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A Pantropical Overview of Soils across Tropical Dry Forest Ecoregions

Anaitzi Rivero-Villar¹, Marínés de la Peña-Domene^{1,2} , Gerardo Rodríguez-Tapia¹, Christian P. Giardina³ and Julio Campo^{1,*} 

¹ Instituto de Ecología, Universidad Nacional Autónoma de México, Mexico City 04510, Mexico; anaitzirv@ieciologia.unam.mx (A.R.-V.); marinespd@iteso.mx (M.d.l.P.-D.); gerardo@ieciologia.unam.mx (G.R.-T.)

² Centro Interdisciplinario para la Formación y Vinculación Social, Instituto Tecnológico y de Estudios Superiores de Occidente, Tlaquepaque 45604, Mexico

³ Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, HI 96720, USA; christian.p.giardina@usda.gov

* Correspondence: jcampo@ecologia.unam.mx; Tel.: +52-55-56229027

Abstract: Pantropical variation in soils of the tropical dry forest (TDF) biome is enormously high but has been poorly characterized. To quantify variation in the global distribution of TDF soil physical and chemical properties in relation to climate and geology, we produced a synthesis using 7500 points of data with gridded fields representing lithologic, edaphic, and climatic characteristics. Our analyses reveal that 75 TDF ecoregions across five biogeographic domains (Afrotropical, Australasian, Indo-Malayan, Neotropical, and Oceanian) varied strongly with respect to parent material: sediment (57%), metamorphic (22%), volcanic (13%), and plutonic (7%). TDF ecoregions support remarkably high variability in soil suborders (32), with the Neotropical and Oceanian realms being especially diverse. As a whole, TDF soils trend strongly toward low fertility with strong variation across biogeographic domains. Similarly, the exhibited soil properties marked heterogeneity across biogeographic domains, with soil depth varying by an order of magnitude and total organic C, N, and P pools varying threefold. Organic C and N pool sizes were negatively correlated with mean annual temperature (MAT) and positively correlated with mean annual precipitation (MAP). By contrast, the distribution of soil P pools was positively influenced by both MAT and MAP and likely by soil geochemistry, due to high variations in soil parent material across the biogeographic domains. The results summarized here raise important questions as to how climate and parent material control soil biogeochemical processes in TDFs.

Keywords: carbon; Entisols; nitrogen; phosphorus; soil climate relationships; soil fertility; Ultisols



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1. Introduction

Tropical landscapes are characterized by enormously high edaphic diversity, with soils ranging from pedologically young Entisols and Inceptisols to pedologically old Ultisols and Oxisols [1–3]. This edaphic variation exerts strong control over ecosystem functioning and dynamics [4], including in the tropical dry forest (TDF) biome, which exhibits high soil heterogeneity. To date, reviews portray TDFs as being dominated by medium- to high-fertility status soils e.g., [5,6], likely because TDF soils are generally less weathered compared to those found in more humid tropical climates, including tropical rain, wet, or moist forests or in tropical savannas [7,8]. This generalization may obscure the highly heterogeneous nature of TDF soils as a result of the wide variety of climate, parent material, topography, and vegetation that defines the TDF biome [9]. So, for TDF soils, as elsewhere, local to regional scale variation relates to both abiotic (edaphic properties, climatic conditions) and biotic (vegetation) conditions [10,11]. Variation in these variables and their interactions across TDFs result in very high heterogeneity in soil properties and soil-ecological processes and, consequently, highly dynamic biogeochemistry [12–15]. This dynamic condition in TDFs is accentuated by severe anthropogenic land use changes [16,17] that can expose

highly erodible and easily degraded soils [18,19] and that result in conditions that no longer support agroecosystem management over time [20,21].

A synthesis of baseline information for TDF soils would provide a critical resource to help guide restoration planning and implementation, conservation policy and management, and, importantly, conceptualizations of restoration science. Optimally, such a synthesis would integrate information about environmental change to complement the global distribution of physical and chemical properties of TDF soil. For example, recent findings indicate that land management can drive large losses of ecosystem carbon (C) from tropical forests, with most of this loss occurring in the Afrotropical and Neotropical regions [22,23]. Ecological restoration not only recovers stand-to-landscape scale biodiversity but also promotes C sequestration and increases in the nutrient capital of a site, which can offset C losses and enhance nitrogen (N) and phosphorus (P) availability [24,25]. The latter is important because soil N and P availability typically controls plant growth and C accumulation in TDF soils [26,27]. Landscape-level variation in soil fertility is an important constraint on the planning of effective TDF restoration strategies, with current knowledge gaps representing an obstacle to achieving diverse restoration goals. This knowledge gap is further complicated by climate change [28], including in the TDF biome, and soil–climate relationships in tropical landscapes increasingly complicate efforts to establish reference conditions to guide restoration efforts. Therefore, restoration-focused research is needed to understand the impact of climate change on the properties and biogeochemical functioning of TDF soils.

