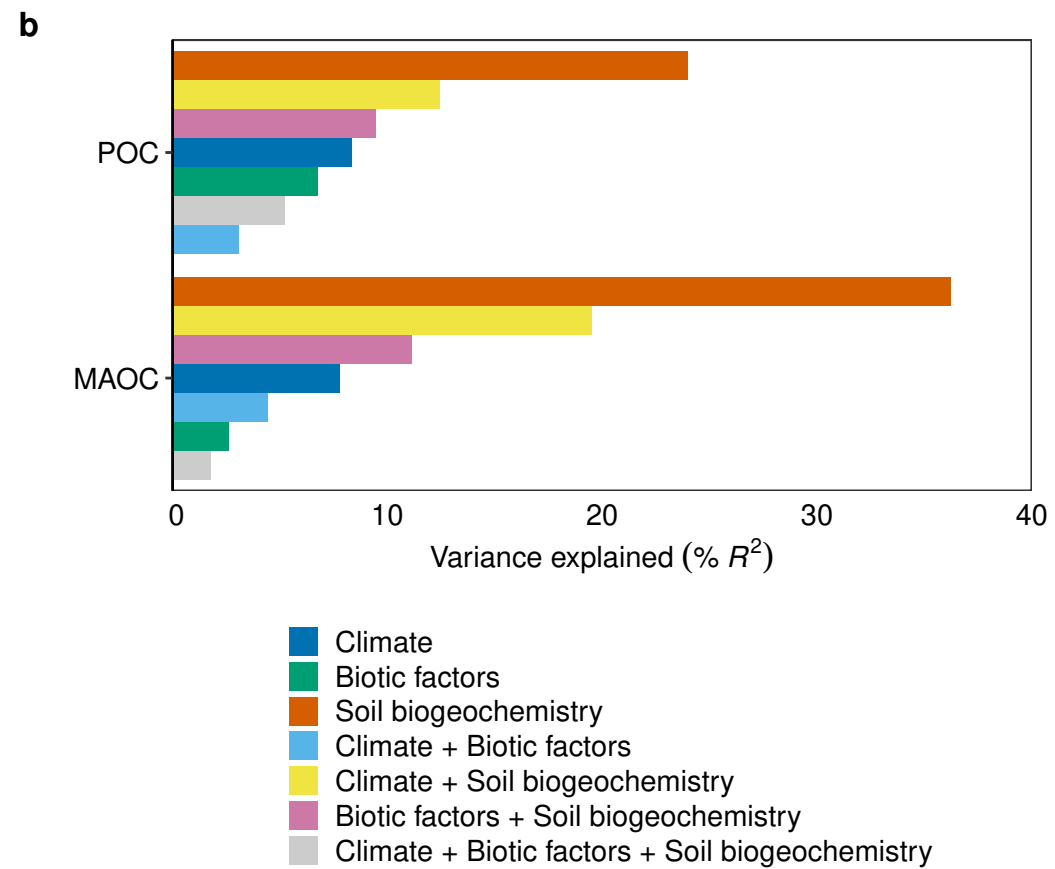
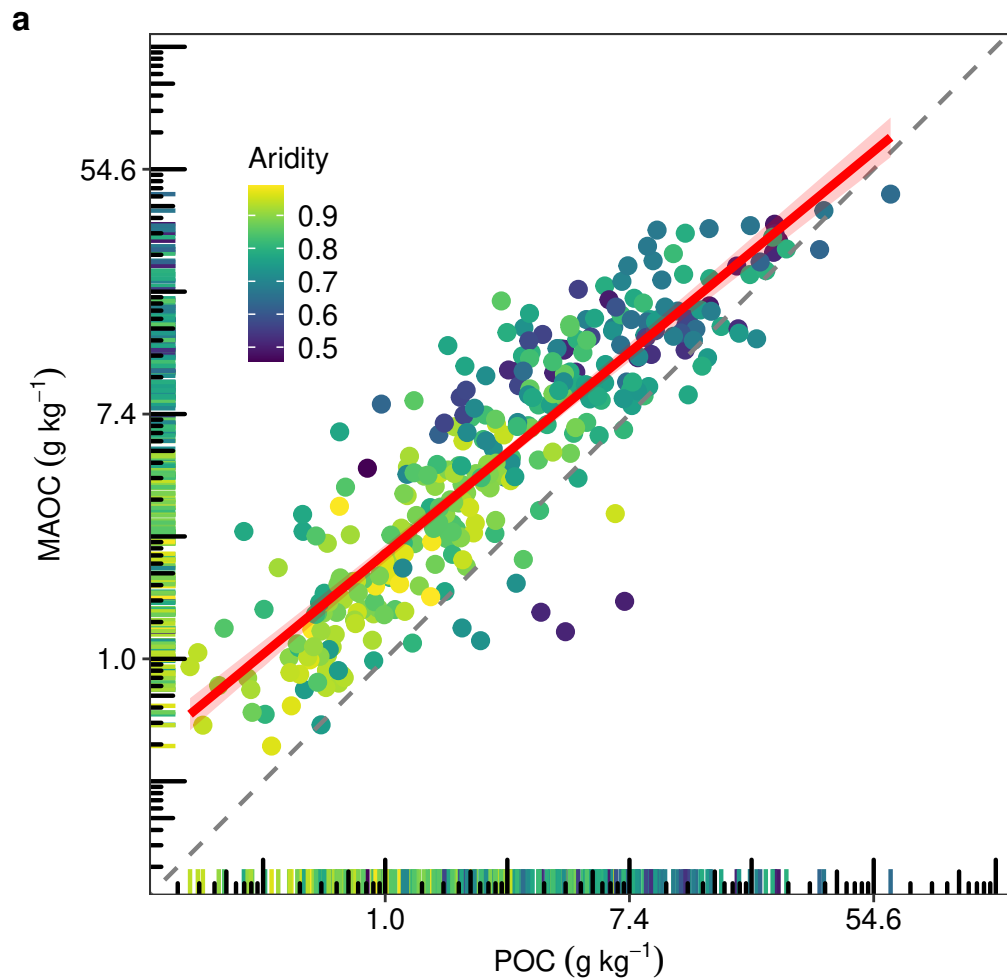
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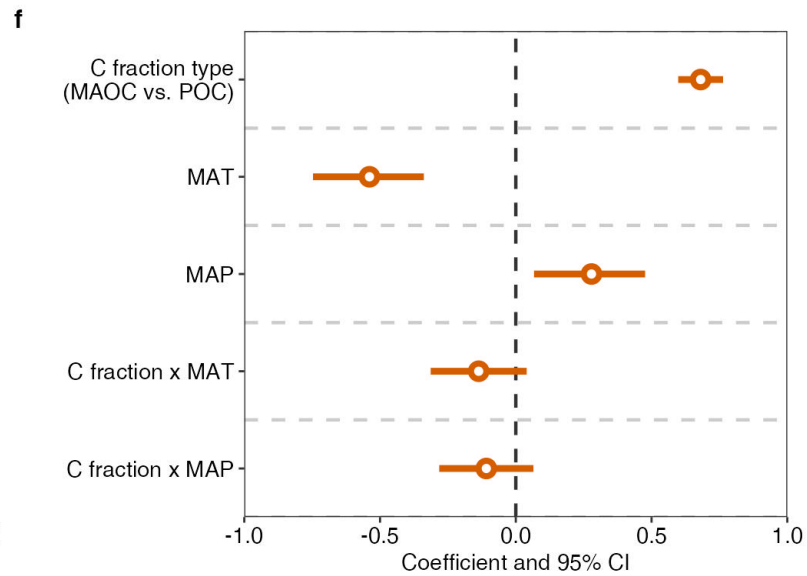
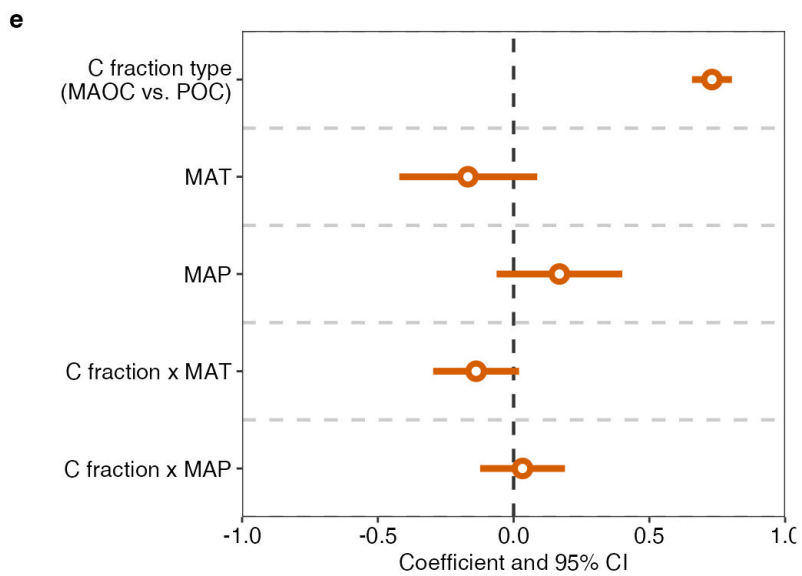
