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- ⁴Instituto Multidisciplinar para el Estudio del Medio 'Ramón Margalef', Universidad de Alicante, Alicante, Spain
- ⁵Departamento de Ecología, Universidad de Alicante, Alicante, Spain
- ⁶Department of Biology, Faculty of Sciences, Universidad Autónoma de Madrid, Madrid, Spain

⁷Department of Environment Systems Science, Institute of Integrative Biology, ETH Zürich, Zürich, Switzerland

⁸Department of Soil and Water Conservation and Waste Management, CEBAS-CSIC, Murcia, Spain

⁹Instituto de Ciencias Agrarias (ICA), Consejo Superior de Investigaciones Científicas, Madrid, Spain

- ¹⁰Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain
- ¹¹Department of Biology, Botany Area, University of Cádiz, Vitivinicultural and Agri-Food Research Institute (IVAGRO), Cádiz, Spain
- ¹²Laboratorio de Biodiversidad y Funcionamiento Ecosistemico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC., Sevilla, Spain
 ¹³Unidad Asociada CSIC-UPO (BioFun), Universidad Pablo de Olavide, Sevilla, Spain

Correspondence

Eduardo Moreno-Jiménez, Department of Agricultural and Food Chemistry, Faculty of Sciences, Universidad Autónoma de Madrid, 28049 Madrid, Spain. Email: eduardo.moreno@uam.es

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Abstract

Soil micronutrients are capital for the delivery of ecosystem functioning and food provision worldwide. Yet, despite their importance, the global biogeography and ecological drivers of soil micronutrients remain virtually unknown, limiting our capacity to anticipate abrupt unexpected changes in soil micronutrients in the face of climate change. Here, we analyzed >1300 topsoil samples to examine the global distribution of six metallic micronutrients (Cu, Fe, Mn, Zn, Co and Ni) across all continents, climates and vegetation types. We found that warmer arid and tropical ecosystems, present in the least developed countries, sustain the lowest contents of multiple soil micronutrients when a temperature threshold of 12–14°C is crossed, which may be occurring on 3% of the planet over the next century. Altogether, our findings provide fundamental understanding of the global distribution of soil micronutrients, with direct implications for the maintenance of ecosystem functioning, rangeland management and food production in the warmest and poorest regions of the planet.

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KEYWORDS

climate change, environmental drivers, global biogeography, metals, micronutrients, soil ecology

1 | INTRODUCTION

Metallic micronutrients are critical regulators of essential ecological processes such as photosynthesis (Fe, Mn; Fischer et al., 2015; Schmidt et al., 2020), respiration (Fe; Dallman, 1986), enzymatic and redox activity (Zn, Cu, Mn, Fe; Hänsch & Mendel, 2009), animal reproduction (Zn; Swain et al., 2016) or biological N fixation (Ni, Co; O'Hara, 2001). In terrestrial ecosystems, plants, animals and microorganisms satisfy their micronutrient requirements from the soil. Hence, low concentrations of soil micronutrients can be associated with mineral deficiencies in natural ecosystems, crops and livestock (Gupta et al., 2008; White & Zasoski, 1999). Consequently, total soil micronutrient contents are critical indicators of ecosystem health. stability and food provision (Luo et al., 2016; Moreno-Jiménez et al., 2019). However, unlike for macronutrients (C, N and P; He et al., 2021; Plaza et al., 2018), the global distribution and the abiotic (i.e., climatic and edaphic) and biotic drivers (i.e., biomes) of soil micronutrients at supracontinental scale are largely unknown (Jones et al., 2013; Thompson & Amoroso, 2010).

