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25 **Vulnerability of mineral-associated soil organic carbon to climate across**
26 **global drylands**

27

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

193
194 Soils in drylands—the largest set of biomes of the planet —store 646 Pg of organic C, more than
195 all living vegetation on Earth ^{1,2}. This vast soil organic C pool supports essential ecosystem
196 services, including food provision and water and climate regulation for more than 2.5 billion
197 people ^{3,4}. Yet, temperature increases and precipitation reductions forecasted for many dryland
198 regions are expected to disrupt the balance of soil organic C, accelerating microbial
199 decomposition, reducing plant C inputs into the soil, and resulting in more CO₂ emissions to the
200 atmosphere ^{5,6}.

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

204 encapsulating and adsorbing organic matter^{8–10}. Plant-derived materials at early stages of
205 decomposition are the main constituents of the mineral-unprotected, particulate organic C (POC)
206 fraction of soil organic matter⁹. The POC fraction is thus directly affected by changes in plant C
207 inputs into the soil and is more exposed to microbial decomposition than the organic component
208 of the mineral-associated organic C (MAOC) fraction, which has, therefore, a lower turnover rate
209^{11,12}. As a result, large scale meta-analyses and observational studies suggest that POC is more
210 sensitive to changes in climate, and particularly to warming, than MAOC^{7,13–16}. Because of the
211 typically large ratio of soil minerals to organic matter in drylands, MAOC is expected to
212 dominate over POC, potentially driving a high persistence of soil organic C in these ecosystems
213^{7,10,17}. However, no studies to date have examined the relationship of POC and MAOC with
214 climate across the diverse environmental gradients that characterize global drylands.

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

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

227 across drylands worldwide (Extended Data Tables 1 and 2)^{19,20}. At each site, we collected
228 topsoil samples (0-7.5 cm) from areas both covered (322) and not covered (326) by perennial
229 vegetation from two to four plots located across a local gradient of extensive grazing pressure
230 (648 samples in total, see Methods). We subjected all samples to a size fractionation procedure
231 to separate and quantify C content in POC and MAOC pools^{9,21}. Using these data, we tested the
232 hypothesis that MAOC, being protected by minerals, is less sensitive than POC to increases in
233 temperature and decreases in precipitation^{7,10,16,22}. We also hypothesize that the presence of
234 vegetation mitigates declines in soil C, particularly POC, by increasing soil C inputs.

235

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

237 Our results show that MAOC was the dominant soil organic C fraction in drylands globally (Fig.
238 1a). In particular, median MAOC content was 5.2 g C kg⁻¹ soil, equivalent to 66% of the total
239 soil organic C content, whereas median POC content was 2.3 g C kg⁻¹ soil. This quantification
240 falls within the range of soil organic C content (MAOC and POC) commonly found in drylands,
241 and is relevant to improve the performance of emerging models of soil organic C formation and
242 persistence using POC and MAOC frameworks^{2, 23-25}.

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

250 MAOC contents significantly declined with temperature at an average rate of 3.2% per °C (95%
251 confidence interval (CI): 1.8, 4.6) and increased with precipitation at an average rate of 6.6% per
252 100 mm (95% CI: 0.6, 12.6).

253 Warming accelerates the microbial decomposition of soil organic matter, and precipitation
254 reduction constrains plant production and organic matter inputs into the soil ^{5,26}. Our results are,
255 therefore, consistent with previously reported reductions in soil organic C content with
256 increasing temperature and reducing precipitation across terrestrial ecosystems ²⁷⁻²⁹. However,
257 and contrary to expectations of smaller sensitivity of MAOC versus POC to changes in climate
258 observed in more mesic systems ^{14,15}, our findings based on a space-for-time substitution
259 highlight that the MAOC and POC fractions may decrease at similar rates in response to climate
260 warming and precipitation reduction across global drylands. Therefore, they suggest that the
261 current paradigm of mineral protection may not determine soil C persistence in dryland
262 ecosystems ^{8,30-32}. The apparent lack of protection by minerals, which contrasts with what was
263 observed in mesic systems richer in organic matter, was consistent across the range of soil
264 organic C content found in drylands (Extended Data Fig. 2). There is recent evidence that
265 MAOC is controlled not only by C stabilization in soil organo-mineral complexes, but also by
266 changes in C inputs driven by climate ¹⁵. In drylands, not only precipitation reduction but also
267 warming may increase water deficit, which may decrease plant productivity ⁵, C inputs into the
268 soil and C accumulation into the MAOC fraction. These is also evidence that dryland soils
269 maintain a high oxidative potential during dry periods, mainly through the stabilization of
270 enzymes, which result in a rapid organic matter decomposition in wet periods ^{28,29} and may
271 further limit C inputs to the MAOC fraction.

272

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

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

284

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

286 We found that POC and MAOC contents were strongly correlated across global drylands ($r =$
287 0.83 , $n = 326$, $P < 0.001$; Fig. 3a). These results strongly suggest that both fractions remain
288 highly coupled in drylands despite their different levels of putative protection against
289 decomposition by microorganisms.

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

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

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

311

312 **Concluding remarks**

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

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

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

329

330

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358

359 **Author contributions**

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370 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
371 C.P. conducted laboratory research and analysis. P.D.M., E.G., and C.P. carried out data
372 analysis, after discussion, suggestions, and contributions from F.T.M., E.M.J., M.D.B., N.G.,
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375 results and contributed to editing the manuscript.

376

377 **Competing interests**

378 The authors declare no competing interests.

379

380 **Figure captions**

381

382 **Fig. 1 | Distribution of soil organic carbon (C) contents in particulate organic C (POC) and**
383 **mineral-associated organic C (MAOC) fractions and their relationships with climate in**
384 **global drylands. a**, Boxplot of POC and MAOC contents. Box, 1st, and 3rd quartiles; central
385 horizontal line, median; upper vertical line end, largest value smaller than 1.5 times the
386 interquartile range; lower vertical line, smallest value larger than 1.5 times the interquartile range
387 ($n = 326$ plots). **b-c**, Relationships between POC and MAOC contents and mean annual
388 temperature (MAT, **b**) and precipitation (MAP, **c**). Lines and shading represent linear regressions
389 and 95% confidence intervals. **d**, Summary of a linear mixed-effects model, controlling for biotic

390 factors and soil biogeochemistry (see Methods). The panel shows coefficients (circles) and 95%
391 confidence intervals (CI, bars) for main and interaction effects of C fraction type (binary
392 variable, either POC or MAOC) and climate (MAT and MAP) on POC and MAOC contents.
393 The variance explained (R^2) by the fixed and random effects relative to the total variance was
394 77% and 12%, respectively ($n = 634$ POC and MAOC observations). Carbon fraction contents
395 were natural-logarithm transformed, and all the predictors were standardized. The positive
396 coefficient of C fraction type (MAOC vs. POC) indicate that MAOC contents are significantly
397 greater than POC contents ($P < 0.001$). For the observed negative association of MAT and
398 positive association of MAP with C content ($P < 0.001$ and $P = 0.039$ respectively), negative
399 coefficients for the interaction of C fraction type with MAT and MAP indicate that increasing
400 MAT has a stronger negative effect on MAOC than on POC contents ($P = 0.053$), while
401 decreasing MAP has a stronger negative effect on POC than on MAOC ($P = 0.181$).

