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RESEARCH ARTICLE

Drivers of plant phenolic concentration across global drylands

Kaarina N. Shilula[1,2] | Hugo Saiz[3] | Emilio Guirado[4] | Nicolas Gross[5] | Yoann Le Bagousse-Pinguet[6] | Lucio Biancari[7,8] | Yolanda Pueyo[9] | Xoaquín Moreira[10] | David J. Eldridge[11] | Victoria Ochoa[12] | Beatriz Gozalo[1] | Sergio Asensio[1] | Betty J. Mendoza[13] | Enrique Valencia[14] | Miguel García-Gómez[15] | Juan J. Gaitán[16] | César Plaza[17,18] | Jaime Martínez-Valderrama[1] | Fernando T. Maestre[4]

Correspondence
Kaarina N. Shilula
Email: kshilula96@gmail.com

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Abstract

1. Plant phenolics play a key role in plant defence mechanisms against both biotic and abiotic stressors. However, their responses to environmental variables and grazing pressure across large geographical scales remain poorly understood.
2. Using data from a global survey of 325 plots spanning six continents, we examined how climatic factors, soil properties, leaf nutrients and grazing pressure shape leaf phenolic concentration in 1854 plant species (1280 herbaceous and 574 woody) across global drylands.
3. Our findings reveal that leaf phenolic concentration in herbaceous plants was mainly influenced by grazing pressure and its interactions with leaf nitrogen and iron, which together explained over 50% of observed variation across global drylands. Conversely, phenolic concentration in woody plants was strongly associated with climatic factors, particularly mean annual precipitation (MAP) and mean annual temperature (MAT), which accounted for 80% of the observed variation. While MAP had a positive effect on leaf phenolic concentration in woody plants, grazing pressure buffered this relationship by reducing the influence of MAP.
4. *Synthesis*. Our study advances the understanding of how biotic and abiotic stressors shape plant defence strategies in global drylands. Our findings shed novel insights about how plant secondary metabolites and their associated functions shift in response to changes in climate and grazing pressure, two key global change drivers with significant implications for ecosystem resilience in drylands worldwide.

KEYWORDS
climate change, global drylands, grazing pressure, herbaceous plants, leaf nutrients, leaf phenolic concentration, plant defence strategies, woody plants

For affiliations refer to page 10.

1 | INTRODUCTION

Global changes, such as increasing aridity and shifts in land use, pose significant challenges to ecosystems and plant communities (Sala et al., 2000; Watson et al., 2005). As primary producers, plants play a critical role in ecosystem functioning, and their ability to adapt to these challenges is fundamental for maintaining the resilience of terrestrial ecosystems (Chapin et al., 1998; Loreau et al., 2001). To address these challenges, plants have evolved mechanisms to tolerate or evade desiccation and damage caused by various abiotic and biotic stressors (Karban & Myers, 1989; Nguyen et al., 2016; Saraví Cisneros et al., 2022). Under stress conditions, such as increased herbivory, plants often inhibit growth and shift their primary metabolic processes towards the production of secondary metabolites (Chiapusio et al., 2018; Chowdhary et al., 2021; Jonasson et al., 1986). Among these compounds, leaf phenolics, a diverse group of carbon-based secondary metabolites, are particularly significant. Found in nearly all plant species, phenolics can constitute between 5% and 40% of dry leaf weight (Peñuelas et al., 2011). These compounds play crucial roles in plant tolerance and resistance to biotic stressors, such as pathogen infections and herbivory (Chowdhary et al., 2021; Pratyusha, 2022), and abiotic stressors, including temperature fluctuations, UV exposure, nutrient deficiencies, drought and flooding (Chowdhary et al., 2021; Jonasson et al., 1986). In response to abiotic stress, plants activate the phenylpropanoid biosynthetic pathway, resulting in high accumulation of phenolics (Naikoo et al., 2019; Nenadis et al., 2015; Sharma et al., 2019). These chemicals alleviate stress by scavenging reactive oxygen species, chelating detrimental ions, stabilising cellular membranes and safeguarding photosynthetic machinery (Naikoo et al., 2019). Phenolics also regulate essential activities like cell division, nutrient absorption, hormone equilibrium and gene expression (Naikoo et al., 2019; Sharma et al., 2019).

Climatic variations can influence leaf phenolics by changing carbohydrate production, can alter the carbon-nutrient balance and influence secondary metabolite levels (Di Ferdinando et al., 2014; Jonasson et al., 1986). Similarly, soil properties, such as water-holding capacity, influence carbon allocation patterns in plants, particularly the synthesis of chemical defences such as phenolics within plants (Hussain et al., 2020). Finally, species richness may also influence phenolic concentration through competitive interactions and niche complementarity (Loreau & Hector, 2001; Tilman, 1982), influencing plant resource allocation towards growth or defence. However, we lack a general understanding of how plant phenolic concentration responds to abiotic and biotic stressors at a global scale.

Grazing pressure also influences leaf phenolics, as leaf phenolic concentration often increases under grazing pressure, enhancing plant resistance to herbivory and serving as a temporary protective measure until nutrient levels are restored (Jonasson et al., 1986). Leaf nutrients, particularly nitrogen and iron, also impact the production of phenolics (Kołton et al., 2022). When nitrogen level is low, plants tend to allocate more resources to the production of carbon-based secondary metabolites such as phenolics, and conversely, when nitrogen is abundant, the production of carbon-based phenolics tends to decrease because some plants allocate more photosynthate towards growth rather than phenolic production (Dudt & Shure, 1994; Herms & Mattson, 1992). On the other hand, iron is involved in enzymatic processes linked to phenolic biosynthesis and redox balance under stress conditions (Kołton et al., 2022; Rout, 2015).

Research on leaf phenolics has garnered substantial interest due to their important role in ecological adaptation and evolutionary processes (Fraenkel, 1959; Kulbat, 2016; Mannino & Micheli, 2020; Stafford, 1991). However, despite their ecological importance and ubiquity, there remains a lack of comprehensive understanding about how abiotic and biotic factors influence leaf phenolic concentration across plant communities on a global scale.

Furthermore, plant responses to stressors and phenolic production often vary with life form. Herbaceous plants frequently prioritise rapid growth and reproduction, while woody plants allocate more resources to structural development and defence mechanisms (Massad, 2013). Understanding how phenolics respond to grazing pressure and environmental factors across global climatic gradients could provide valuable insights into the role of biotic and abiotic drivers on phenolic production across diverse plant functional groups.