Here, we examine the remarkable spatial variation in the physical, chemical, and biological properties of soils across TDF biogeographic domains. Our analysis relied on (i) global data from multiple repositories, that allowed us to construct a database of 7500 points with gridded fields of lithologic, edaphic, and climatic characteristics in 75 TDF ecoregions and (ii) an examination of the sensitivity of TDF structure and function to climate variations [23,29,30], by relying on a pantropical assessment of how mean annual temperature (MAT), mean annual precipitation (MAP), and an aridity index relate to TDF soil pH, cation exchange capacity (CEC), and C and nutrient stocks. Our analyses combine data from across the Afrotropical, Australasian, Indo-Malayan, Neotropical, and Oceanian biogeographic domains, cover a wide variety of climates, lithologies, and soils, and were grouped according to their biogeographic distributions [31]. Our analyses were designed to quantify soil properties that often show marked heterogeneity across biogeographic domains. We were especially interested in exploring soil fertility, climate interactions, regional drivers of transformation and abandonment, and overall controls on a broad mosaic of secondary tropical forests in different successional stages [32].

2. Materials and Methods

2.1. Selection of Ecoregions

This study includes 75 ecoregions that contain TDFs, grouped into one of five biogeographic domains: Afrotropical, Australasian, Indo-Malayan, Neotropical, and Oceanian. We relied on definitions of TDFs that have been identified following (i) Olson et al. [33], (ii) assessments by regional authors and experts, or (iii) the FAO [34] assessment of TDFs (Table S1). Australia was excluded according to the World Wild Fund for Nature (WWF), whose delimitation of world ecoregions ‘Tropical and subtropical dry broadleaf forest’ is only distributed in the New Caledonia Island and remains in isolated patches.

2.2. Selection of Sample Points

From each ecoregion, a 1 km² grid was created, and then the centroid of each cell was calculated as a sample point. We selected 100 sample points from all the centroids in a random block design to fully assess the range of climatic and edaphic variation within each ecoregion (Figure 1). We assumed similar conditions within each ecoregion because they are defined as regions that are characterized by specific ecological patterns, including soil health, flora and fauna, climatic conditions, etc. [33]. All spatial analysis were conducted in

ArcGIS 10.2.1. Because the surface of each ecoregion differs greatly among them, we could not select different numbers of sample points for each ecoregion as this would result in an overrepresentation of values from larger ecoregions.

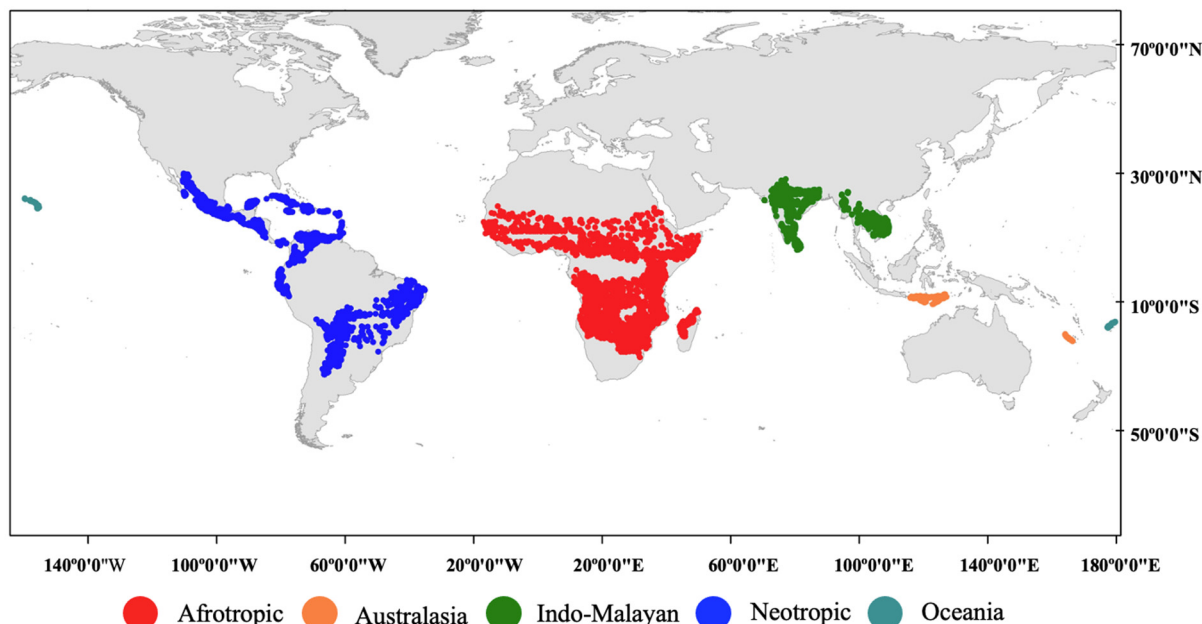


Figure 1. Tropical dry forest ecoregions. Each circle indicates the distribution of the 100 sample points within each ecoregion and colors indicate the five studied biogeographic domains.