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

413 **Fig. 3 | Coupling and drivers of particulate organic C (POC) and mineral-associated**
414 **organic C (MAOC) in global drylands. a**, Relationship between POC and MAOC contents.
415 Dots represent individual dryland plots, with the colors of the dots illustrating their aridity ($1 -$
416 annual precipitation/potential evapotranspiration) values. The line and shading represent the
417 fitted linear regression and 95% confidence interval, respectively. **b**, Variance explained (R^2) by
418 linear mixed-effects models for POC and MAOC contents partitioned into the fraction
419 attributable to unique and shared among groups of drivers (climate: mean annual temperature
420 and mean annual precipitation; biotic factors: net primary productivity, type of vegetation,

421 woody cover, plant richness, grazing pressure, and herbivore richness; and soil biogeochemistry:
422 clay and silt, pH, chemical index of alteration, exchangeable Ca, non-crystalline Al and Fe,
423 available N and P, and microbial biomass carbon). The variance explained (R^2) by the fixed and
424 random effects relative to the total variance was 69% and 20% for POC ($n = 317$) and 84% and
425 11% for MAOC ($n = 317$), respectively.

426

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506 **Methods**

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

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

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

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

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

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

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

563 **Soil analyses.** All the bulk soil samples were analyzed as follows. Clay and silt contents were
564 determined by sieving and sedimentation ⁴³. Soil pH was measured in a water suspension at a
565 soil-to-water ratio of 1:2.5 ⁴⁴. The chemical index of alteration, which is an indicator of the
566 degree of weathering, was calculated as the molecular proportion of Al₂O₃ versus Al₂O₃ + CaO +
567 Na₂O + K₂O ⁴⁵, using total Al, Ca, Na, and K contents and after correcting Ca for soils with
568 carbonates ¹⁸; total Al, Ca, Na and K contents were determined by inductively coupled plasma
569 atomic emission spectroscopy (ICP-AES) after digestion in nitric and perchloric acids ^{44,46}.

570 Exchangeable Ca content was determined by ICP-AES after extraction with ammonium acetate
571 at pH 7.0 ^{44,47}. Non-crystalline Fe and Al contents were determined by ICP-AES after extraction
572 with acid ammonium oxalate ⁴⁸. Available N (ammonium and nitrate) content was determined by
573 extraction with 0.5 M K₂SO₄ and the indophenol blue method using a microplate reader ⁴⁹.

574 Available P content was determined by the Olsen method ⁵⁰. Microbial biomass C was
575 determined by substrate-induced respiration ⁵¹ using an automated microrespirometer ⁵².