The responses of leaf phenolic concentration to changes in abiotic and biotic stressors are of particular importance in drylands, which cover more than 40% of Earth's surface and support about 38% of the global human population (Reynolds et al., 2007). Grazing is a fundamental activity in drylands because more than 1 billion dryland inhabitants rely on livestock for their livelihoods (Neely et al., 2009), which demands substantial forage production (Adeel et al., 2005; Giridhar & Samireddypalle, 2015; Middleton et al., 2011). Forage quality is also crucial for ensuring an adequate supply of energy and nutrients for livestock (Berauer et al., 2020), and has a direct impact on livestock production and nutritional value (Ball et al., 2001). Forage quality is determined largely by leaf phenolic concentration (Horvat et al., 2022), making it an important consideration in livestock production systems. For example, high concentrations of phenolics could reduce forage protein digestibility (Skidmore et al., 2010), leading to lower feed intake and reduced animal performance (Waghorn & McNabb, 2003). Despite this, the factors affecting leaf phenolic concentration in drylands have not been widely studied so far.

Most studies of leaf phenolics in drylands to date have been restricted to local or regional scales (Chen et al., 2013; Mattera et al., 2024; Moreira et al., 2020; Saraví Cisneros et al., 2022; Varela et al., 2016). For example, warming has been shown to enhance the community-level expression of phenolic compounds in annual herbs in Mediterranean savannas (Moreira et al., 2020), while UV radiation has been identified as a primary driver of phenolic variation, rather than grazing pressure, in ecosystems such as Inner Mongolia and the Tibetan Plateau (Chen et al., 2013). Another study by Saraví Cisneros et al. (2022) conducted in Patagonian rangelands assessed phenolic profiles in tall and medium evergreen shrubs and grasses. They found that, across morphotypes, phenolic structural complexity was conserved despite large differences in concentration and richness. However, no study has simultaneously evaluated how grazing pressure and environmental factors shape leaf phenolics across global drylands. Doing so is critical for understanding how forage quality may shift under global change and for better understanding physiological plant responses to biotic and abiotic stressors.

Here we used a global survey conducted on 325 plots in dryland ecosystems from six continents in 25 countries (Algeria, Argentina, Australia, Botswana, Brazil, Canada, Chile, China, Ecuador, Hungary, Iran, Israel, Kazakhstan, Kenya, Mexico, Mongolia, Namibia, Niger, Palestine, Peru, Portugal, South Africa, Spain, Tunisia and the United States of America) (Maestre, Eldridge, et al., 2022). This survey included 1854 plant species (574 woody and 1280 herbaceous), and we evaluated how climate and grazing —two key drivers of desertification, along with soil properties and plant biodiversity attributes influence leaf phenolic concentrations. We considered key predictors of phenolics (Albert et al., 2009; Chen et al., 2013; Dudt & Shure, 1994; Moreira et al., 2020; Muzika, 1993), including climatic variables (mean annual precipitation, MAP; mean annual temperature, MAT), soil attributes (water-holding capacity), plant nutrient contents (macro- and micronutrients), biodiversity (plant species richness) and grazing pressure. We aimed to identify the main drivers of leaf phenolics across dryland sites and to explore interactive effects between grazing pressure and other environmental variables (climate, leaf nutrients and soil properties) on phenolic concentrations. We hypothesised that both grazing pressure and an increase in temperature would increase the concentration of leaf phenolics as a response to herbivory and environmental stress, as observed across local and regional scales (Chen et al., 2013; Moreira et al., 2020; Saraví Cisneros et al., 2022). We also hypothesised that grazing pressure would influence leaf phenolics more in herbaceous (grasses, herbs and forbs) than woody (trees and shrubs) plants, as herbaceous plants usually prioritise rapid growth and reproduction, while woody plants allocate more resources to structural support and defence mechanisms. Furthermore, herbaceous plants in drylands are generally preferred and grazed more than woody plants, withstanding greater consumption pressure (Biancari et al., 2024).

2 | MATERIALS AND METHODS

2.1 | Study sites and grazing gradients

This survey was conducted at 98 study sites located in 25 countries from six continents except Antarctica. At each of the 98 study sites, two to four 45 m × 45 m plots located across a local grazing pressure gradient (ungrazed and low, medium and high grazing pressure) were surveyed. These grazing gradients were established either by placing plots at different distances from artificial water points to determine the grazing gradient or by setting up grazing exclosures (see (Maestre, Bagousse-Pinguet, et al., 2022) for details). The distance from water points is known to be a good proxy of grazing pressure in drylands from all around the world (Pringle & Landsberg, 2004; Stumpp et al., 2005; Tefera et al., 2007). The plots were established in areas representative of the vegetation found at each site, with soils derived from the same parent material and sharing the same soil type whenever possible, to avoid undesirable confounding factors, such as having different soil types between plots subjected to varying grazing intensities (Maestre, Eldridge, et al., 2022). Additional details on study site selection and environmental characteristics can be found in Maestre, Bagousse-Pinguet, et al. (2022). Mean annual precipitation (MAP) and mean annual temperature (MAT) of each site were obtained from WorldClim 2.0 (www.worldclim.org) (Fick & Hijmans, 2017). The study sites had a range in MAP from 26 mm/year to 891 mm/year, and MAT from −1.2 to 29.2°C.