2.3. Climatic and Edaphic Metrics

For each sample point, climatic, lithological, and edaphic data were obtained from different maps and satellite data repositories, including NASA Earth Observations (<https://neo.sci.gsfc.nasa.gov/>, accessed on 23 April 2021) [35], Climate Hazards Center, UC Santa Barbara (<https://www.chc.ucsb.edu/about>, accessed on 7 October 2021) [36], Numerical Terradynamic Simulation Group (NTSG), University of Montana (<https://www.ntsg.umt.edu/>, accessed on 14 October 2021) [37], Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) (data at 5.6 km resolution), Composition of the Geological map of the world (<https://ccgm.org/en/home/168-lithological-map-of-the-world-9782917310250.html>, accessed on 23 September 2021) [38] (data at 1 km resolution), Biogeochemical Dynamics NASA (<https://daac.ornl.gov/>, accessed on 23 September 2021) [39], and SoilGrids (<https://soilgrids.org/>, accessed on 23 April 2021) [40] (data at 1 km resolution). Soils are described at the suborder level within USDA soil taxonomy and were grouped according to their fertility (low, medium, and high) and water retention capacity (low, medium, and high). Eight climatic metrics were examined, including mean annual temperature (MAT), mean daily minimum temperature in the coolest month, and mean daily maximum temperature in the warmest month (hereafter known as minimum and maximum temperature, respectively), site water availability metrics including MAP, precipitation in the driest month, precipitation in the wettest month, total precipitation in the rainy season, and Lang aridity index (that is, the ratio between annual precipitation and temperature). Our approach integrates the climatic variability for an 11-year period (2004 to 2014) at the pantropical scale from satellite projections and we calculated average climate variables for each site. We also computed several metrics of soils from SoilGrids data that account for the physical and water retention properties encompassing the following: soil depth, bulk density, coarse fragments, clay content (representing soil texture), field capacity, water retention capacity, and the wilting point, as well as compiled information on soil pH and fertility properties, such as CEC, organic C, total N stocks, and total P stocks. Each metric was processed and harmonized to standard units.

2.4. Data Analysis

All statistical analyses were conducted in R version 4.0.3 [41]. To assess the climatic and edaphic characteristics across the 75 ecoregions, we compared ecoregions with respect to each of the five biogeographic domains. One-way ANOVA was used to explore soil and climate variations across each ecoregion and biogeographic domain.

The key axes of the multi-dimensional space of soil properties were identified using principal component analysis (PCA) [42]. Each variable was standardized. From the PCA results, the explained variance of each component was extracted and the loadings of the soil properties indicated the contribution of each variable to the component. A total of 7497 sample points (three points had no climatic and/or edaphic data) were obtained; this dataset allowed us to capture the high climatic and edaphic variation across world tropical dry forest biogeographic domains. PCA was performed using the PCA function implemented in the R package. Finally, we analyzed the predictive importance of three climate variables (MAT, MAP, and Lang aridity index) on five soil fertility properties (pH, CEC, organic C, total N, and total P) using Pearson's correlation analysis.

3. Results

The seventy-five ecoregions of this study are distributed in five biogeographic domains and four continents (Figure 1). The largest biogeographic domain is the Afrotropical region (14,600,868 km²), which accounts for 67.3% of the global cover of TDFs, and which includes 23 distinct ecoregions (Table S1). The second largest is the Neotropical region, which accounts for 24.4% of global TDFs, and which includes the most abundant variety of ecoregions [34]. This is followed by the Indo-Malayan biogeographic domain (7.9% and 12 ecoregions); meanwhile, the Australasian and Oceanian biogeographic domains combine to represent less than 0.5% of global TDFs and include six different ecoregions.

3.1. Global Lithological Classes and Soils

Identified TDF ecoregions have developed on at least twelve different lithological classes, with sampling points including: sedimentary (59%), metamorphic (22%), volcanic (11%), and plutonic (7%) geologies (Figure 2). Significant regional differences in lithology distribution were observable, e.g., Oceania is the biogeographic domain with lowest lithological variety, while Neotropical ecoregions have some representation of all the lithological classes. Sedimentary geology dominates the Neotropical, Australasian, Afrotropical, and Indo-Malayan landscapes (76%, 60%, 49%, and 47%, respectively), with abundant carbonate-containing rock units in the Australasian and Neotropical domains (21% and 14%, respectively). In contrast, sedimentary geology represents 8% in ecoregions of Oceania (with carbonate-containing rocks contributing only 3.5%).

Soil taxonomic diversity is enormous across TDF biogeographic domains of Africa, America, and Asia (Figure 3), with a total of 32 soil suborders identified across the TDF biome. A total of 69% of the soils corresponds to five suborders (Udults, Ustalfs, Ustolls, Usterts, and Ustox). The Neotropical biogeographic domain has the highest soil diversity, which accounts for 28 of the 32 known suborders (data not shown). In contrast, Australasia shows the lowest variety of soils with only eight suborders. Interestingly, Oceania has twice the number of soil suborders as Australasia in a much smaller area (13,308 and 90,548 km², respectively; Table S1). Soils with low fertility and medium water retention capacity dominate TDF ecoregions at the pantropical scale (Figure 3b).

There was high variation in soil properties at the pantropical scale and across biogeographic domains (Table S2 and Tables S3–S7, respectively). The deepest soils were from the Afrotropical domain (mean = 2.53 m), while Oceania demonstrated the shallowest soils (mean = 0.30 m; Figures 4a and S1). Oceania's soils had the lowest bulk density, while the Indo-Malayan biogeographic domain supported the highest density soils (1.23 and 1.52 g cm^{−3}, respectively; Figures 4b and S1). Coarse fragments were most abundant in Indo-Malayan soils, while soils of Australasia showed the lowest content of fragments (Figures 4c and S1). Clay content was highest in soils of the Indo-Malayan and

Neotropical biogeographic domains (38.8 and 38.2 percent, respectively), and lowest in soils of the Afrotropical region (29.9 percent; Figures 4d and S1).