Until now, three factors have restricted our understanding of the global distribution and ecological drivers of soil micronutrients. First, previous studies have focused on distribution at national/local scale and primarily within agricultural systems (Ballabio et al., 2018; Hengl, Leenaars, et al., 2017; Navarro-Pedreño et al., 2018; Ramzan & Wani, 2018; White & Zasoski, 1999), revealing a wide range of environmental drivers, from soil parameters (e.g., texture; Kabata-Pendias & Pendias, 2001; McBride, 1989; Shuman, 2005) to climate (Moreno-Jiménez et al., 2019; Tan et al., 2020), parent material (Augusto et al., 2017; Kabata-Pendias & Pendias, 2001; Luo et al., 2016; Moreno-Jiménez et al., 2019) and biota (Choudhury et al., 2021; Hemkemeyer et al., 2021) that operate in different regions. As such, we lack an unifying perspective of the variation in micronutrient abundance in soils at global scale, covering large terrestrial climatic and vegetation gradients. This limits our ability to identify global "hotspots"-and more importantly "coldspots"-of soil micronutrient contents that could limit the concentration of critical nutrients in plants and animals (Fageria et al., 2002; Graham, 1991; White & Zasoski, 1999). Similar approaches at relatively large scale have been done in some specific subcontinental areas, for example, sub-Saharan Africa (Hengl, Leenaars, et al., 2017), but never at the global scale. Second, previous work has not considered the simultaneous distribution of multiple soil microelements at a global scale and using standardized data. This knowledge is essential to better anticipate if consistent environmental patterns arise supporting potential co-limitations in particular regions worldwide. Third, data availability on micronutrients at a large/global scale is very limited because they are not systematically assessed within the usual soil parameters in global surveys, but some others such as C, N, pH or

texture. Finally, previous studies have not evaluated whether controls of micronutrients by climate exhibit linear or nonlinear patterns. This is important because nonlinear patterns between climate (e.g., temperature) and micronutrients will signal climatic zones with different sensitivity to further climatic change (Groffman et al., 2006). For example, previous studies have evidenced that above certain aridity levels soil nutrients decrease abruptly, identifying aridity thresholds above which drastic reductions of soil fertility may occur if further aridification occurs (Berdugo et al., 2020). Unravelling this type of thresholds allows to set tangible targets delimiting climatic boundaries for ecosystems (Allen, 2009), which are especially relevant in the context of the current climate crisis. Understanding the global distribution of multiple soil micronutrients, along with their drivers, could have important implications for establishing policies to ensure food security, as micronutrient scarcity is a major nutritional issue in least developed regions (Alloway, 2009; Hengl, Leenaars, et al., 2017; Thompson & Amoroso, 2010) where food production relies largely on soil resources. However, the previous four factors have restricted the understanding of soil micronutrient distribution and drivers at large scales (continental and global).

To better understand the global distribution and abundance of soil metallic micronutrients, we collected 1306 topsoil composite samples (~10 cm depth) from 383 natural ecosystems across the globe. These ecosystems include all types of climatic conditions (arid, temperate, tropical, polar and continental) and vegetation types (forest, grasslands and shrublands) across all continents (Figure S1). We determined in these soil samples the total content of cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), nickel (Ni) and zinc (Zn). We focused on the respective total soil micronutrient content for three reasons: (1) total stocks provide a long-term perspective (years to centuries) on the availability of micronutrients in terrestrial ecosystems; (2) unlike available elements, total stocks are more stable over time, not being as influenced by seasonal dynamics as available nutrients; and (3) at a global scale, total soil micronutrient concentrations are known to be correlated with the fraction of soil micronutrient which is immediately bioavailable for plants and animals across a wide range of environments (see Table S2 for examples and associated explanation in the Supplementary Material).

We aimed to (1) evaluate whether the total contents of six different soil metallic micronutrients follow common or contrasting patterns globally, (2) map the occurrence of soil micronutrients at a global scale and (3) identify the environmental factors associated with the content of soil metallic micronutrients at a global scale, and their potential relationship with changes in climate, with particular attention to potential climatic thresholds. Ecosystem ecology theory predicts that warmer topsoils in older tropical ecosystems should have a reduced content of bedrock-associated elements compared with colder and higher latitude ecosystems in which soils are often rejuvenated through periodic glaciation processes (Hartemink, 2002; Schlesinger, 2005; Uhlig et al., 2020). According to this, microelement contents are expected to increase with distance to the equator. However, this prediction has not been empirically tested.

2 | METHODS

2.1 | A global standardized field survey

We analyzed 1306 composite topsoil samples (top ~10 cm) from 383 sites collected between early 2016 and late 2019 in global standardized field surveys across all continents, vegetation (shrublands, grasslands and forests) and climatic (arid, continental, temperate, polar and tropical) types (Figure S1; Table S1). These locations were selected to cover the wide range of environmental conditions found on Earth. For example, soil pH and fine texture ranged from 3.4% to 9.9% and 0.2% to 88.2%, respectively, and mean annual temperature (MAT) and precipitation ranged from -6.7 to 29.3°C and 4 to 2161 mm, respectively.