To confirm our local grazing gradients and to quantify grazing pressure in situ, we estimated it using a combination of herbivore dung/pellet counts, dung mass per unit area and the number and size of livestock tracks, following the protocol described in Maestre, Bagousse-Pinguet, et al. (2022). Recent grazing pressure by large herbivores (e.g. cattle, buffalo, zebra) was determined by counting dung in two 25 m^2 (5 m × 5 m) quadrats located along each 45 m transect. For smaller herbivores (e.g. rabbits, goats, sheep), pellets were counted within smaller 1 m × 1 m quadrats (Maestre, Eldridge, et al., 2022). The dung and pellets were separated into herbivore types using experts or field guides (Hess, 1954; Triggs, 1996). Dung and pellet mass were calculated at each plot by either taking direct measurements or by counting dung/pellets. In plots where dung/pellet mass was low or where the main herbivores did not produce clearly defined pellets, all dung and pellets in the quadrats were collected, dried, weighed and expressed as a mass per hectare for each herbivore type (Maestre, Eldridge, et al., 2022; Sheidai-Karkaj et al., 2022). The total oven-dried mass of dung per hectare for each herbivore was therefore calculated (Maestre, Eldridge, et al., 2022). Historic grazing was determined by quantifying the size and density of livestock tracks (Landsberg et al., 2002; Maestre, Eldridge, et al., 2022), as the intensity and size of livestock tracks are said to be useful indicators of the history of livestock grazing (Pringle & Landsberg, 2004; Val et al., 2018). The width and depth of all livestock tracks crossing each of the 45 m transects were measured to derive a total cross-sectional area of tracks for each site; this was done to determine the historical pressure intensity. Local grazing pressure gradients at the surveyed sites result mainly from livestock, primarily involving goats, sheep and cattle. However, wild herbivores, including kangaroos, deer, zebras, antelopes, elephants, rabbits and giraffes, were also observed in the surveyed plots. In dryland rangelands, the coexistence of wild herbivores and livestock is common (Acebes et al., 2016; Mizutani et al., 2012). The analyses of dungs/pellets and livestock tracks confirmed our local grazing gradients (from ungrazed to high), see Maestre, Eldridge, et al. (2022) for a full description.

No specific permits were required to conduct the fieldwork associated with this study. However, all shipments of leaf and soil samples were carried out in accordance with national and international regulations. Export permits were obtained in each country when required, and all shipments entering Spain were accompanied by the corresponding import permits issued by the Spanish Ministry of Agriculture, Fisheries and Food.

2.2 | Vegetation surveys

At each plot, we placed 2–4 transects separated by 10 m each (see Maestre, Eldridge, et al., 2022). At each transect, 25 (1.5 m × 1.5 m), consecutive quadrats were placed. Within these quadrats, the cover of every perennial species in relation to the quadrat size was visually estimated (to 1%). In total, 100 quadrats were sampled within each plot. Total plot-level species plant richness was determined by counting the unique perennial plant species identified in the quadrats.

Plant phenolic concentration was assessed on the tallest individual of each perennial plant species within 20 quadrats, randomly chosen from the 100 quadrats surveyed per plot (5 quadrats per transect). This means that, in theory, up to 20 individuals of a species could be sampled per plot, but the actual number of replicates per species depended on how frequently it occurred in the sampled quadrats. This approach allowed for representative sampling of dominant and co-dominant species across diverse dryland ecosystems (Gross et al., 2024). For each selected individual, the youngest mature, undamaged leaves were collected from the top. In the field, the harvested leaves from the same individuals were placed in a wet paper towel and stored in a labelled plastic Ziploc bag with a small amount of water to avoid desiccation. These plastic bags were placed in a cooling box before being transported to the laboratory. Once in the laboratory, the plastic bags with leaves were stored in a dark refrigerator before being analysed, ideally within 48 h of sampling (Maestre, Eldridge, et al., 2022). The leaves were thereafter oven-dried for 48 h at 40°C, ground with liquid nitrogen and stored at room temperature prior to chemical analysis. Drying at this temperature halts enzymatic activity and preserves secondary metabolites such as phenolics (Chua et al., 2019). While we acknowledge that phenolic profiles can be sensitive to post-harvest conditions, previous work (e.g. Lattanzio et al., 2006; Salminen & Karonen, 2011) supports the stability of total phenolic concentration in oven-dried tissue.

The total phenolic content was determined colorimetrically using the Folin–Ciocalteu method (Moreira et al., 2020; Waterman & Mole, 1994). Specifically, phenolics were extracted from 20 mg of plant tissue with 70% methanol in an ultrasonic bath for 15 min, followed by centrifugation (Moreira et al., 2020). The total phenolic concentration was then measured using a Biorad 650 microplate reader (Bio-Rad Laboratories, PA, USA) at 740 nm, with tannic acid serving as the standard. Each sample was tested in three technical replicates to account for variations due to the experimental procedure, and phenolic concentration was expressed on a dry weight basis. To investigate the effects of environmental factors, grazing pressure, leaf nutrients and soil parameters on plant phenolics at the community level, total phenolics were measured across all species and then converted to community-weighted mean (CWM) (Moreira et al., 2020). Due to the global scope of this study, many species were sampled only locally and therefore have low sample sizes. Consequently, the statistical power to infer variability across sites is limited for most taxa. For this reason, our analyses and interpretations focused on community-weighted and trait-based metrics rather than species-specific trends.

The leaves used for phenolic analyses were also used for leaf nutrient analyses. Leaf nutrients such as nitrogen, phosphorus, potassium, calcium, magnesium, manganese, copper, zinc and iron were extracted using an open-vessel wet digestion method with nitric-perchloric acid. The extracted elements were then suspended in water and quantified using inductively coupled plasma optical emission spectrometry (Hesse, 1971; Kuo, 1996) with a Perkin Elmer Optima 4300 DV instrument (Perkin Elmer, Waltham, Massachusetts, USA; Maestre, Bagousse-Pinguet, et al., 2022).

2.3 | Soil properties

Soil sampling was carried out in all the plots surveyed for vegetation during the dry season (soils were dry at the time of sampling). Soil sampling followed a stratified random approach. In each plot, five 50 cm × 50 cm quadrats were randomly positioned beneath the canopy of the dominant perennial vegetation (based on percentage cover) and in open areas without perennial vegetation, resulting in a total of 10 quadrats per plot. From each quadrat, a composite topsoil sample was created by collecting five 145 cm^3 soil cores (from a depth of 0–7.5 cm), which were bulked and homogenised in the field. Upon field sampling, soil samples were put in Ziploc bags (one sample per bag) labelled with the plant species under which they were sampled and put in cooler ice packs to transport to the laboratory (where possible). See (Maestre, Bagousse-Pinguet, et al., 2022; Maestre, Eldridge, et al., 2022) for additional details on how the soil survey was conducted.

To measure water-holding capacity, 10 g of dry soil per sample was weighed and placed in a funnel lined with moist filter paper. Each sample then received 10 mL of deionised water, and the funnels were covered with parafilm to prevent evaporation. The soils were allowed to drain for 24 h into a test tube. After this period, the soils were weighed again to determine their water-holding capacity (Maestre, Bagousse-Pinguet, et al., 2022).