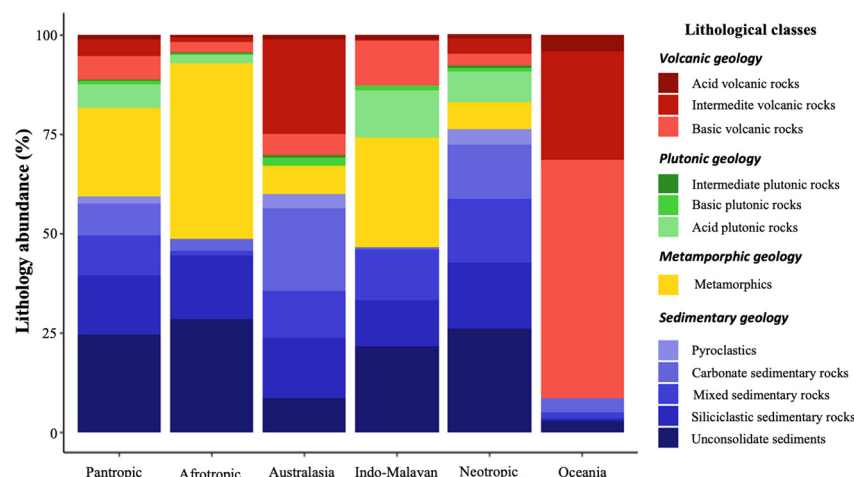


Figure 2. Lithology in tropical dry forest ecoregions within biogeographic domains and at the pantropical scale.

Significant variation in soil water retention was observed amongst biogeographic domains (Figure 5). For example, although average field capacity varied within a narrow range across biogeographic domains (from 399.7 mm in the Afrotropical realm to 418.7 mm in Australasia), differences were significant (Figures 5a and S2). In addition, soils of the Afrotropical domain were associated with the lowest mean wilting point and mean water holding capacity (Figures 5b,c and S2). In contrast, soils of Indo-Malayan biogeographic domain had the highest mean wilting point, while soils of Australasia had the highest mean water holding capacity.

Mean soil pH varied from 5.7 to 6.6 in the following the order: Australasian < Oceanian < Afrotropical < Neotropical < Indo-Malayan (Figures 6a and S3). Mean soil CEC was lowest in the Afrotropical domain, followed by Australasia; it was highest in soils of the Indo-Malayan biogeographic domain (Figures 6b and S3). Soils of the Neotropical and Oceanian domains constituted an intermediate, statistically homogeneous group ($p > 0.05$). Additionally, an increasing and significant gradient in soil organic C and total N stocks was found increasing from lowest to highest: Afrotropical ~ Indo-Malayan < Neotropical < Australasian < Oceanian (Figures 6c,d and S3). In contrast to C and N stocks detected across biogeographic domains, the Afrotropical region (and also Australasia) had the poorest P soils, while Oceania had the richest P soils (Figures 6e and S3).

The PCA analyses allowed us to identify soil features that were the most distinguished in each biogeographic domain, generating a clear separation between them. On the one hand, we found that Afrotropical soils were characterized as being the deepest, while Oceania is the biogeographic domain that had the most fertile soils with largest stocks of C, N, and P (Figure 7). On the other hand, Indo-Malayan soil separated in response to soil water retention metrics and clay content. The first two principal components explain 77 percent of data variation (Table 1). Across the entire dataset, the first principal component summarized 42 percent of the variation in soil metrics, particularly the variables that loaded most strongly into the first PC axis, which were soil bulk density and depth ($r = 0.98$, $p < 0.01$ and $r = 0.93$, $p < 0.05$, respectively) and the organic C and the total N stocks ($r = -0.98$, $p < 0.01$; in both cases). The second principal component (PC2) accounts for 34 percent of the variation, and the highest correlation to this axis was obtained from the wilting point, the clay content, and the CEC ($r = 0.96$, $p < 0.01$ in the cases of wilting point and clay content; and $r = 0.94$, $p = 0.05$, in the case of CEC).