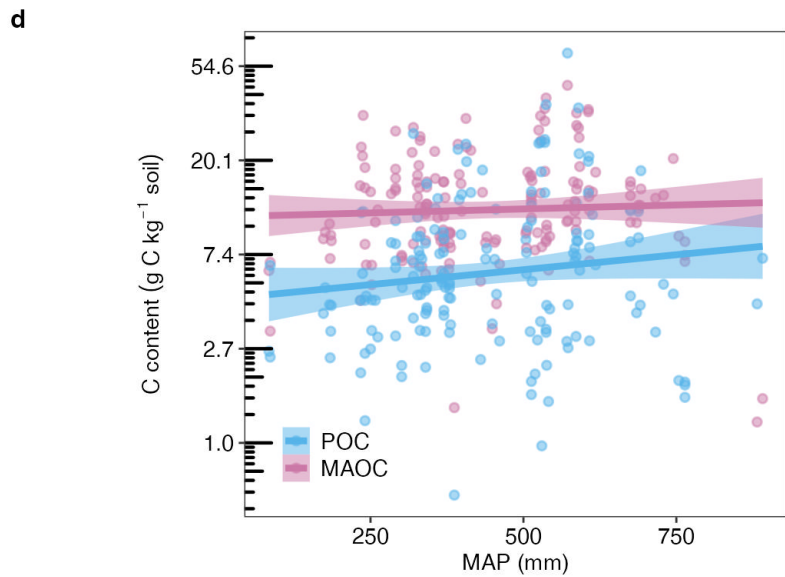
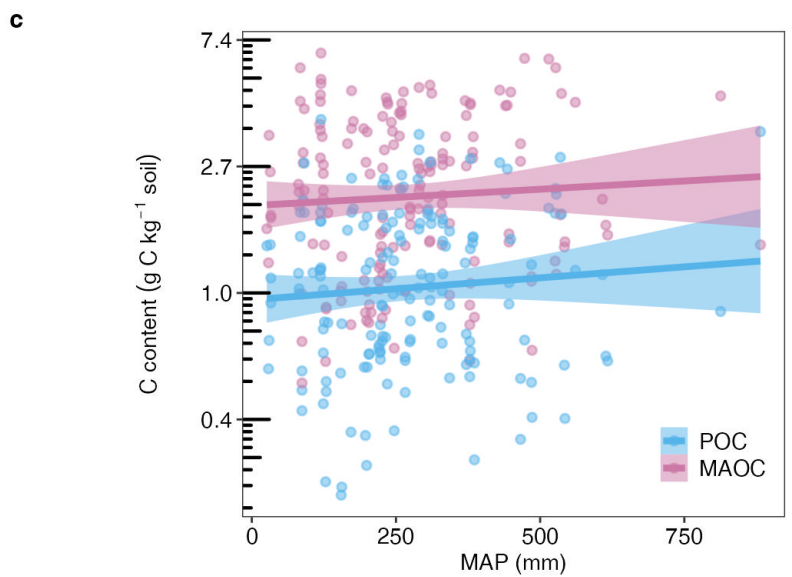
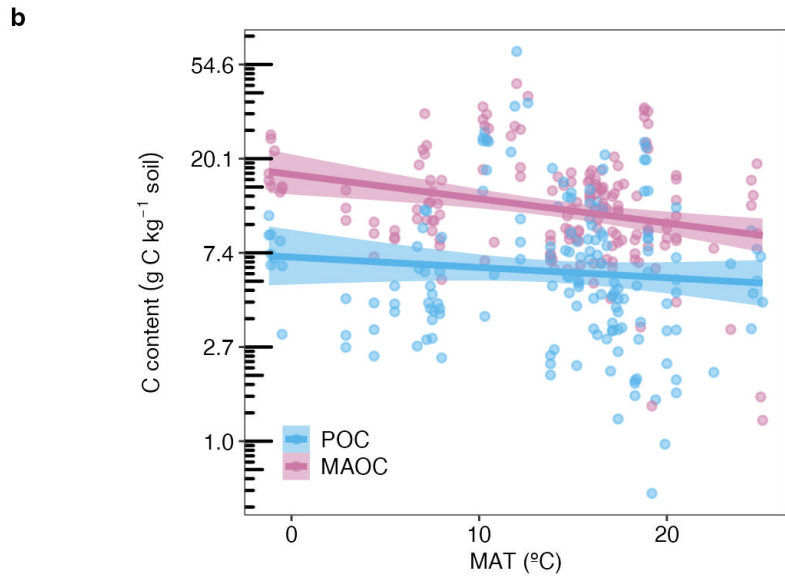
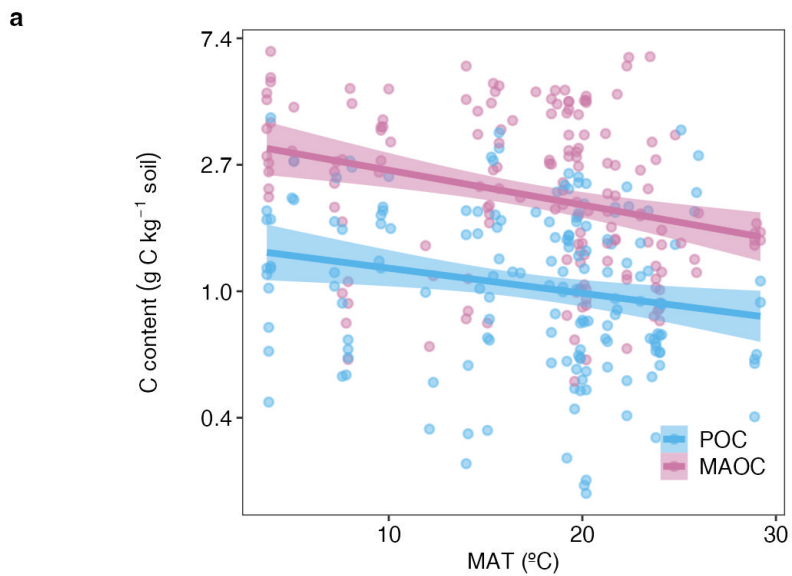
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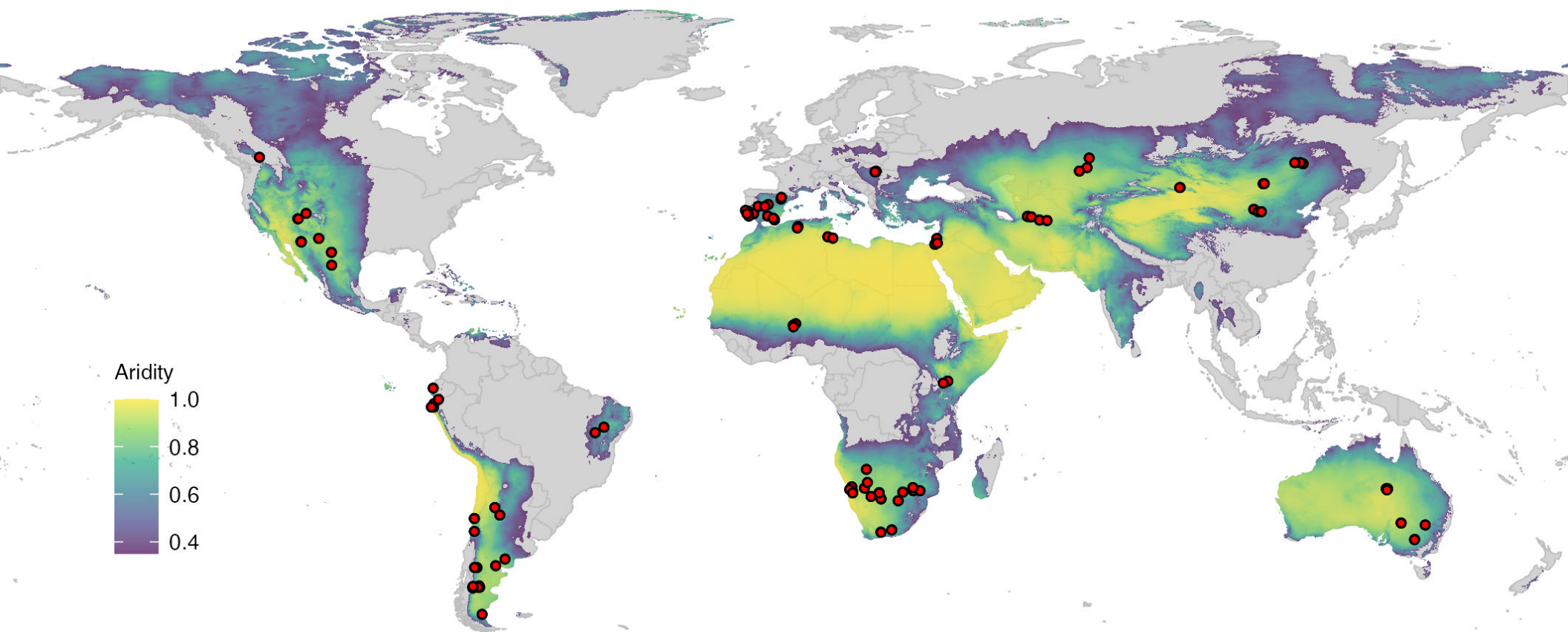