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

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

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

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

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

628

629 **Data availability**

630 The data associated with this study are publicly available in

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

632

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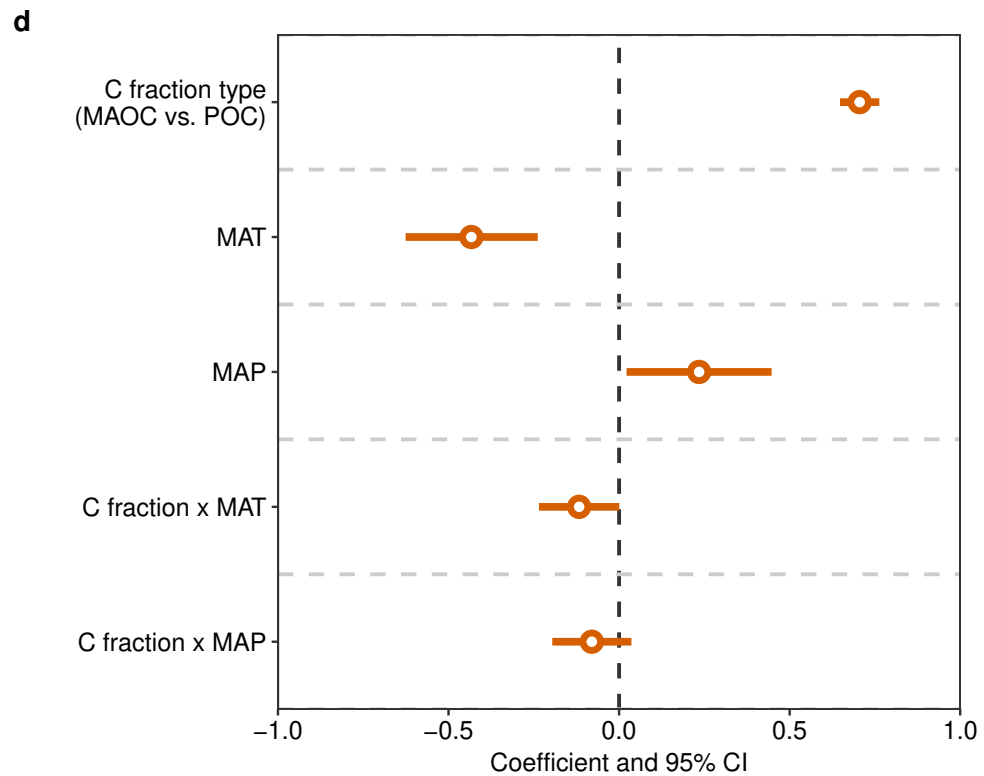
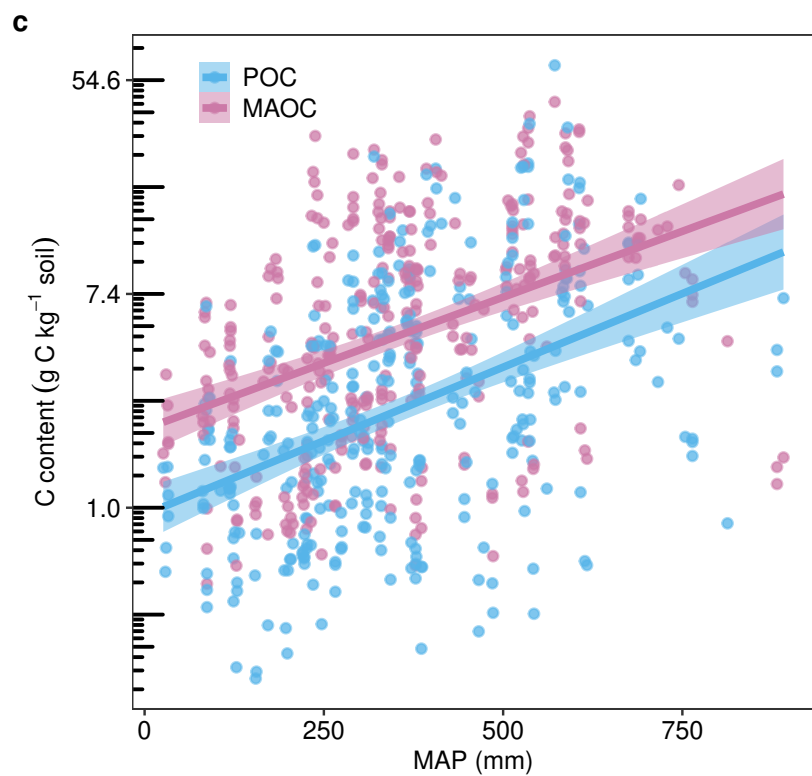
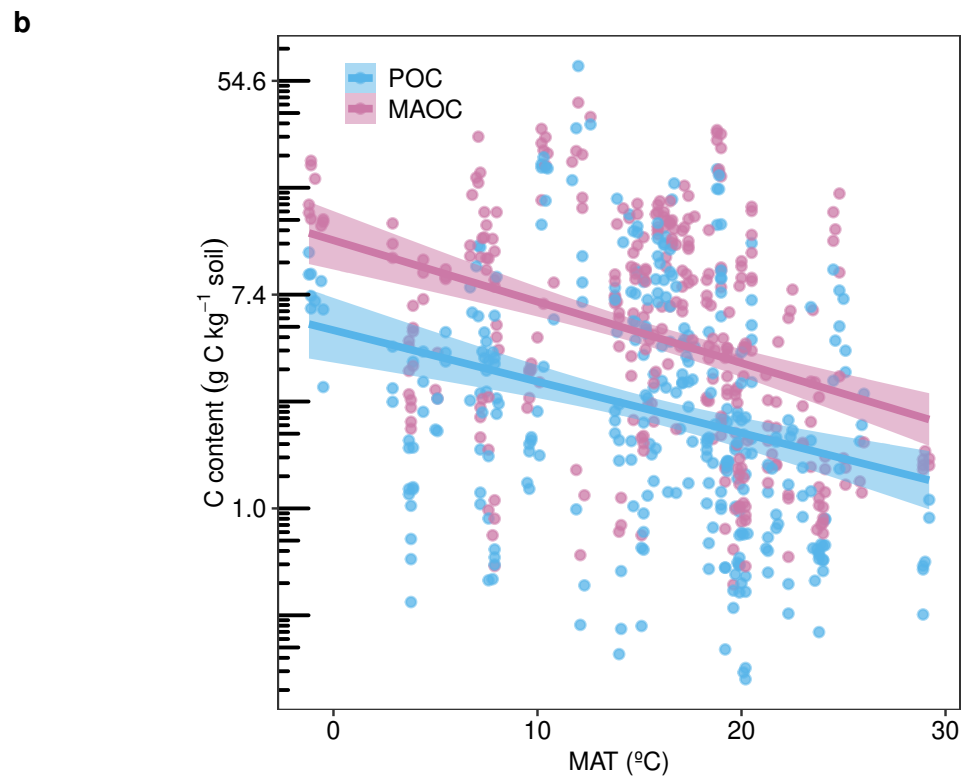