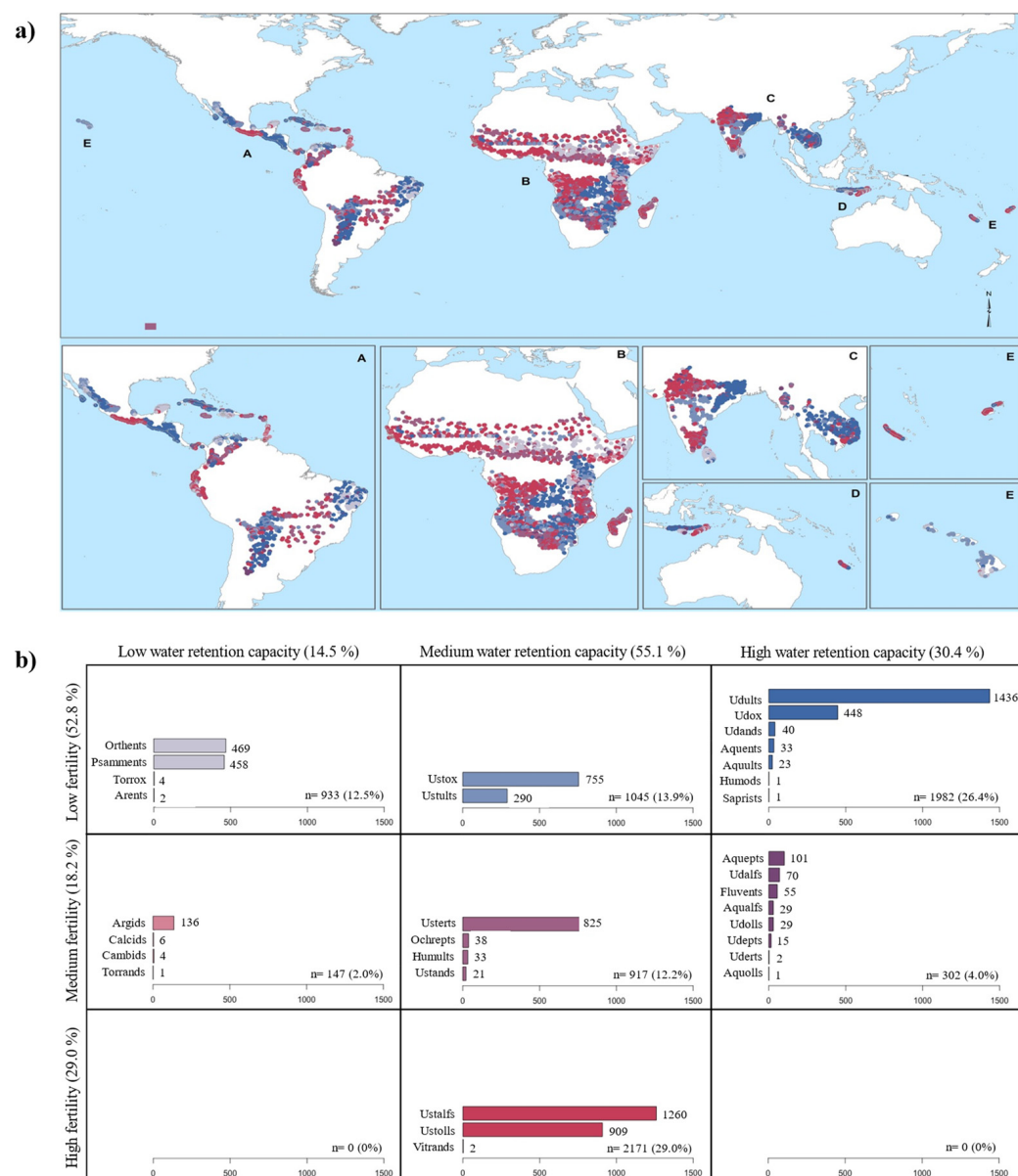


Figure 3. Soil distribution according to their fertility and water retention capacity in tropical dry forest ecoregions at the pantropical scale (a); filled color symbols indicate the combination of the soil fertility with the water retention capacity (as is indicated in panel (b)) and capital letters indicate the biogeographic domain: (A), Neotropical; (B), Afrotropical; (C), Indo-Malayan; (D), Australasian; and (E), Oceanian. Global soil suborders in tropical dry forest ecoregions; the horizontal grids indicate the soil fertility (low, medium, and high) and the vertical ones indicate the water retention capacity (low, medium, and high) (b).

3.2. Climate and Soil Fertility Relationships

Our results show that the MAT across ecoregions range from 22.0 to 37.7 °C with a pantropical mean of 29.2 °C (Table S2). The MAP is 1143.7 mm (range from 320.5 to 2294.1 mm) and, on average, TDF ecoregions suffer 7.4 dry months (precipitation is less than 100 mm) and 4.4 months of hydric stress for vegetation. The hottest ecoregions are the Afrotropical and Indo-Malayan biogeographic domains, both with a MAT of 30.4 °C, while Australasia and Oceania show the lowest MATs (Figure 8a). In addition, the Afrotropical region is the driest biogeographic domain (MAP of 913 mm); meanwhile, the wettest biogeographic domains are Australasia and Oceania (MAP of 1589 and 1516 mm, respectively).

(Figure 8b). We found an increasing and significant gradient of aridity: Australasian ~ Oceanian < Indo-Malayan < Neotropical < Afrotropical (Figure 8c).