2.4 | Statistical analyses

The community weighted mean (CWM) of total leaf phenolics for each plot was calculated using the *weighted.mean* function in R software, version 4.2.3 (R Core Team, 2023). This calculation used species-level phenolic values, weighted by the relative cover of each species. Initially, individual total phenolic measurements were averaged at the species level, followed by the calculation of plot-level estimates as community mean trait values (Mean j):

$$\text{Mean}\ j = \sum_i^n piTi$$

Here, *pi* and *Ti* represent the relative abundance and the trait value of species *i* in plot *j*, respectively, and S represents species richness in plot *j* (Lavorel & Garnier, 2002; Pérez-Harguindeguy et al., 2013).

To compare leaf phenolic contents between woody and herbaceous plants, we used plot-level community-weighted mean (CWM) values calculated for each plant group at each plot. Descriptive statistics, including the range (minimum and maximum) and mean phenolic concentration, were derived from these plot-level estimates using Microsoft Excel. The range was determined by identifying the minimum and maximum CWM values within each plant group, and the mean was calculated as the average across all plots for woody and herbaceous plants, respectively. Additionally, a *t*-test was performed to determine whether the differences in mean phenolic concentration between woody and herbaceous plants were statistically significant.

All quantitative predictor variables, such as mean annual precipitation (MAP), mean annual temperature (MAT), soil water-holding capacity, leaf carbon, leaf iron, leaf nitrogen and species richness, were standardised across plots prior to analysis to ensure that parameter estimates could be interpreted on a comparable scale.

Generalised linear mixed models (GLMM) with the *lme* function were performed to determine the influence of the predictor variables on leaf phenolics (Bolker, 2015; Bolker et al., 2009; Brown, 2021). The model incorporated interactions between grazing pressure and climatic, soil, leaf nutrient and biodiversity variables, as well as quadratic terms for mean annual precipitation (MAP^2) and mean annual temperature (MAT^2). The inclusion of quadratic terms allows the model to capture potential non-linear relationships, such as diminishing or threshold effects of climatic factors on plant phenolic concentration. The model also included site as a random effect to account for the non-independence of data collected at the same site. Multicollinearity was evaluated among all predictors in the global model; we excluded variables with variance inflation factors (VIFs) > 10 to prevent distortion of coefficient estimates (Kim, 2019). Only predictors that had VIF values lower than 10 were considered for further model selection.

To determine the relative importance of the predictors and identify the best-fitting model, multi-model inference (Burnham & Anderson, 2002; Katsanevakis, 2006) was performed using the *dredge* function in the MuMIn package (Bartoń, 2024). Geographical coordinates, which include latitude and longitude, were kept as fixed variables in all models. Longitude was included with the sine and cosine transformations to account for the cyclical nature of the variable.

The relative importance of the variables included in our models was assessed using the *sw* function of the MuMIn package (Bartoń, 2024), which provides a summary of the important weights based on model averaging, including model estimates, standard errors, *p* values and variance inflation factors. The best-fitting model, chosen based on the lowest Akaike Information Criterion (AIC), was extracted from the model set. After this step, only the most influential variables on leaf phenolic content remained in the model. To visualise the best-fitting model's results, coefficient plots were created using the *ggplot2* package (Xia et al., 2018), which displays the variables (climate, soil, leaf nutrients, biodiversity and their interactions) that influence leaf phenolic concentration, along with their respective coefficients and standard errors. This helps to understand the relative significance and influence of these factors on plant phenolic concentration, with variables with higher coefficients being more important. Variance partitioning was therefore established from the best model to identify the predictors contributing most to explaining variation in phenolics across dryland regions. To categorise variance partitioning, interactions between variables such as grazing and leaf nutrients, grazing and climate, grazing and biodiversity, leaf carbon and climate, and climate and leaf nutrients were redistributed equally among their primary contributing factors. This approach grouped the total variance explained into fewer, broader categories: grazing, climate, leaf carbon, leaf nutrients, biodiversity and soil. This procedure enabled a clearer visualisation of the results while preserving the interpretability of each category's contribution.

3 | RESULTS

Plot-level estimates showed that woody plants had significantly higher leaf phenolic concentration (7.51 to 186.85 mg g^{-1}, with an average of 71.66 mg g^{-1}) compared to herbaceous plants (4.76 to 123.22 mg g^{-1}, with an average of 33.79 mg g^{-1}; $t = 13.51$, $\text{df} = 411.26$, $p < 0.001$).

3.1 | Predictors of leaf phenolic concentration across global drylands

Grazing pressure accounted for 52.2% of the variation in leaf phenolics in herbaceous species, while leaf nutrients accounted for 42.8% of the variation observed (Figure 1), with leaf iron having a positive effect and leaf nitrogen showing a negative impact on leaf phenolics concentration (Figure 1). The relationship between leaf nutrients and leaf phenolics was, however, dependent on grazing pressure. As grazing pressure increased, the positive effect of leaf iron on leaf phenolics became negative, implying that higher iron content resulted in lower levels of leaf phenolics. Conversely, the interaction between leaf nitrogen and grazing pressure reduced the negative effects of leaf nitrogen on leaf phenolics. This suggests that with higher grazing pressure, higher leaf nitrogen content is associated with increased concentration of leaf phenolics (Figure 2).

Climatic variables explained 4% of the observed variation in the leaf phenolic concentration of herbaceous species, with their interaction with grazing pressure accounting for a minor fraction of this variation (Figure 1). Increasing soil WHC was associated with declines in leaf phenolic concentration irrespective of grazing pressure, whereas increases in MAP were strongly grazing pressure