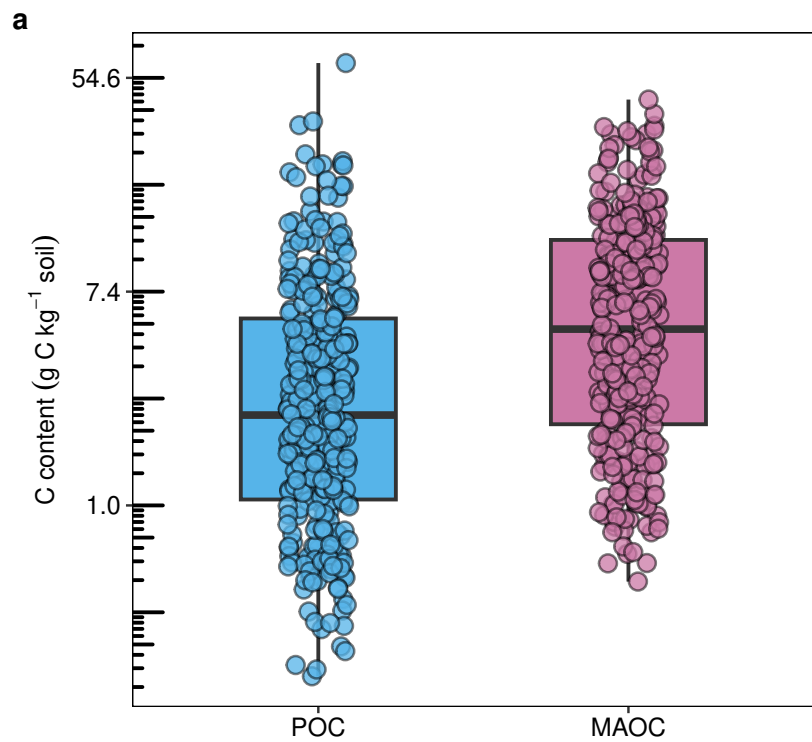
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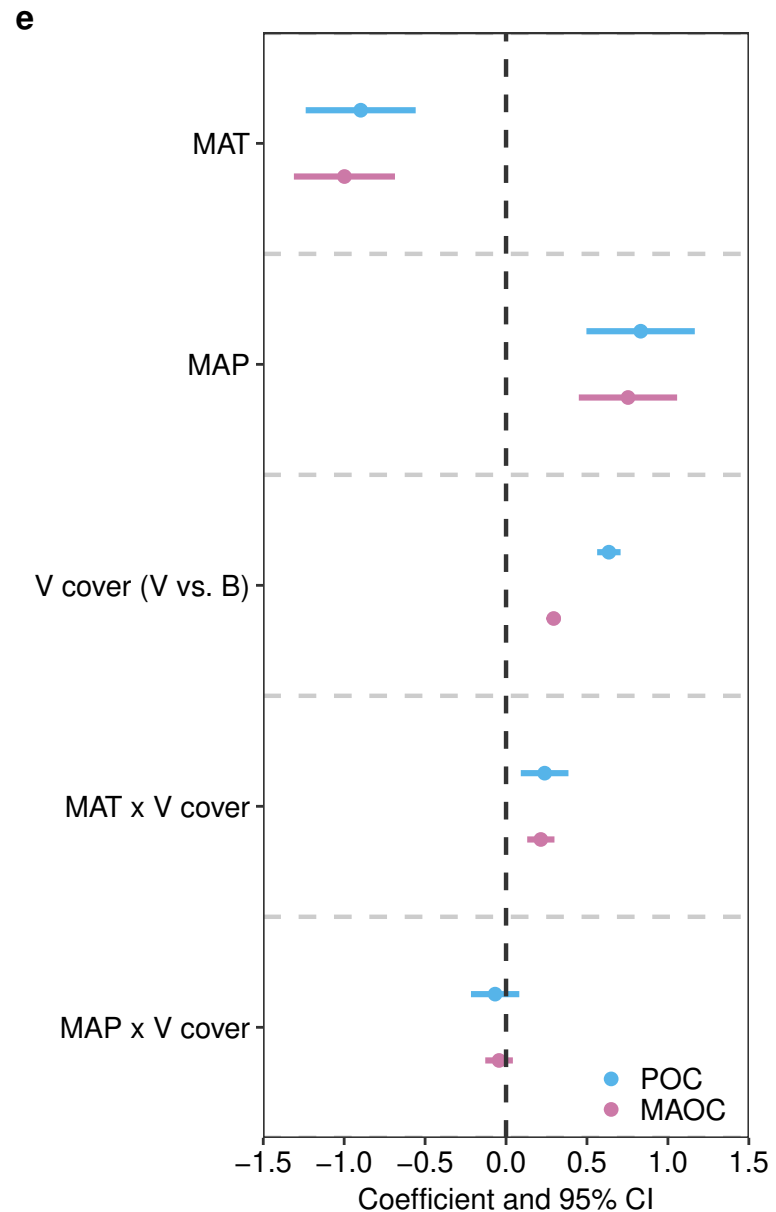
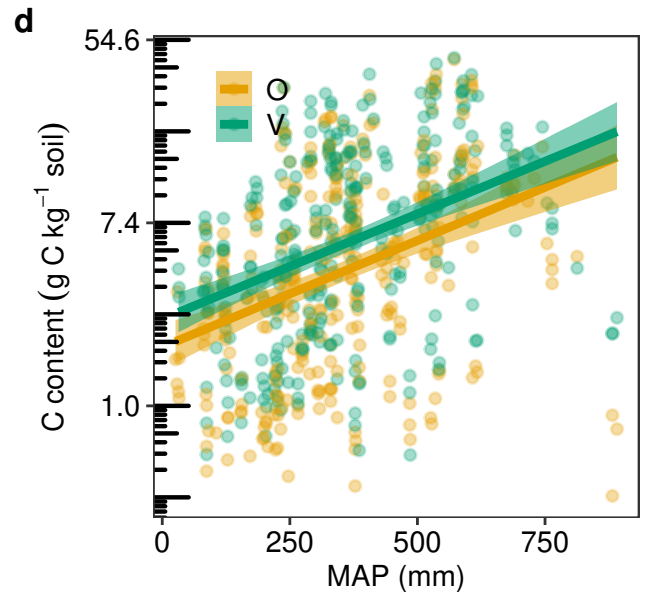
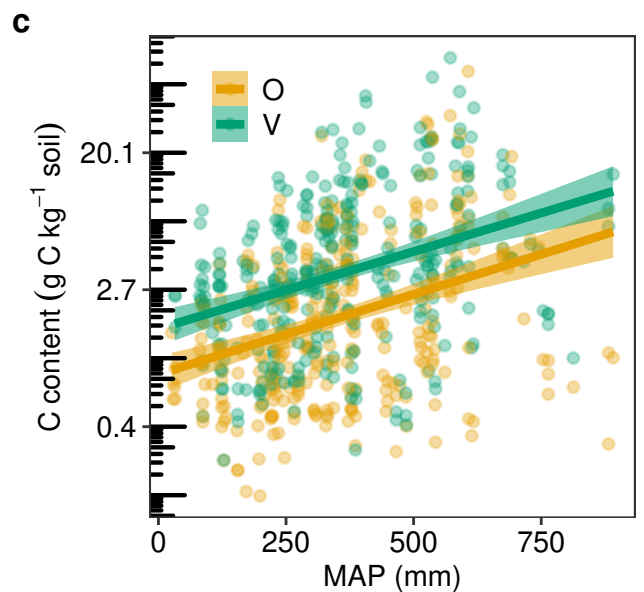
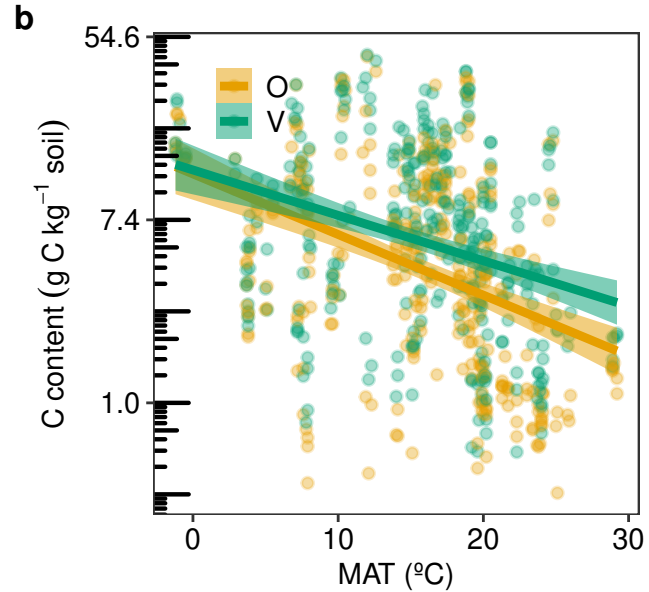
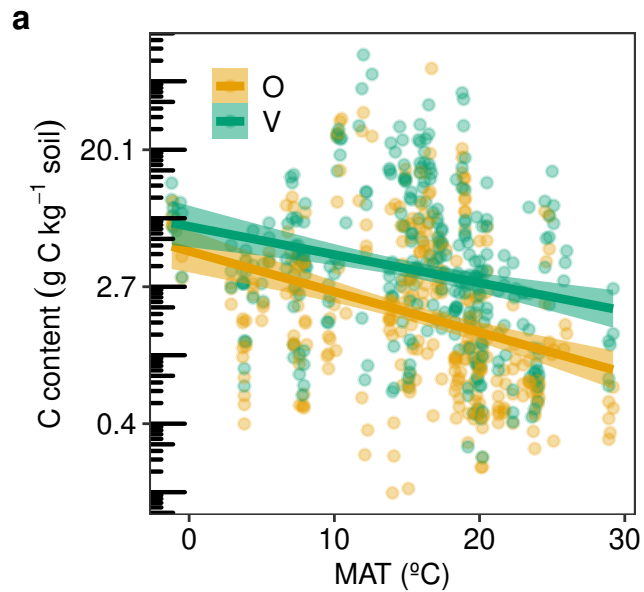