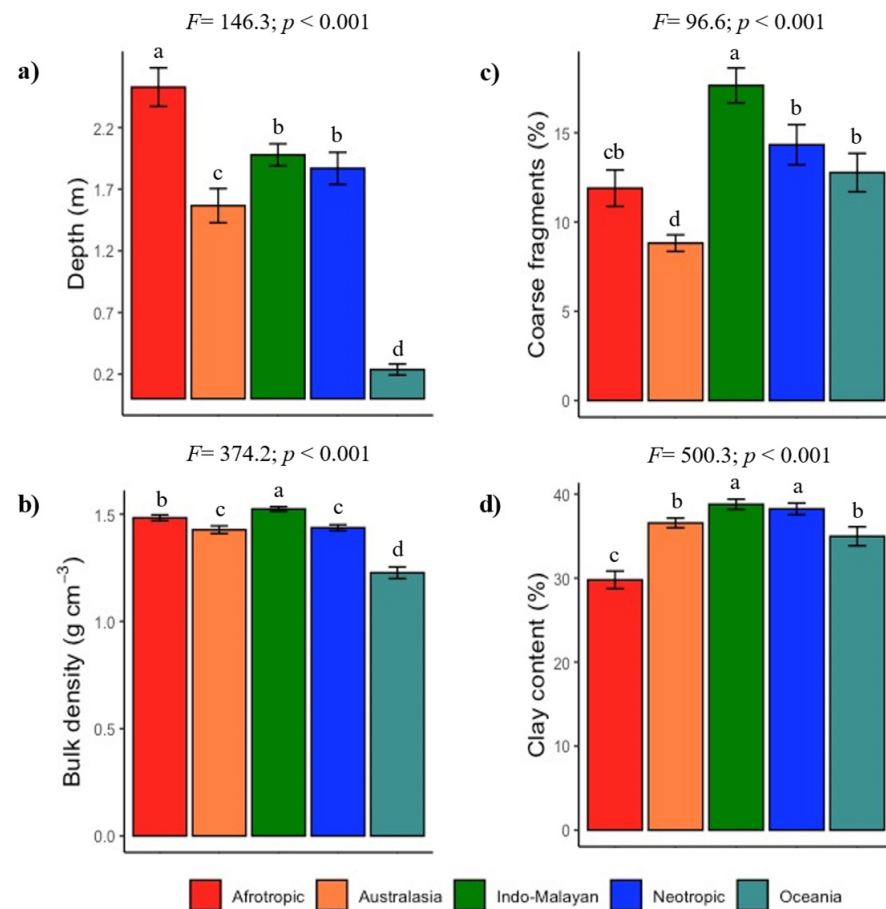


Figure 4. Spatial variation in soil physical properties. Panels indicate the soil depth (a), bulk density (b), and coarse fragment (c) and clay (d) contents. Values are mean $\pm$ 1SE and different letters indicate significant difference ($p < 0.05$) across biogeographic domains.

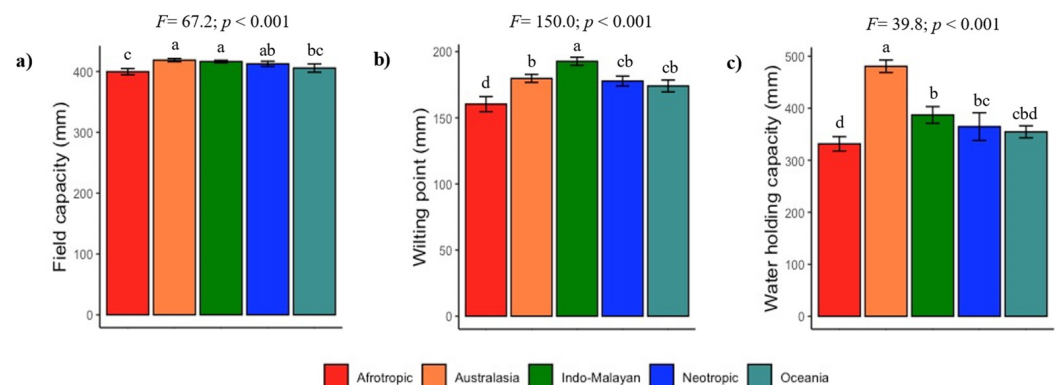


Figure 5. Spatial variation in soil water retention capacity. Panels indicate soil field capacity (a), wilting point (b), and water retention capacity (c). Values are mean $\pm$ 1SE and different letters indicate significant difference ($p < 0.05$) across biogeographic domains.

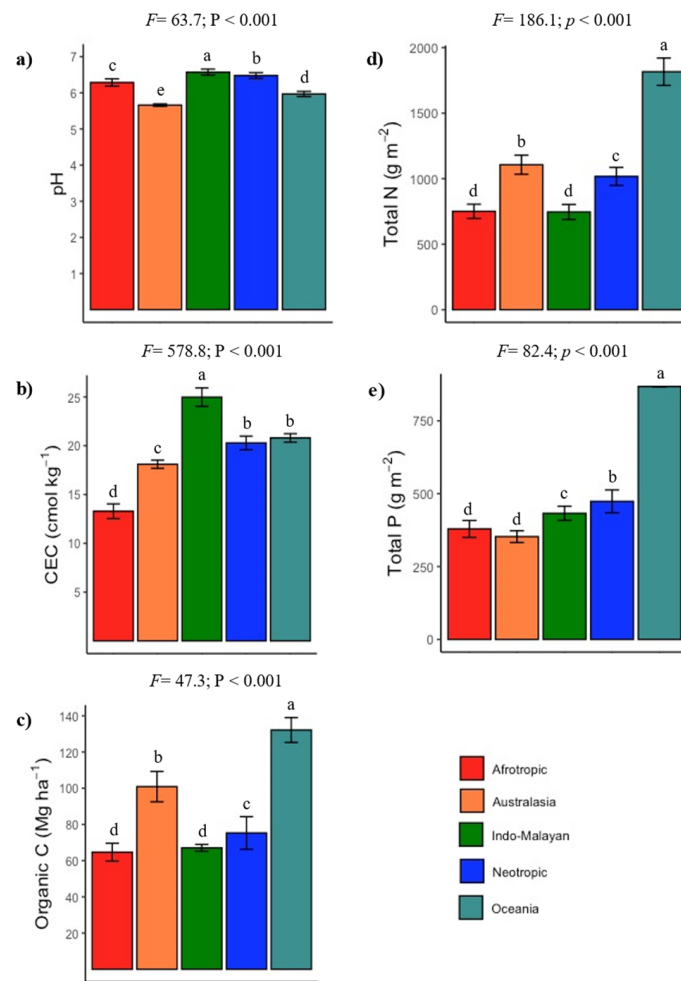


Figure 6. Spatial variation in soil fertility properties. Panels indicate soil pH (a), cation exchange capacity (b), organic carbon (c), total nitrogen (d), and total phosphorus (e) contents. Values are mean $\pm$ 1SE and different letters indicate significant difference ($p < 0.05$) across biogeographic domains.

Table 1. Eigenvalues, cumulative percent variation, and eigenvectors of the first three principal components (PCs) for the soil metrics in tropical dry forest ecoregions at the pantropical scale.