2.2 | Total soil micronutrient analysis

The total content of metallic soil microelements, including cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), nickel (Ni) and zinc (Zn), was determined after acid digestion in a microwave using inductively coupled plasma atomic emission spectroscopy. The total soil metal recovery was assessed in a certified reference material (CMR048-050G; sandy soil supplied by Sigma-Aldrich) and ranged 82%–103% for the elements. As a guideline, total soil micronutrient averages $30 \text{ mg} \text{ Cu} \text{ kg}^{-1}$, $38,000 \text{ mg} \text{ Fe} \text{ kg}^{-1}$, $600 \text{ mg} \text{ Mn} \text{ kg}^{-1}$, $50 \text{ mg} \text{ Zn} \text{ kg}^{-1}$, $40 \text{ mg} \text{ Ni} \text{ kg}^{-1}$ and 8 mg Co kg⁻¹ in the literature (Lindsay, 1979).

2.3 | Environmental drivers

We considered a wide range of environmental factors such as geographic position, climate, vegetation, lithologies and soil properties. Absolute latitude (distance from equator) was determined in the field. Elevation was extracted from Advanced Land Observation Satellite (Hamasaki, 1999). Climatic information (MAT, seasonal temperature, precipitation and precipitation seasonality) was extracted from the WorldClim database v2 (https://www.worldclim. org/data/index.html; Fick & Hijmans, 2017). The overall accuracy of the Worldclim climate models was very high for temperature variables with overall correlation coefficient (between estimated and observed values) ≥0.99 and root-mean-square error between 1.1 and 1.4°C. Precipitation in arid areas can be highly variable in time and space, with some regions showing abrupt changes across spatial scales. In general, prediction error increased with station elevation and distance to the nearest neighboring station (in the training set) for all variables. Generalized additive models of cross-validation errors showed that higher elevations tended to be associated with lower interpolation accuracy, even after accounting for the effects of isolation and spatial variation in errors, although this effect differed between variables (Fick & Hijmans, 2017). MAT was highly positively and significantly correlated with soil MAT (r = .971; p < .001). Vegetation type (forest vs. no forest), plant richness (number of perennial plant species) and plant cover (%) were determined in the field. Soil pH was measured in all the soil samples with a pH meter in a soil to water suspension and soil total organic carbon and fine texture content (% of clay+silt) were also determined in the laboratory (Anderson & Ingram, 1989; Kettler et al., 2001). Lithology information was extracted from Hartmann and Moosdorf (2012).

2.4 | Statistical analyses

2.4.1 | Differences on total soil micronutrients among terrestrial ecosystems

The concentration of total soil micronutrients was compared among different terrestrial ecosystems using Adonis Permutational Analysis of Variance (Oksanen et al., 2019) with a block design, with sites as a random factor. This nested analysis is aiming to statistically account for having more than one sample per plot.

2.4.2 | Environmental factors associated with the content of soil micronutrients

We used a machine learning approach, Random Forest (rfPermute package; Archer, 2021), to investigate the environmental associations between environmental factors and the content of soil micronutrients. Environmental predictors included the variables associated with spatial, climate, vegetation, lithologies and soil properties were described above.

We then used partial Spearman correlations (ppcor R package; Kim, 2015) to further investigate the relationships between environmental factors and the content of soil elements accounting for spatial autocorrelation (averaged distance among locations in decimal degrees calculated from latitude, and cosine and sine of longitude). Figures were created using "ggplot2" packages, v3.3.5. Spearman rank correlations can be used to associate two variables regardless of whether they are ordinal, interval or ratio. Moreover, spearman rank correlations are a nonparametric approach which does not require normality of data or homogeneity of variances and measures the strength and direction of the association between two ranked variables.

2.4.3 | Global mapping

To predict the extent of the micronutrients (Cu, Fe, Mn, Zn, Co and Ni), we used a random forest regression analysis (Lahouar &