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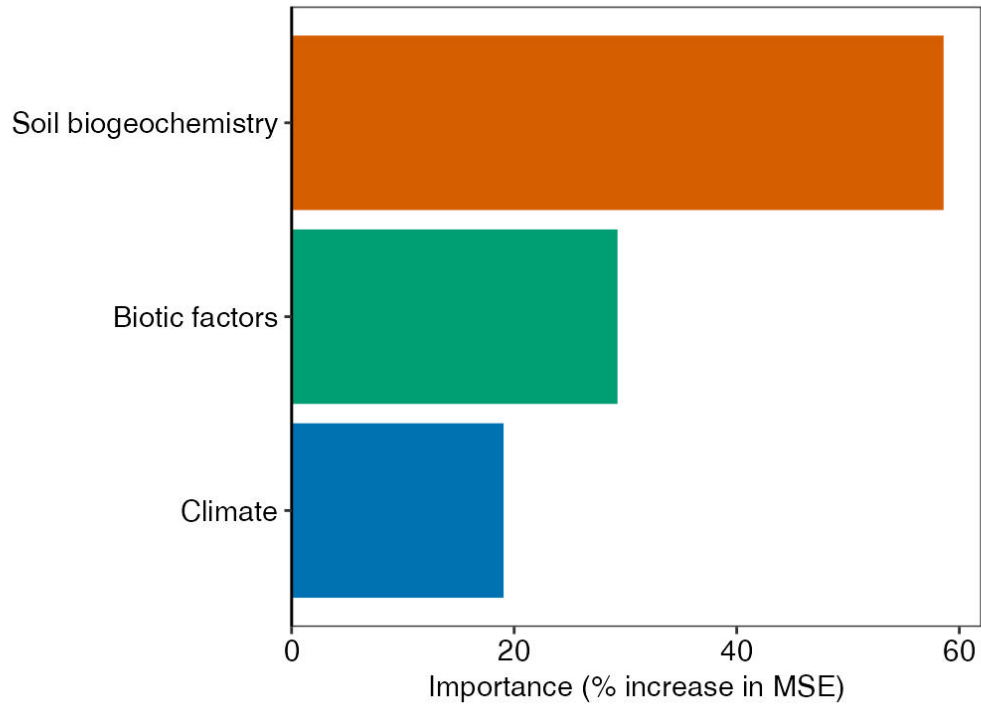




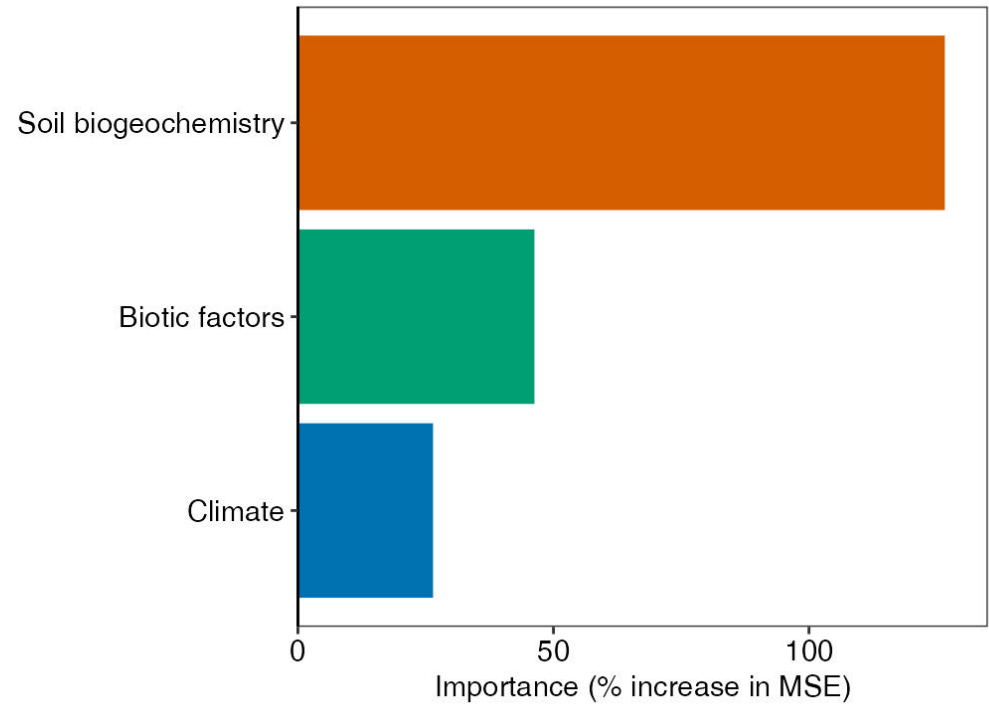


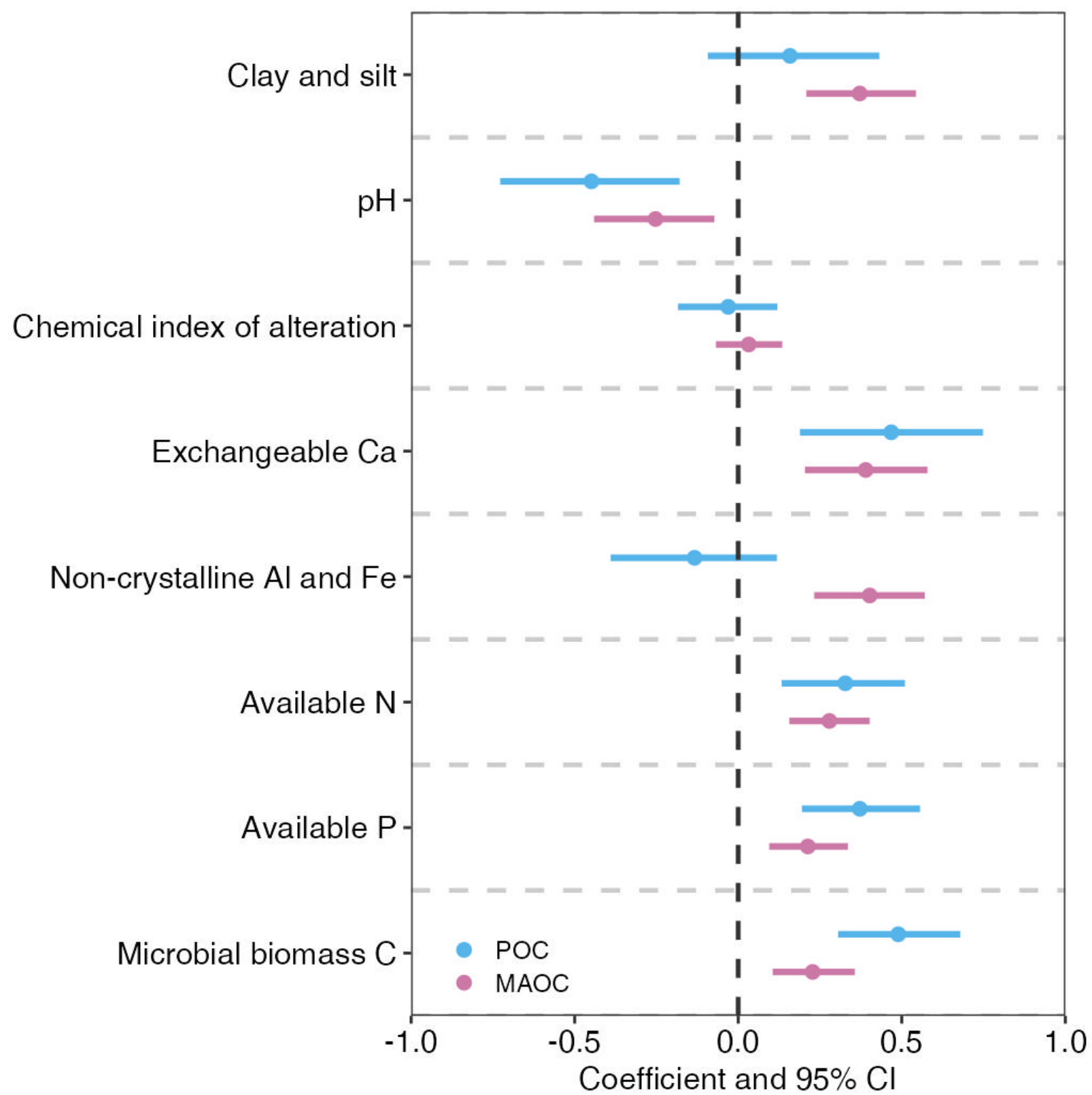


POC



MAOC