	PC1	PC2	PC3
Eigenvalue	5.168	4.307	2.169
Cumulative variation percent	43.06	76.99	98.69
Eigenvectors			
Soil depth	−0.925	0.355	0.128
Bulk density	−0.982	0.017	0.162
Coarse fragments	−0.434	−0.452	−0.772
Clay content	−0.121	−0.958	0.019
Field capacity	−0.215	−0.842	0.487
Water holding capacity	0.025	−0.473	0.877
Wilting point	−0.227	−0.963	0.011
pH	−0.662	−0.097	−0.732
Cation exchange capacity	−0.025	−0.936	−0.334
Organic carbon	0.976	−0.187	−0.101
Total nitrogen	0.979	−0.147	−0.119
Total phosphorus	0.834	−0.14	−0.533

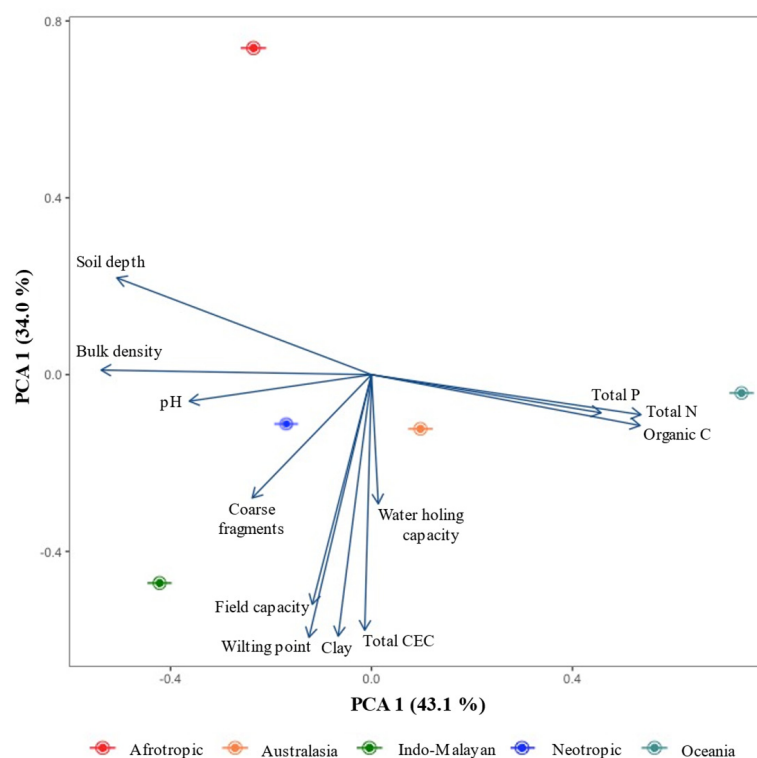


Figure 7. Principal component analysis (PCA) biplot of the edaphic metrics in tropical dry forest ecoregions at the pantropical scale.

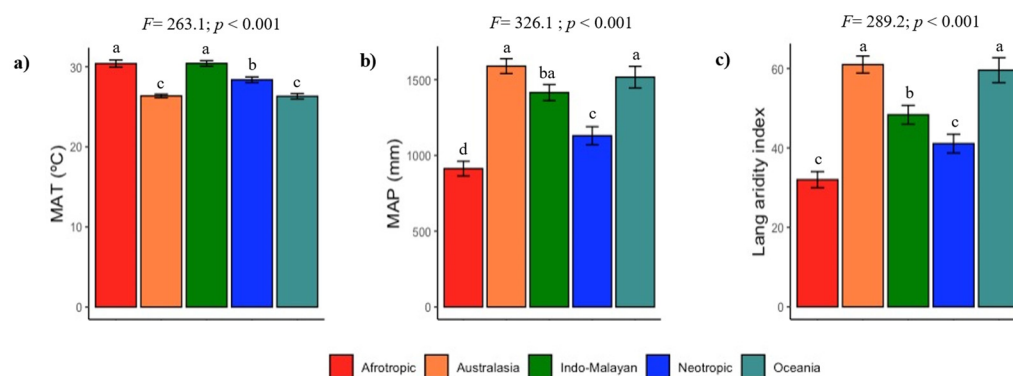


Figure 8. Spatial variation in mean annual temperature (a), mean annual precipitation (b), and Lang aridity index (c). Values are mean $\pm$ 1 SE and different letters indicate significant difference ($p < 0.05$) across biogeographic domains.

Of all properties, soil pH was the property most strongly related to climate (values increased with MAT and decreased with MAP and aridity index) (Figure 9a–c, Table S8). In contrast, CEC was the least climate-sensitive soil characteristic, with no statistically significant relationship with MAP (Figure 9d–f). CEC did show a relationship with precipitation in the driest month and precipitation in the wettest month (Table S8). Total soil C and N stocks decreased with increasing MAT, while increasing with MAP (Figure 9g–i). Total soil C responded the most strongly to precipitation variables, increasing with precipitation in the driest month (Table S8). Total soil P was also strongly related to precipitation in the driest month and minimum temperature (Figure 9m–o, Table S8); the size of pools of this rock-derived nutrient decreased with both increasing aridity index and decreasing MAP (Figure 9n,o).