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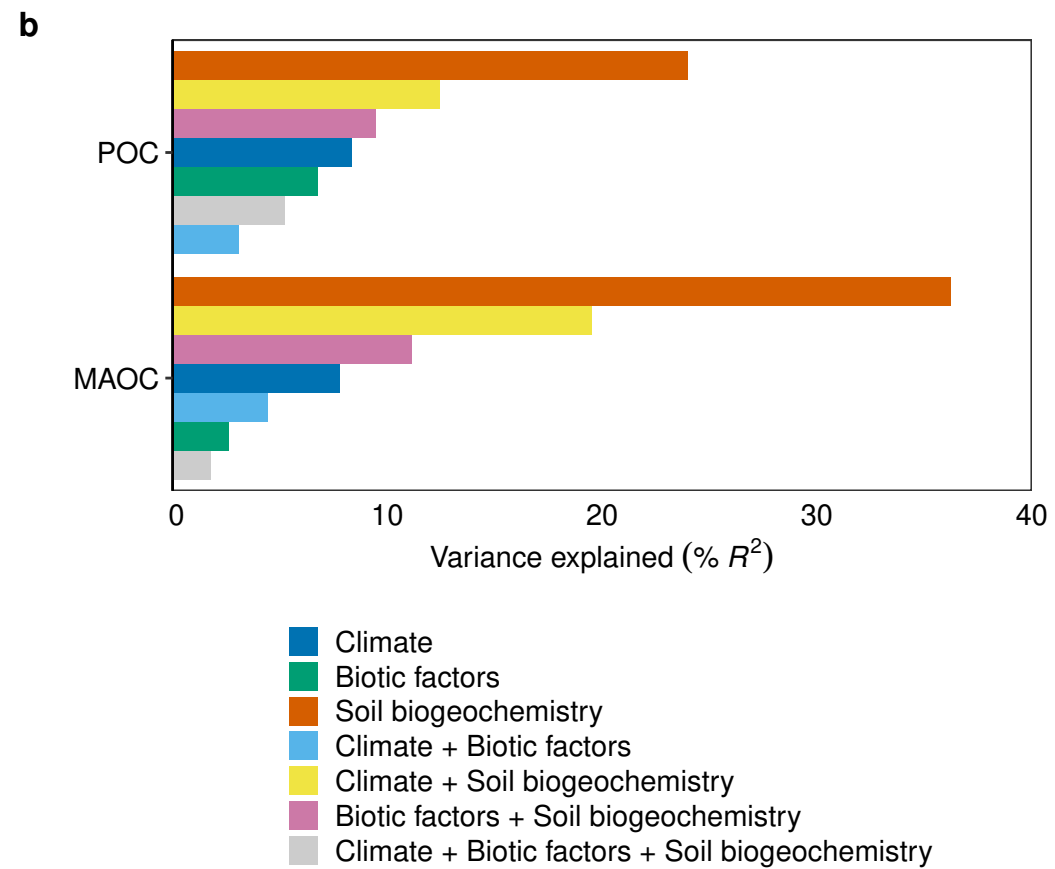
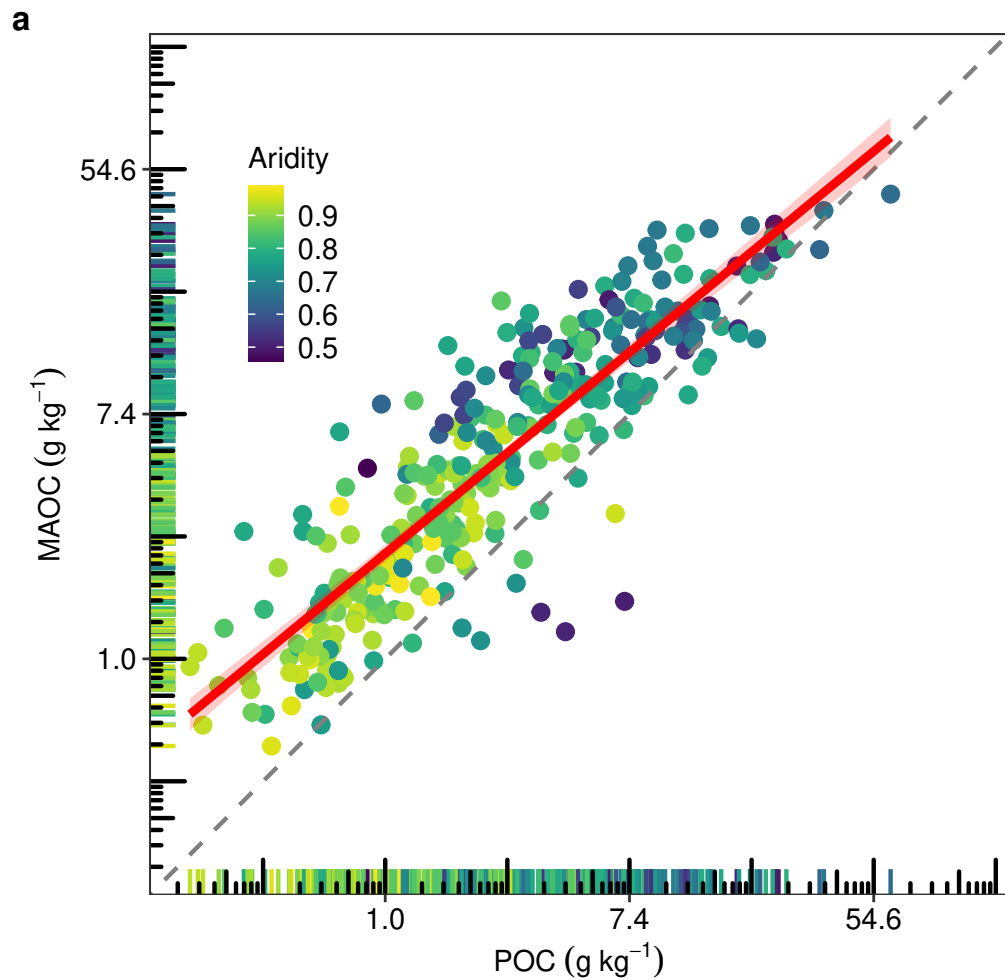
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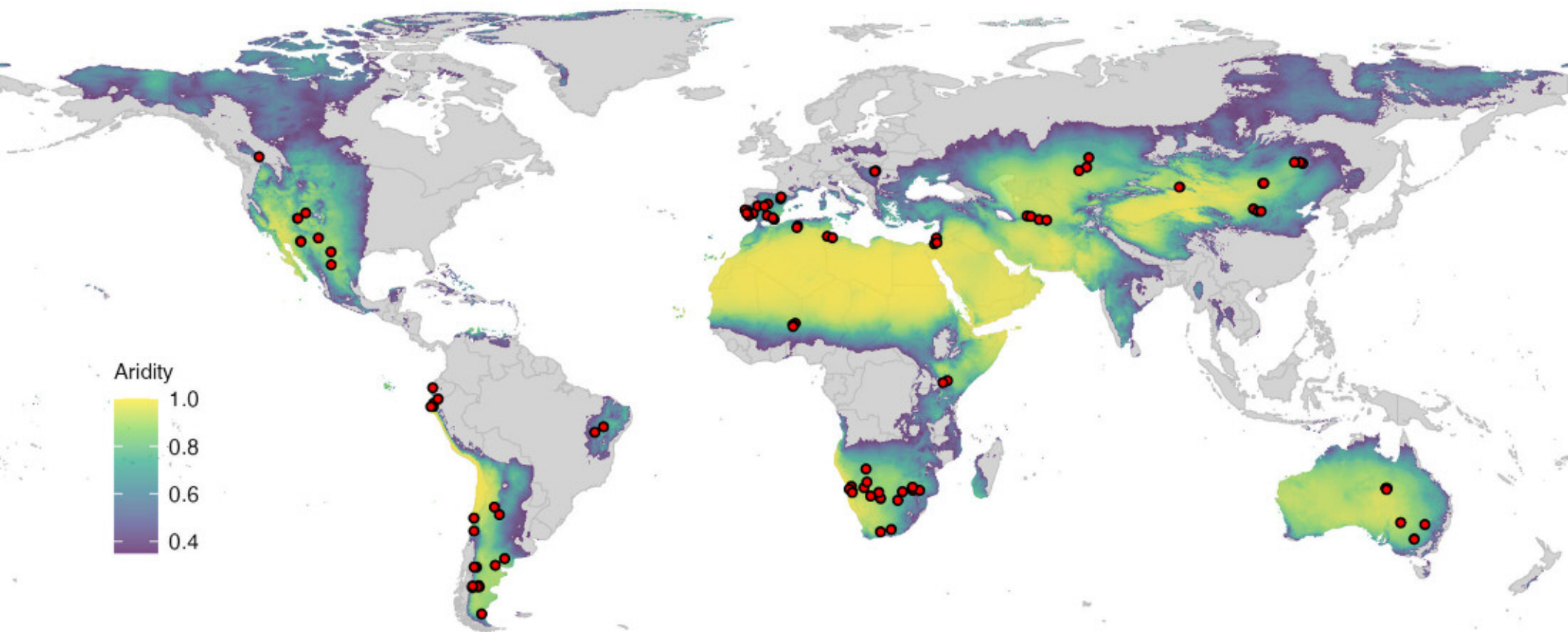
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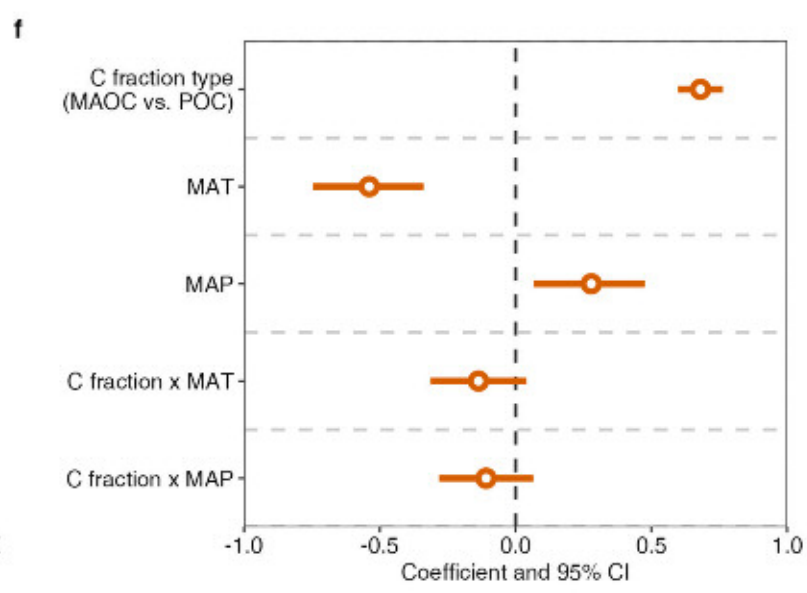