Variable	n	Min	Q1	Median	Mean	Q3	Max
MAT (°C)	326	-1.2	10.4	16.6	15.5	19.9	29.2
MAP (mm)	326	26	233	332	357	505	891
Net primary productivity (NDVI, unitless)	326	0.06	0.13	0.17	0.19	0.25	0.43
Woody cover (%)	326	0	15	46	48	83	100
Plant richness (number of species)	326	0	8	16	19	26	57
Herbivore richness (number of species)	326	0	1	2	2	3	6
Clay and silt (g kg ⁻¹)	326	10	120	271	325	512	870
pH	326	4.5	6.1	7.0	6.9	7.8	9.9
Chemical index of alteration (%)	326	42	74	81	79	87	97
Exchangeable Ca (mg kg ⁻¹)	321	39	843	1730	3394	3443	42446
Non-crystalline Al and Fe (mg kg ⁻¹)	326	28	475	932	1357	1620	9889
Available N (mg kg ⁻¹)	326	1	8	14	21	26	143
Available P (mg kg ⁻¹)	323	0.1	5.5	11.5	13.6	17.8	87.6
Microbial biomass C (mg kg ⁻¹)	326	16	101	186	245	331	1065

Variable	Category	Number of observations
Vegetation type	Grassland	94
	Shrubland	160
	Forest	72
Grazing pressure	Zero	43
	Low	88
	Medium	97
	High	98