Slama, 2015) using as inputs the variables elevation (Hamasaki, 1999), plant cover (Buchhorn et al., 2020), plant richness (Kier et al., 2009), pH, clay content, organic C, lithology (Hengl, Mendes de Jesus, et al., 2017), MAT, temperature seasonality, mean annual precipitation and precipitation seasonality (Fick & Hijmans, 2017). This model was built by finding the set of covariate combinations that most robustly predicted the training samples with a configuration of 999 decision trees in the model and 999 replicates. To assess the accuracy of the predictions calculated from the random forest model, we calculated how much the parameter space of the predictors differed from the original dataset. The modeling approach was then validated by returning the predicted values (x-axis) versus the observed values (y-axis) (Piñeiro et al., 2008). To provide a visualization of the most reliable predictions about the distribution of micronutrients, we generate a mask with the help of Mahalanobis distance, the distance from any multidimensional point to the center of the known distribution that we have previously calculated and the distance from any multidimensional point formed by the 1306 locations that were used in the model. Outliers were masked from the 0.9 quantile of the chi-square distribution with 11 degrees of freedom (Mallavan et al., 2010). The maps were validated with respect to the modeling approach by returning predicted values versus observed values (Piñeiro et al., 2008). The model obtained a high predictive power (Cu R^2 = .86, Fe R^2 = .91, Mn R^2 = .88, Zn R^2 = .90, Co R^2 = .88, Ni $R^2 = .88$).

2.4.4 | Calculation of thresholds with temperature

To provide evidence showing that soil micronutrients exhibit threshold patterns, we used the method proposed by Berdugo et al. (2020). In short, we first fitted the micronutrient content to temperature using a linear model, and we compared this fitting with a segmented model, which is a model in which the slope is changed in a given point of the predictor (here temperature). To perform this comparison, we used the Akaike information criteria (AIC) from these fittings. Akaike criteria provide a metric on the goodness of fit of a given model by explicitly penalizing for extra parameters, thus finding a compromise between model complexity and variance explained. When comparing AICs, the model with lowest AIC is selected. Models with AIC values differing less than 2 units are considered similarly good and the less complex is selected. If the segmented model showed a significantly better fit than linear models to the data, then we extracted the threshold as the fitted breakpoint of the segmented regression. To additionally provide estimates of the uncertainty of the thresholds found, we bootstrapped the segmented regression considered to exhibit the best AIC 100 times (Table S3).

Because the existence of outliers may strongly influence the position of the thresholds, we repeated this procedure with and without outliers (defined as already explained with Mahalanobis method, see previous section). Both results were very similar (Table S3). - Global Change Biology - WILEY

2.4.5 | Calculation of the area potentially affected by micronutrient decline

To obtain the land area that could be affected by processes declining soil micronutrients if temperature thresholds are exceeded due to climate change in the next decades, the MAT variable from the Worldclim v.2 database (Fick & Hijmans, 2017) at global scale was reclassified into three classes around the temperature threshold identified in the previous subsection, (1) below 12°C, (2) between 12 and 14°C and (3) greater or equal to 14°C with the table reclassification algorithm used by the QGIS software (QGIS.org, 2022). Subsequently, the data were reprojected to Eckert IV (Snyder, 1997), a pseudocylindrical projection of equivalent areas for global maps. The lateral meridians are semicircles that give the projection a rounded shape and smooth corners where the lateral meridians coincide with the poles. This projection is used for maps that require precise measurement of areas (Seong et al., 2002).

3 | RESULTS AND DISCUSSION

3.1 | Global-scale patterns in soil micronutrients

In general, we found that most terrestrial ecosystems supported relatively low levels of total soil micronutrients, with only a few ecosystems maintaining high contents of these elements (Figure 1; Figure S2), compared to our average values in the samples included in this study or to reference average in soils (see Section 2). The total content of topsoil micronutrients varied considerably across ecosystem types, with warm (arid grasslands, shrublands and forests) and tropical (tropical and subtropical forests) ecosystems containing the lowest total micronutrient contents (Figure 1a). Moreover, we found that all micronutrients were strongly correlated with one another (Figure S3), which indicates unifying patterns that could lead to the potential co-limitation of micronutrients within certain regions. These findings substantially expand studies observing correlations between soil micronutrients at smaller spatial scales (regional, national, subcontinental or continental; Navarro-Pedreño et al., 2018; Ramzan & Wani, 2018; Wani et al., 2013). This intense correlation of micronutrients at a global scale is particularly striking if we consider some previous observations suggesting that soil fertility and ecosystem processes are directly co-limited by micronutrients (Crowther, Riggs, et al., 2019; Kaspari, 2021; Radujković et al., 2021).