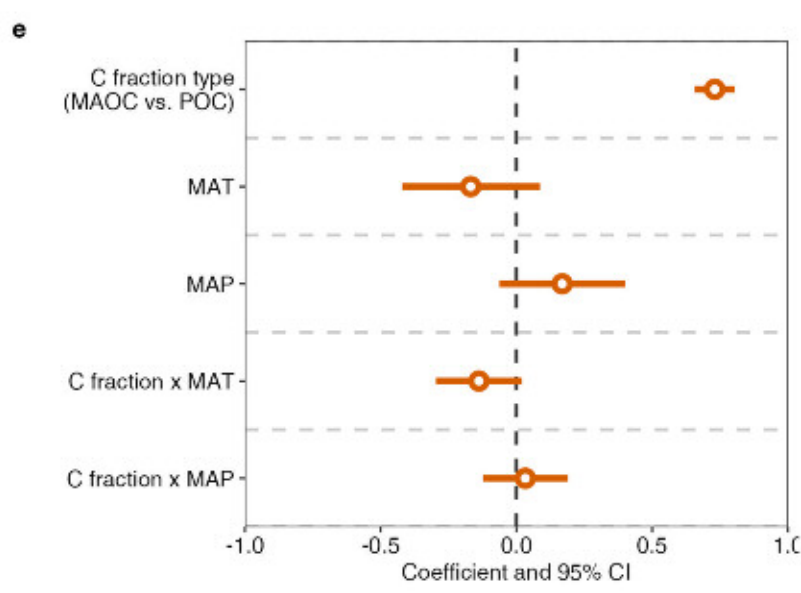
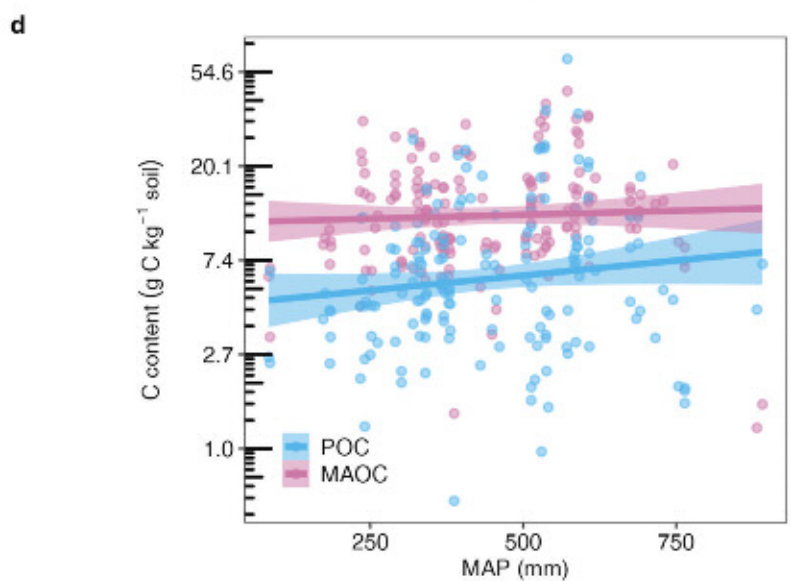
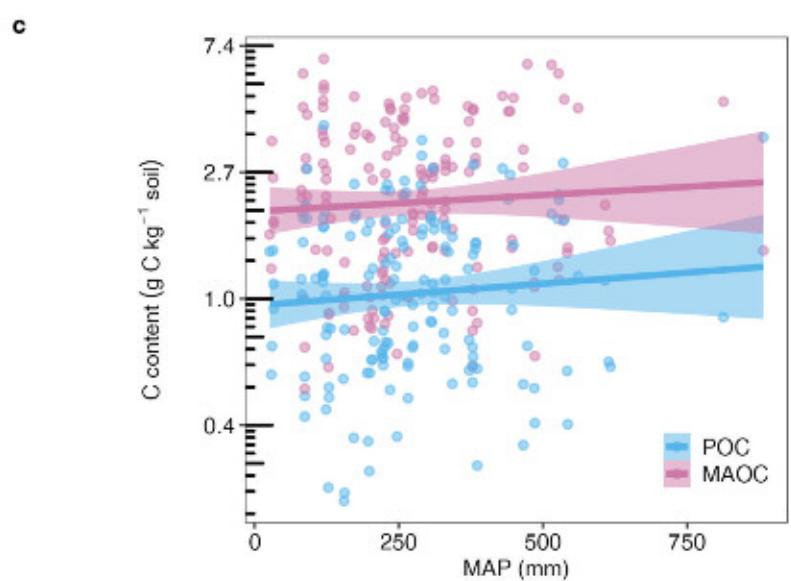
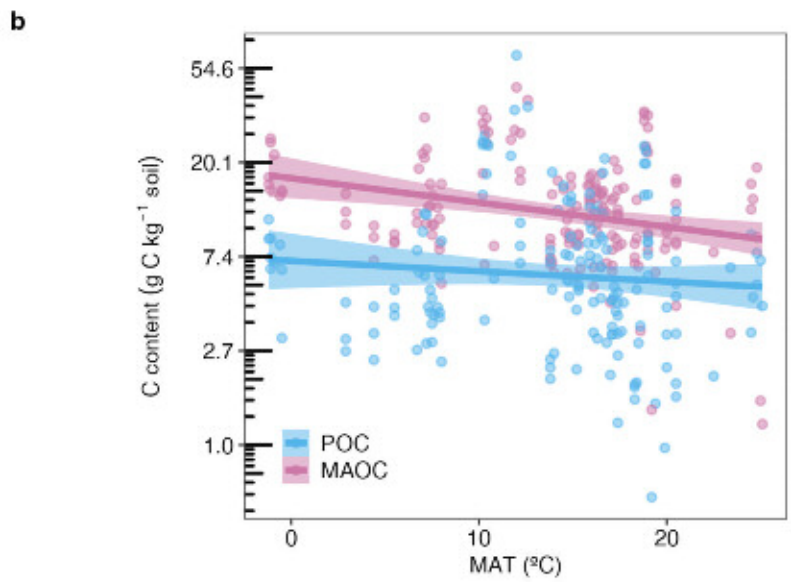
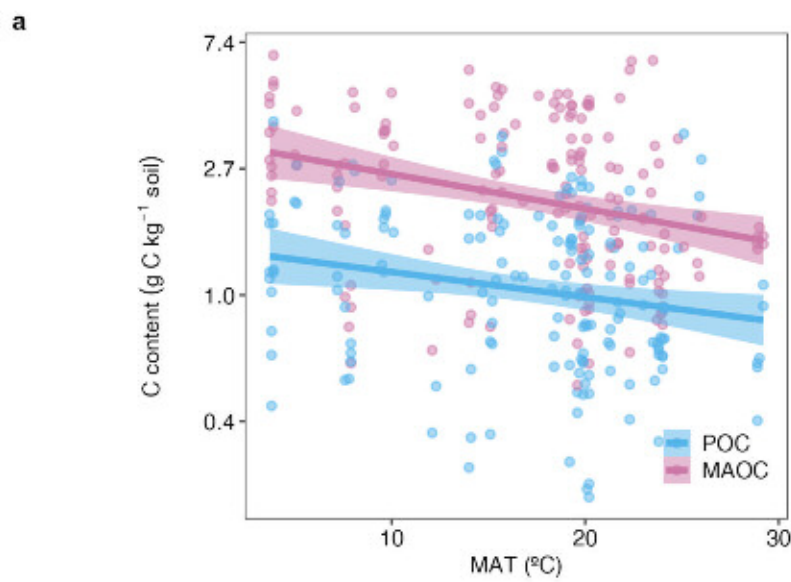
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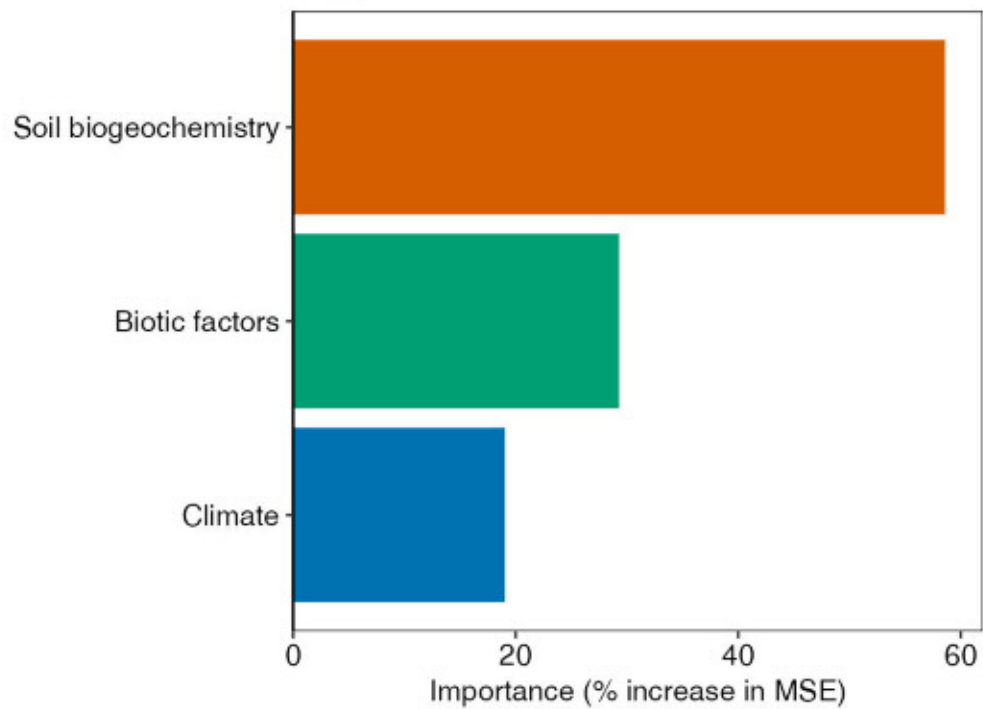