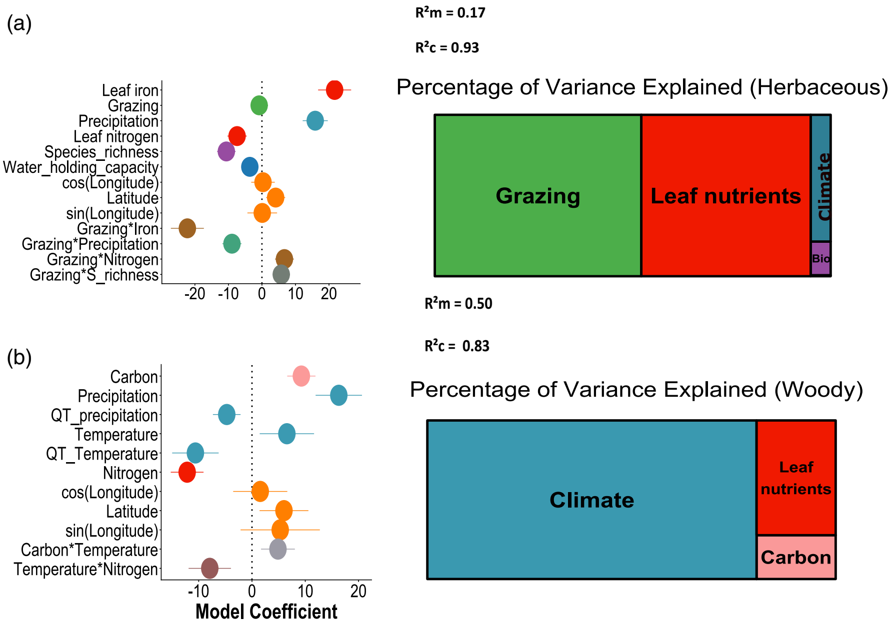

FIGURE 1 Coefficient estimates of model predictors (left panels) and variance partitioning models (right panels) illustrating the relative contribution of each predictor variable to the explained variance in leaf phenolic concentration of herbaceous (a) and woody (b) plants. In the left panels, dots to the left of the dotted line represent negative effects, while dots to the right indicate positive effects; dots on the dotted line indicate non-significant effects. The horizontal lines on the dots show ±1 standard error. Quadratic terms (QT) for precipitation and temperature were included to account for potential non-linear relationships. In variance partitioning, the contribution of interactions such as grazing with leaf nutrients, grazing with climate, grazing with biodiversity (Bio), carbon with climate and climate with leaf nutrients was evenly distributed among their primary contributing factors. The conditional R^2 values (R^2c) reflect the total variance explained by both fixed and random effects, while the marginal R^2 values (R^2m) represent the variance explained by fixed effects alone.

dependent. Specifically, increasing precipitation was associated with increasing leaf phenolics, but only under low grazing pressure (Figure 2). Biodiversity and soil WHC had minimal explanatory power, contributing less than 2.0% of the overall variation of phenolics on herbaceous plants (Figure 1). While species richness generally had a negative impact on leaf phenolics, the interaction between species richness and grazing pressure showed that this effect varied with grazing pressure (Figure 2).

As grazing pressure increased, the negative impact of species richness on leaf phenolics was reduced. There was a significant negative relationship between soil WHC and leaf phenolic content (Figure 1), as soil WHC increased, leaf phenolic concentration decreased (Table S1).

Climatic factors were the main drivers of leaf phenolics in woody species, accounting for 80.6% of the variation observed (Figure 1). Both MAP and MAT showed a strong positive effect on leaf phenolics, suggesting that increased precipitation and temperature were associated with higher phenolic concentration. Leaf nutrients explained 14.0% of the variation in the phenolic concentration of woody species, with nitrogen showing a negative effect on leaf phenolics (Figure 1). An interaction between MAT and leaf nitrogen was associated with a decrease in phenolic production, suggesting that higher MAT and nitrogen levels together reduced leaf phenolic concentration (Table S2). Leaf carbon content accounted for 5.4% of the variation in phenolic concentration in woody species (Figure 1). The interaction between leaf carbon and MAT observed suggests that higher temperatures strengthened the positive relationship between leaf carbon and phenolic concentration (Figure 3). This means that as MAT increased, plants with higher leaf carbon tended to produce more phenolics.

4 | DISCUSSION

Our results supported our hypothesis, that is, grazing pressure more strongly influences phenolic concentration in herbaceous plants than in woody plants, particularly when they interacted with factors like leaf iron, leaf nitrogen, MAP and species richness. Herbaceous plants, which favour rapid growth and reproduction, are often preferred by herbivores, while woody plants, which grow more slowly, allocate resources towards long-term survival and invest in chemical defences (Coley et al., 1985; Saraví Cisneros et al., 2022). Consistent with previous research (Coley et al., 1985; Dudt & Shure, 1994), woody plants exhibited higher phenolic levels than herbaceous plants, likely reflecting the adaptive advantages of defence compounds in slow-growing species that experience greater environmental stress.

Grazing pressure and leaf nutrients emerged as the primary drivers of phenolic concentration in herbaceous plants across global drylands. This includes the observed interactions between grazing pressure and leaf nitrogen as well as grazing pressure and leaf iron. While nitrogen alone had a negative effect on leaf phenolics, its