Our study provides new insights into the global biogeography and ecology of soil microelements. First, we used linear models and machine learning to examine how the effects of climatic and soil characteristics influence the distribution of total topsoil micronutrients across the globe (Figure 1b; Figure S4). We found that texture, soil carbon, MAT and temperature seasonality (the annual range in temperature of a site) are among the most important factors controlling the global distribution of total soil micronutrients, with warmer and more seasonal ecosystems with less carbon and coarse texture supporting the lowest contents of soil



FIGURE 1 Global patterns in soil metallic micronutrients. (a) Includes a violin plot representation of soil metallic micronutrients (Cu, Fe, Mn, Zn, Co and Ni, in mg kg⁻¹) across different terrestrial ecosystems. Ecosystems were grouped according to Koppen classification (Table S1). The violin plots are histograms, where the width along the *x*-axis indicates the normalized fraction of data at the value corresponding to each ecosystem. There are statistical differences for all the elements among different terrestrial ecosystems (p < .001). (b) Includes partial Spearman correlations (rho) between soil metallic micronutrients and abiotic (geographic, edaphic and climatic) and biotic drivers, and controlling for Spatial autocorrelation (included as the averaged distance between all locations in decimal degrees). White cells indicate p > .05. MAP, mean annual precipitation; MAT, mean annual temperature; sc, carbonate sedimentary rocks; ss, siliciclastic sedimentary rocks; su, unconsolidated sediments.

microelements. Based on our capacity to predict the global distribution of microelements, we built the first global atlas of total soil micronutrients (Figure 2), which allows us to identify global hotspots (abundance of micronutrients) and, more importantly, coldspots (defined as regions with low stocks of several micronutrients) of micronutrient supply. Moreover, our maps highlight that multiple countries that are considered among the least developed from Africa, Asia and South America, match entire regions with low soil stocks of micronutrients, with potential implications for their economies as discussed below.

3.2 | Global patterns in soil micronutrients follow ecosystem ecology theory

Our analyses revealed that the content of soil microelements was positively associated with the distance from the equator, supporting ecosystem ecology theories never tested before for micronutrients at a global scale. The chemical composition of parent rock substrates is affected by glaciation intensity (Augusto et al., 2017; Schlesinger, 2005); however, these glaciation processes are known to be more important in regions far from the equator. As such, levels of soil metallic micronutrients are expected to increase with latitude, as parent material and micronutrient stocks were rejuvenated during glacial events that affected temperate but not tropical ecosystems. In this sense, parent rock constitutes a significant input of nutrients to topsoils during pedogenesis after every glaciation event. This agrees with the hypothesis that bedrock-associated micronutrients are dependent on glaciation events, while old, circumequatorial soils that are free from the effects of glaciation are impoverished in all these elements. In agreement with this, we found a positive correlation between micronutrient content and both the latitude (Figure 1b) and elevation (Figure 1b), another feature linked to intense soil erosion and presence of shallow rocks, which promotes soil rejuvenation (Egli & Poulenard, 2016).



FIGURE 2 Global representation of metal micronutrients (Cu, Fe, Mn, Zn, Co and Ni) from a random forest model. Bar plots represent the mean \pm standard deviation of micronutrient contents (mgkg⁻¹) for least developed countries (LDC) and all other countries (AOC) according to United Nations (https://unctad.org/webflyer/least-developed-countries-report-2020). Map lines delineate study areas and do not necessarily depict accepted national boundaries. White regions represent outliers in the map. Asterisks represent significant differences of soil micronutrients between AOC and LDC (***p <.001, from the Kruskal–Wallis test comparison).

3.3 | The global distribution of soil micronutrients as a function of temperature thresholds

Temperature emerged as a key driver of the global distribution of multiple soil micronutrients, with warmer ecosystems closer to the tropics supporting lower levels of soil microelements. While the positive relationships between fine soil texture and soil organic C content with higher micronutrient concentration were expected (Kabata-Pendias & Pendias, 2001; Shuman, 2005; Stevenson, 1991; White & Zasoski, 1999), much less was known about the links between temperature and micronutrient contents (Luo et al., 2016; Moreno-Jiménez et al., 2019). Further analyses provided unparalleled evidence for the existence of important nonlinear relationships between MAT and the content of multiple soil microelements, supporting an undescribed temperature threshold regulating the content of soil microelements worldwide. In particular, our results show that the total content of metallic micronutrients decreases with higher temperature, but stress that this decrease is especially important after crossing a temperature threshold of 12– 14°C of MAT (Figure 3). This finding signals the existence of very different micronutrient regimes driven by temperature and has direct implications on assessing the vulnerability of soil micronutrients to climate change, which will increase temperature worldwide (Pachauri et al., 2014). Indeed, our results suggest that the expected decline—based on a space for time substitution as a valid approach in ecological modeling (Wogan & Wang, 2018)—of soil