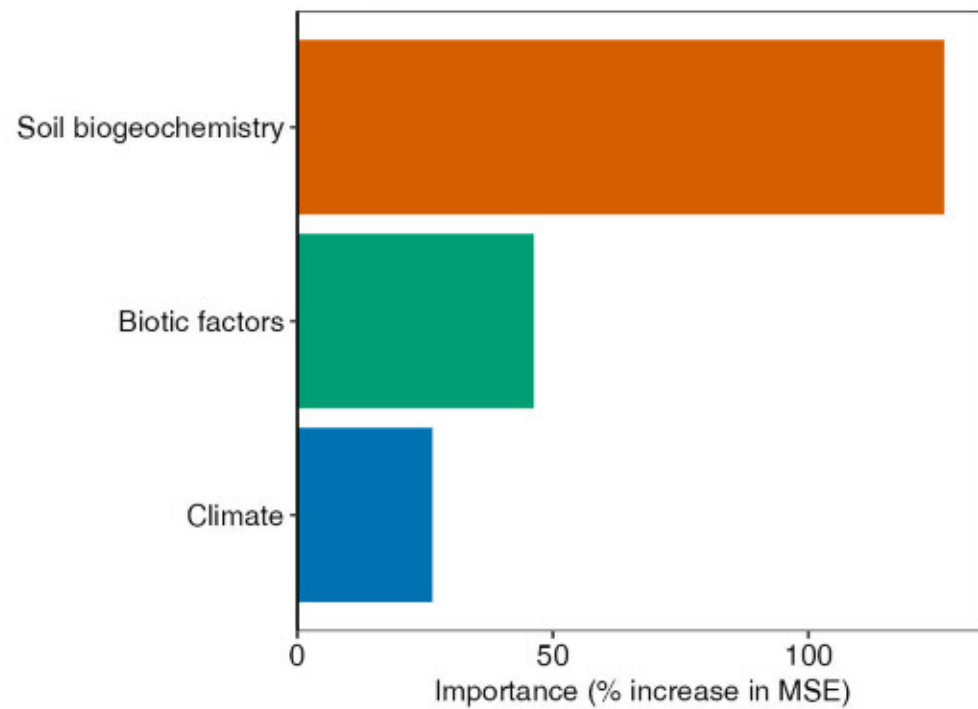


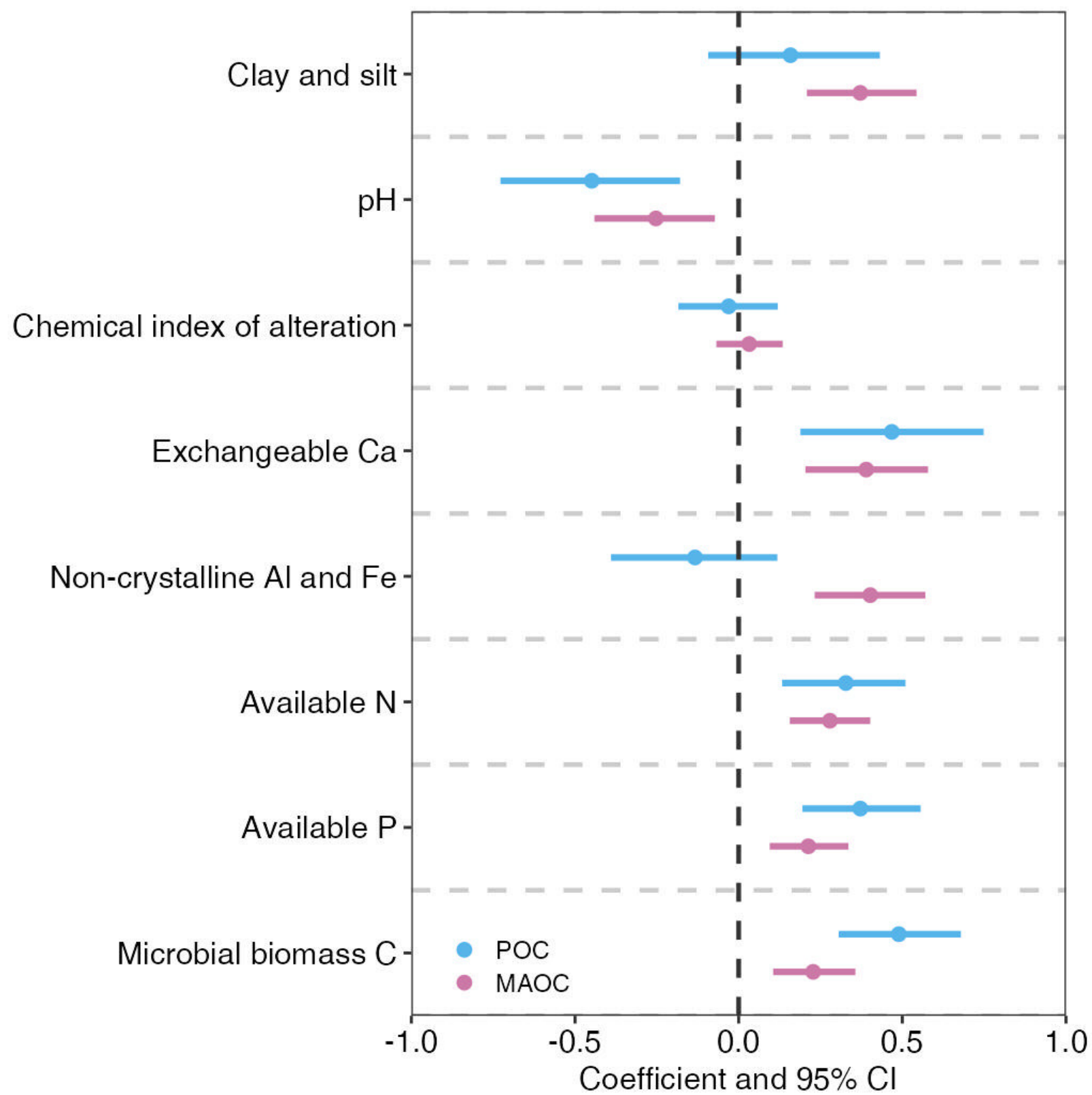


POC



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 |