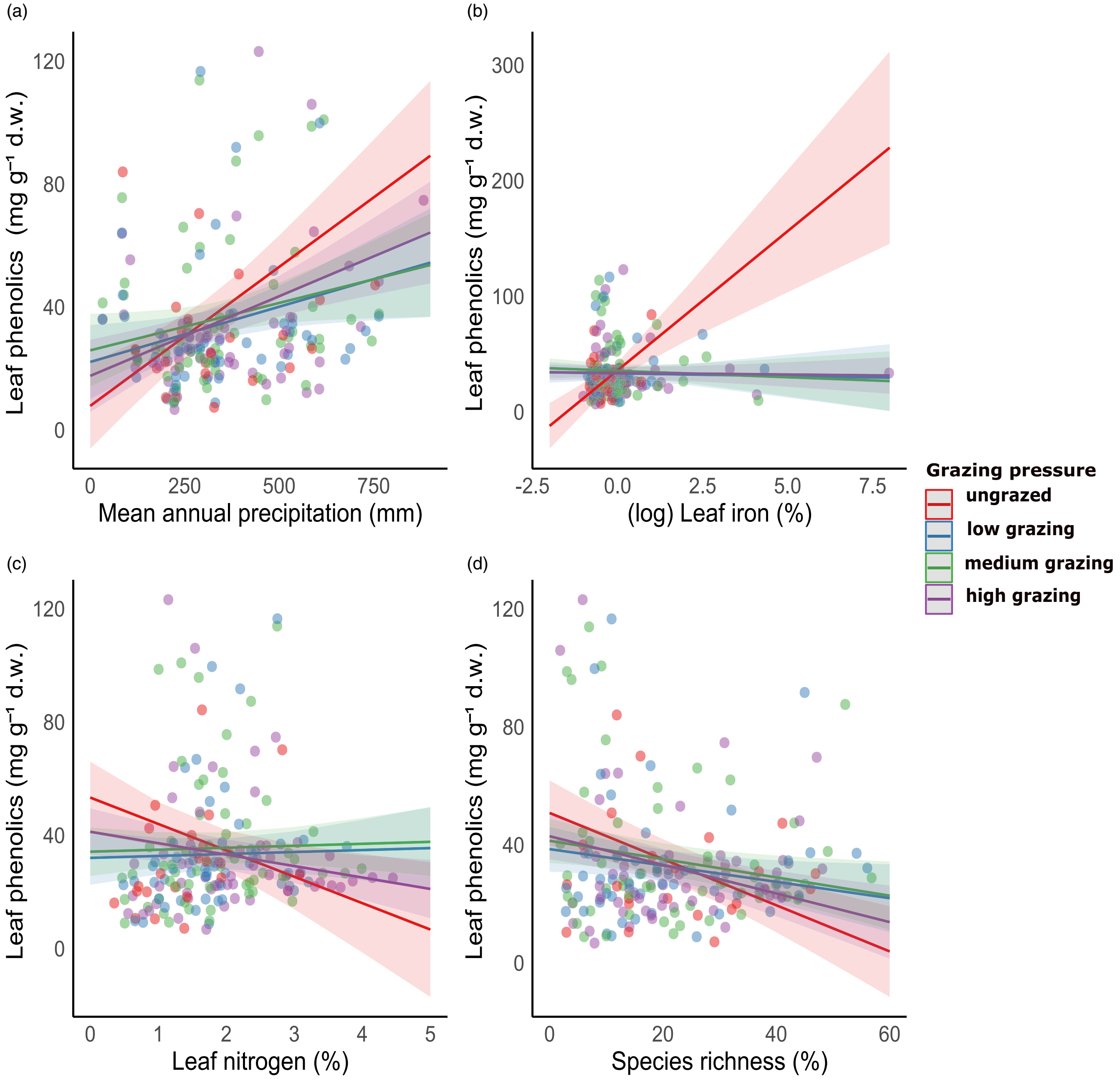

FIGURE 2 The effect of mean annual precipitation (MAP, a), leaf iron (b), leaf nitrogen (c) and species richness (d) on leaf phenolic concentration of herbaceous plants, as well as their interaction with grazing pressure, with 95% confidence intervals shown as shaded regions around the regression lines. The data points represent the observed values for each variable, and the regression lines show the estimated relationships between leaf phenolics and MAP, leaf iron, leaf nitrogen and species richness at different grazing pressure levels.

interaction with grazing led to a positive effect, which suggests that grazing pressure mitigates the negative impact of nitrogen on phenolic production. This relationship indicates that grazing pressure influences plants' nutrient-use strategies (Bi et al., 2020). Leaves with high nitrogen concentration may be more attractive to herbivores, potentially promoting a greater investment in defensive mechanisms to mitigate herbivory pressure (Li et al., 2024; Mattson, 1980). Plants may invest more resources in growth rather than in secondary metabolites like phenolics (Herms & Mattson, 1992), as leaf nitrogen is often associated with a higher growth rate, which may enable plants to tolerate herbivory. In such cases, plants might rely less on phenolic-based defences, as their growth strategy reduces the need for high phenolic investment (Mattson, 1980). This aligns with the findings by Valim et al. (2020), who showed that plants adjust their defence strategies by prioritising the synthesis of nitrogen-rich defensive molecules and reallocating nitrogen resources in response to herbivore-induced stress. These findings also correspond well with the Carbon-Nutrient Balance (CNB) concept articulated by Bryant et al. (1983), which asserts that the nature and intensity of chemical defences utilised by plants are determined by the relative availability

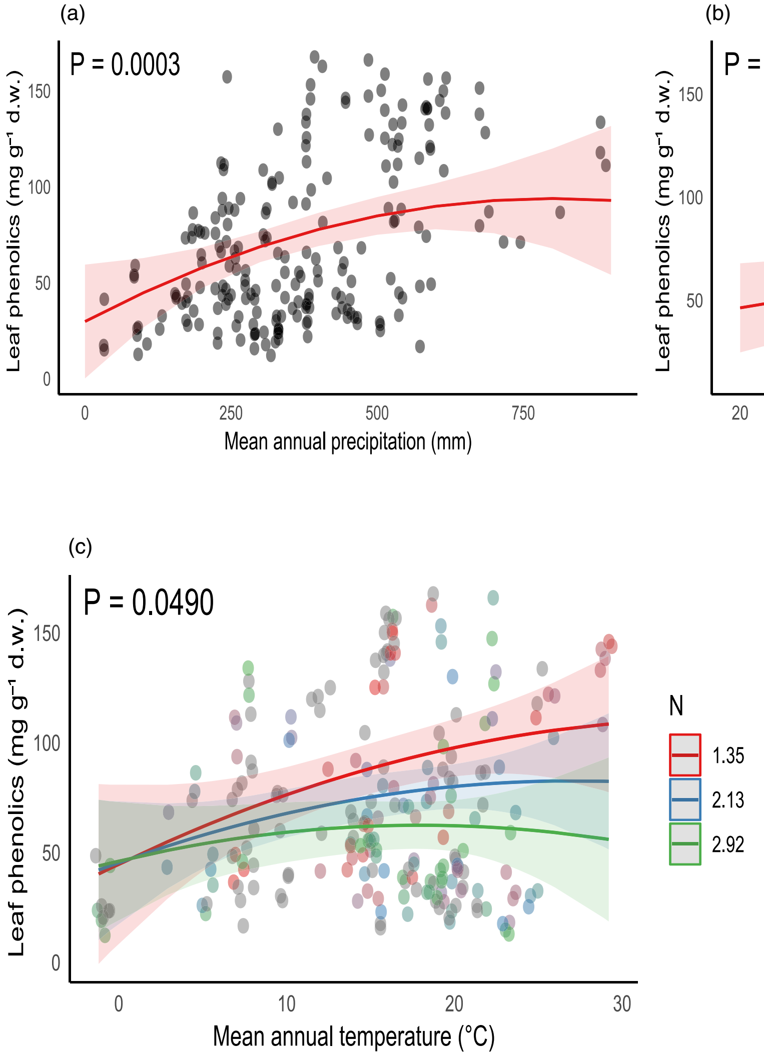

FIGURE 3 The effects of environmental or physiological factors on leaf phenolics of woody plants: (a) mean annual precipitation, (b) leaf carbon and (c) the interaction between mean annual temperature and leaf nitrogen (N). Leaf N was divided into three representative values corresponding to the 33rd percentile (1.35), median (2.13) and 66th percentile (2.29) of its distribution. The fitted trendline (red line) shows the predicted values, and the shaded region around it shows the 95% confidence interval. The data points show the real values, and the *p*-values show the significance of each relationship.