FIGURE 3 Relationships between mean annual temperature and total micronutrient concentration in soils showing abrupt responses. The relationship is fitted using a segmented regression where two fitting lines with significantly different slopes (blue lines) are plotted around a breaking point (temperature value), with color of the points is proportional to temperature (*x*-axis) from yellow to purple. The vertical gray ribbons mark the 95% confidence interval of the breaking point position. Inset labels indicate the element of concern. Note that *y*-axis ticks are shown in logarithmic scale.

micronutrients due to climatic warming is much stronger in sites of the world that have currently an average temperature of around 13°C than in other areas.

We estimated that the terrestrial surface whose MAT is between 12 and 14°C-that can be potentially affected in the next decades by processes declining soil micronutrients, if we consider the current predictions of raising MAT with climate change (Pachauri et al., 2014)—represents around 3% of the Earth surface, equivalent to 3.86 million km² (Figure 4). Such regions are particularly located in the Northern hemisphere, for example, in South and Central Europe, Middle US and Central Asia. Meanwhile, regions with MAT ≥14°C currently account for 51% of the terrestrial surface on Earth and encompass large areas of developing countries. The peak of micronutrients at ~13°C is probably associated with soil conditions wherein organic matter is accumulated, processed and integrated into the soil in a regular cyclic manner. This range of temperature corresponds to temperate regions where soils are well developed (Anderson, 1988; Crowther, van den Hoogen, et al., 2019). We hypothesized that, beyond this temperature threshold, the amount of micronutrients is largely reduced as a consequence of extreme rates of weathering

coupled to high levels of precipitation that exacerbates micronutrient leaching, like in tropical climates (Harmsen & Vlek, 1985; Sanchez & Buol, 1975), or the lack of capacity to retain organic matter in soil in low-development soils with low clay content such as those from arid climates (Dregne, 1976; Moreno-Jiménez et al., 2019). High temperatures (indicated by MAT) stimulate soil organic matter decomposition (Davidson & Janssens, 2006; García-Palacios et al., 2021), productivity and thus micronutrient allocation to plants (Cleveland et al., 2011; Epstein et al., 1997) and impoverishment of soils on clay fractions (Dregne, 1976; Harmsen & Vlek, 1985). This explains the lower metallic micronutrient content observed in warmer soils, particularly in arid and some tropical and subtropical ecosystems (Figure 1a). Similarly, low MAT was also associated with low contents of micronutrients in topsoils, for example, in cold forests, which could be attributed to the relatively low occurrence of minerals and relatively high contents of undecomposed organic matter (Jonasson & Shaver, 1999; Nadelhoffer et al., 1997). Our work opens a new perspective on the importance of temperature thresholds for driving the content of soil micronutrients globally, hypotheses that will need to be tested by future experimental work.

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FIGURE 4 Representation of the annual mean temperature reclassified into two classes (blue less than 12°C and red greater than or equal to 14°C) and the range from 12 to 14°C in yellow. The pie chart represents the percentage of the surface area occupied by each group. Blue surface: 68.63 million km²; Red surface: 76.45 million km²; Yellow surface: 3.86 million km². Data obtained from Worldclim v.2 (Fick & Hijmans, 2017).

We also found a negative relationship between temperature seasonality and soil metallic micronutrient content, probably due to enhanced weathering by changes in temperature. This seasonality is particularly characteristic of arid environments. Such an effect is potentially related to more intense rates of weathering of parent material (Anderson, 2019) that can lead to losses of nutrients (Bluth & Kump, 1994; Hartmann et al., 2014). Overall, warmer and more seasonal temperatures were associated with lower total soil micronutrient concentration. In the context of climate change, where temperatures and weather extremes (i.e., seasonality) are expected to increase, micronutrients may exacerbate nutrient limitations in some regions. Even if soil development and weathering processes are considered to occur at over geological timescales, that is slower than the current climate change, there is evidence that changes associated with climate change can explain soil properties rather than soil age (Delgado-Baguerizo et al., 2020) and warmer and more extreme temperatures may exacerbate micronutrient losses in some regions.

3.4 | A world with less soil micronutrient total stocks

Low stocks of total soil micronutrients can have long-term consequences (depletion of stocks; Jones et al., 2013), as micronutrients associated with the bedrock are only rejuvenated over millions of years of geochemical processes. This may have the most impact in least developed countries from Africa, Asia and South America, where entire regions with low soil stocks of micronutrients are particularly vulnerable to further soil degradation. This could be exacerbated by rising temperatures under the current climate change and elevated concentrations of atmospheric CO_2 (Clair & Lynch, 2010; Myers et al., 2014; Pachauri et al., 2014). Our global micronutrient

maps are particularly important to anticipate potential limitations and implications for food and fiber production, natural resource management, such as livestock grazing, and also the future establishment of new croplands aiming to feed a growing human population. Our micronutrient atlas anticipates that, on average, less developed countries in the Global South tend to have lower stocks of multiple soil micronutrients than more developed countries. Our results further suggest that food production, which depends directly or indirectly on soil nutrient and micronutrient content, may be most limited by the lower micronutrient contents observed in least developed countries. For instance, many of the soils included in this study are associated with land used for livestock grazing and local populations in developing regions rely on this source of proteins for their diets (Johnsen et al., 2019), while micronutrient deficiency in grazers is a serious problem in these countries (Gupta et al., 2008; Randolph et al., 2007), probably linked to the low micronutrient content in soils. Also, soils in these developing regions may potentially be transformed to agriculture in the future to satisfy food demands in increasingly populated countries (Prestele et al., 2016; Stehfest et al., 2019), but featuring low stocks of micronutrients. The processes that have caused depletion of soil micronutrients in warm soils may start acting as well in other regions that currently are affected by temperatures around 12-14°C, where climate change may exacerbate soil micronutrient losses when temperature rises over the identified temperature threshold. Our findings provide context to understand the global imbalances in food nutritional quality, as people in certain tropical and subtropical regions often suffer from nutrient-deficient diets (Fageria et al., 2002; White & Broadley, 2005), and ultimately suggests that the lower total content of soil micronutrients in least developed countries could potentially further hamper the development of these developing countries, and impact the well-being of millions of people.

Our global survey reveals consistent patterns of metallic micronutrients across global soils. We identified striking consistencies in the distribution of different micronutrients, which are less abundant in warmer arid and tropical soils closer to the equator. A global temperature threshold appears to govern the content of micronutrients in soils, dividing the world in two distinct micronutrient regimes through a clear climatic boundary that negatively influences the content of micronutrients in warmer ecosystems and suggests potential future exacerbation of micronutrient limitations in a warmer world. This work further highlights the fundamental importance of conserving soil micronutrients particularly in least developed countries where many regions are already co-limited by multiple nutrients that ultimately determine ecosystem processes and food production.

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AUTHOR CONTRIBUTIONS

Manuel Delgado-Baquerizo and Eduardo Moreno-Jiménez conceptualized the idea and led the writing up. Manuel Delgado-Baquerizo and Fernando T. Maestre designed and coordinated the field surveys. Felipe Bastida and César Plaza coordinated the micronutrient soil analyses. Manuel Delgado-Baquerizo, Eduardo Moreno-Jiménez, Emilio Guirado and Miguel Berdugo curated the data, performed the analysis, visualized the figures and elaborated the tables. Fernando T. Maestre and Thomas W. Crowther provided specific insights during the drafting. All coauthors provided feedback during the subsequent drafting.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data are available in Figshare https://figshare.com/s/8ff4083eb0 ddb84ba056.

CODE AVAILABILITY

All analyses were conducted using standard code packages referred to in Section 2.

ORCID

Eduardo Moreno-Jiménez https://orcid. org/0000-0002-2125-1197 Fernando T. Maestre https://orcid.org/0000-0002-7434-4856 Maren Flagmeier https://orcid.org/0000-0001-6655-5111 Emilio Guirado https://orcid.org/0000-0001-5348-7391 Miguel Berdugo https://orcid.org/0000-0003-1053-8907 Felipe Bastida https://orcid.org/0000-0001-9958-7099 Marina Dacal https://orcid.org/0000-0002-1321-9373 Raúl Ochoa-Hueso https://orcid.org/0000-0002-1329-6926 César Plaza https://orcid.org/0000-0001-8616-7001 Matthias C. Rillig https://orcid.org/0000-0003-3541-7853 Thomas W. Crowther https://orcid.org/0000-0001-5674-8913 Manuel Delgado-Baquerizo https://orcid.org/0000-0001-5674-8913

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SUPPORTING INFORMATION

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