of carbon and nutrients in their environments. In nutrient-deficient conditions, plants would diminish growth and nutrient absorption, yet photosynthesis may proceed mostly unaffected, leading to an excess of carbon. This excess carbon is then diverted to the synthesis of secondary metabolites such as phenolics. On the contrary, when nitrogen is readily available and growth is stimulated, carbon tends to be allocated towards growth and protein synthesis rather than defence, leading to a lower concentration of carbon-based compounds like phenolics (Koricheva et al., 1998). Stamp (2003) revisited and synthesised these and related hypotheses, including the Growth–Differentiation Balance Hypothesis (GDBH), emphasising that plant defensive responses are context-dependent and shaped by both internal resource status and external pressures such as herbivory. Our observation that leaf nitrogen was negatively related to phenolic concentration reflects these underlying resource allocation trade-offs.

The interaction between grazing pressure and leaf iron was associated with low leaf phenolic concentration, suggesting a more complex role for iron in phenolic synthesis under grazing. Although iron is critical for physiological processes (Briat et al., 2007; Neilands, 1974; Rout, 2015), its contribution to phenolic production during grazing appears to be context-dependent. Herbaceous plants may prioritise resource allocation towards growth, and iron enhances photosynthesis and metabolism over defence, especially in resource-limited environments (Li et al., 2021; Tripathi et al., 2018). This focus on growth is typically intensified under higher grazing pressure (Hernán et al., 2019), which could explain the negative relationship between leaf iron and the concentration of phenolics observed.

Although MAP had a positive effect on leaf phenolic concentration of herbaceous plants, its interaction with grazing pressure reduced this effect, suggesting that grazing acts as a buffer to the MAP–phenolic relationship. This contrasts with previous studies showing that leaf phenolic concentration tends to increase under drought (Aninbon et al., 2016; Espadas et al., 2019; Sarker & Oba, 2018, 2019) and grazing pressure (Fagerström et al., 1987). The stronger association between higher MAP and phenolic production could be attributed to plants adopting a less conservative resource-use strategy in ecosystems with higher water availability. In such environments, plants may invest more resources in producing phenolic compounds as a defence against herbivory (Lin et al., 2023). However, when grazing pressure is high, plants may shift their investment towards alternative structural defence strategies that are more immediately effective against herbivores, for example, spinescence, pubescence, sclerophylly and raphides (Hanley et al., 2007). These structural defences may reduce the need for chemical defences like phenolics, particularly in arid environments.

Higher species richness was associated with lower phenolic production, which may suggest that in ecosystems characterised by high species richness, plants may prioritise growth and resource acquisition rather than investing in defensive secondary metabolites such as phenolics, resulting in reduced phenolic production (Bazzaz et al., 1987; Herms & Mattson, 1992). However, the interaction with grazing pressure made this relationship less negative or even positive. Grazing pressure can act as a trigger for phenolic production, as plants prioritise defence to mitigate herbivory (Carmona et al., 2011). The interaction between grazing pressure and species richness highlights the dynamic nature of plant resource allocation, where herbivore pressure can reduce the negative effect of competition on phenolic production (Díaz et al., 2001). This aligns with ecological theories stating that since plants in diverse ecosystems face both direct resource competition and indirect herbivory pressures, higher species richness may increase competition for resources (Tilman, 1982).

Higher soil water-holding capacity was associated with lower leaf phenolic concentration. These findings agree with Chadha et al. (2019), who found that plants under higher WHC (100% WHC) exhibited lower phenolic concentration compared to those at lower WHC (25% WHC). Soils with higher WHC minimise water stress (Martínez-Vidaurre et al., 2024), decreasing the necessity for plants to produce phenolics (Yang et al., 2018).

In woody plants, climate was the primary factor influencing phenolic concentration, with both MAT and MAP showing positive effects. This agrees with studies indicating that temperature increases phenolic levels in woody species such as *Salix myrsinifolia* (Veteli et al., 2002) and *Betula nana* (Graglia et al., 2001). Like herbaceous plants, woody plants unexpectedly showed a positive relationship between MAP and phenolic concentration, despite the general expectation that phenolic concentration increases in response to drought stress (Kumar et al., 2023; Misra et al., 2023). This could be explained by the fact that plants in dryland environments employ diverse strategies to cope with water limitations beyond the production of phenolic compounds. For instance, drought-adapted species may rely on structural adaptations, deeper root systems or osmotic adjustments to maintain water balance (Comas et al., 2013; Peguero-Pina et al., 2020). These findings suggest that the positive relationship between MAP and phenolics in woody plants could result from species-level trade-offs between growth, defence, and resource-use strategies.

The positive correlation between leaf carbon and phenolic concentration observed is consistent with the fact that phenolic compounds are synthesised through carbon-based metabolic pathways, primarily via the shikimate and phenylpropanoid pathways (Caretto et al., 2015; Read et al., 2009). High carbon allocation to leaves provides the necessary precursors for phenolic synthesis, which plants use as a defence strategy against herbivory and environmental stressors (Caretto et al., 2015; Coley et al., 1985). According to the CNB theory, when carbon availability is relatively high compared to nitrogen, plants tend to allocate excess carbon towards secondary metabolite production, including phenolics, as a way to maximise fitness under resource-limited conditions (Bryant et al., 1983; Estiarte & Peñuelas, 1999; Prescott, 2022; Read et al., 2009). This is consistent with findings by Chen et al. (2013), who reported that plants growing under high nitrogen availability typically exhibit lower levels of phenolic compounds due to a shift in resource allocation towards primary metabolic processes. Therefore, the observed impact of leaf carbon on leaf phenolics highlights the importance of understanding resource allocation strategies in plants as they adapt to varying environmental conditions and resource availability.

It is important to note that we used tannic acid as the reference standard in the Folin–Ciocalteu assay. We acknowledge that gallic acid may have been a more suitable choice due to its simpler structure and higher number of hydroxyl binding sites per unit mass (Chun & Kim, 2004; Prior et al., 2005; Rover & Brown, 2013). Tannic acid is a polymeric gallotannin with a variable structure and larger molecular weight (~1700 g/mol) that can lead to lower chromophore development and consequent underestimation of total phenolic concentration (Chun & Kim, 2004; Prior et al., 2005; Rover & Brown, 2013). However, as the final phenolic concentration values are usually proportional to the number of reacting phenolic hydroxyl groups (Karadag et al., 2009), the approach followed, which has been used in multiple studies in the past (Everette et al., 2010; Singleton et al., 1999), is suitable to estimate phenolic concentration in dryland plants. As such, we believe the effects found in our model are indicative of important drivers of phenolic content in global drylands.

5 | CONCLUDING REMARKS

Grazing pressure, combined with leaf nutrients such as nitrogen and iron, played a pivotal role in driving phenolic production in herbaceous plants across global drylands. These findings highlight the strategies plants employ to balance growth and defence under environmental stressors. They also illustrate the significant influence herbivores exert not only on plant community dynamics but also on biochemical pathways important for plant defence, especially under conditions of high nutrient availability. While herbaceous plants prioritise phenolic production under grazing and nutrient-rich conditions, woody plants rely more on climatic factors like temperature and precipitation, reflecting their longer lifespans and greater investment in defence compounds for survival. The unexpected positive relationship observed between mean annual precipitation and phenolic concentration in woody plants evidences the complex interplay between environmental factors and secondary metabolite synthesis. Our findings show the importance of considering both biotic and abiotic (e.g. herbivory, climatic and soil conditions) drivers in understanding plant defence mechanisms across different plant functional types. The information provided in this study contributes to a better understanding of plant adaptation strategies in response to ongoing global changes, including increased grazing pressure and climate shifts.

AUTHOR CONTRIBUTIONS

Fernando T. Maestre designed and coordinated the global field survey. Kaarina N. Shilula, Fernando T. Maestre, Hugo Saiz and Emilio Guirado conceived the research idea, with inputs from Lucio Biancari, David J. Eldridge, Nicolas Gross, Yoann Le Bagousse-Pinguet, Xoaquín Moreira and Yolanda Pueyo. Kaarina N. Shilula wrote the manuscript, with substantial inputs from Fernando T. Maestre, Enrique Valencia, César Plaza, Nicolas Gross, Yoann Le Bagousse-Pinguet, Yolanda Pueyo, Lucio Biancari, Miguel García-Gómez and David J. Eldridge. Victoria Ochoa, Beatriz Gozalo, Sergio Asensio, Betty J. Mendoza and César Plaza carried out sample analysis. Hugo Saiz, David J. Eldridge, Jaime Martínez-Valderrama, Enrique Valencia and Juan J. Gaitán contributed to data management. Kaarina N. Shilula, Lucio Biancari, Hugo Saiz, Nicolas Gross and Yoann Le Bagousse-Pinguet developed and implemented the statistical analysis. All authors discussed and reviewed the manuscript and gave final approval for the publication.

AFFILIATIONS

[1]Instituto Multidisciplinar para el Estudio del Medio 'Ramón Margalef', Universidad de Alicante, Alicante, Spain; [2]Departamento de Ecología, Universidad de Alicante, Alicante, Spain; [3]Departamento de Ciencias Agrarias y del Medio Natural, Escuela Politécnica Superior, Insituto Universitario de Ciencias Ambietales (IUCA), Universidad de Zaragoza, Huesca, Spain; [4]Environmental Sciences and Engineering, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal, Kingdom of Saudi Arabia; [5]INRAE, VetAgro Sup, Unité Mixte de Recherche Ecosystème Prairial, Université Clermont Auvergne, Clermont-Ferrand, France; [6]Aix Marseille Univ., CNRS, Avignon Université, IRD, IMBE, Technopôle Arbois-Méditerranée, Aix-en-Provence, France; [7]IFEVA, Facultad de Agronomía, Universidad de Buenos Aires, CONICET, Buenos Aires, Argentina; [8]Cátedra de Ecología, Departamento de Recursos Naturales y Ambiente, Facultad de Agronomía, UBA, Buenos Aires, Argentina; [9]Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza, Spain; [10]Misión Biológica de Galicia (MBG-CSIC), Pontevedra, Galicia, Spain; [11]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia; [12]Instituto Universitario de Investigación en el Olivar y Aceite de Oliva (INUO), Universidad de Jaén, Jaén, Spain; [13]Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain; [14]Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Madrid, Spain; [15]Departamento de Ingeniería y Morfología del Terreno, Escuela Técnica Superior de Ingenieros de Caminos, Canales y Puertos, Universidad Politécnica de Madrid, Madrid, Spain; [16]Universidad Nacional de Luján-CONICET, Buenos Aires, Argentina; [17]Instituto de Ciencias Agrarias (ICA), CSIC, Madrid, Spain and [18]Department of Agricultural and Food Chemistry, Faculty of Sciences, Universidad Autónoma de Madrid, Madrid, Spain

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CONFLICT OF INTEREST STATEMENT

The authors declared no conflict of interest.

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DATA AVAILABILITY STATEMENT

The data used in this manuscript are available in figshare: https://figshare.com/articles/dataset/Data_for_Drivers_of_phenolic_concentration_across_global_drylands/28295999 (Shilula, 2025).

ORCID

Kaarina N. Shilula https://orcid.org/0009-0002-8109-3335
Lucio Biancari https://orcid.org/0000-0002-6539-6267
Yolanda Pueyo https://orcid.org/0000-0001-6970-7790
Xoaquín Moreira https://orcid.org/0000-0003-0166-838X
David J. Eldridge https://orcid.org/0000-0002-2191-486X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Statistical summary of GLMM analyses of leaf phenolic concentration. The predictors include leaf iron (Fe), grazing pressure (categorized as low (GRAZ1), medium (GRAZ2), and high (GRAZ3)), mean annual precipitation (MAP), leaf nitrogen (N), species richness, water-holding capacity, cosine of longitude (cosLong), latitude (Lat_decimal), and sine of longitude (sinLong). *p*-values below 0.05 are in bold.

Table S2. Summarises the results of GLMM analyses evaluating the effects of various environmental and leaf nutrients predictors on leaf phenolic concentration.

Figure S1. Geographic distribution of the 98 surveyed sites, including examples (insets a–g) illustrating local grazing gradients.

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