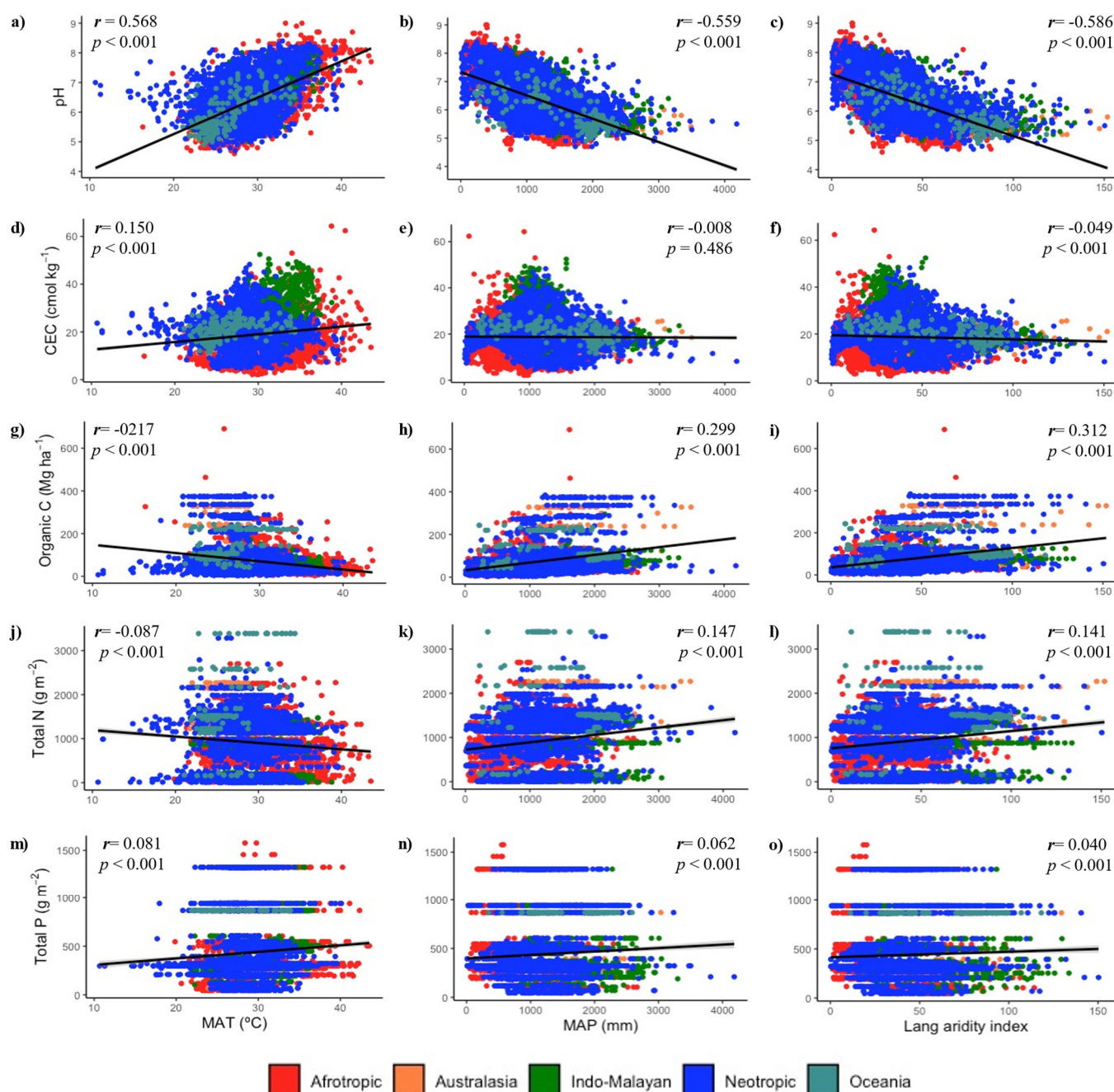


Figure 9. Relationships between soil pH (a–c), cation exchange capacity (d–f), organic carbon (g–i), total nitrogen (j–l), total phosphorus (m–o) contents and main climate drivers of the tropical dry forest distribution and function. Colored points show data for each biogeographic domain. Black lines show pantropical bivariate relationships.

4. Discussion

Waring et al. provided a synthesis of variation in and environmental controls over soil biogeochemistry across Neotropical TDF [9], providing an expanded understanding of the factors that regulate Neotropical soils, we expand on this analysis to examine global scale environmental controls on TDF soil diversity and soil physical and chemical properties. In this analysis, we examined 75 ecoregions within five biogeographic domains (Afrotropical, Australasian, Indo-Malayan, Neotropical, and Oceanian) to assess how soil physical and chemical properties varied with climatic and geological characteristics. We defined TDF according to the World Wildlife Fund's global priority ecoregions assessment [33]. This ap-

proach resulted in important edaphic differences among biogeographic domains that reflect the high parent material diversity and climatic variability across the TDF biome [9,10,43].

4.1. Soil Diversity in the Tropical Dry Forest Biome

Our study results show that, at a pantropical resolution, TDF ecoregions capture enormous variability in the composition of soil parent material (Figure 2), accounting for twelve of the sixteen global lithological classes [44] and reinforcing the idea that tropical forest biogeochemistry is often highly heterogeneous at local and regional scales [10,45]. Despite this high variability in rock types, with the highest diversity of lithologies in the Neotropical realm, TDF landscapes are generally associated with sedimentary geologies with abundant carbonate-containing rock units. This lithological variation influences spatial variability in soil properties and terrestrial biogeochemistry [6,46] as well as the supply of rock-derived nutrients that are essential for plant growth and microbial activity [47], and that can limit ecosystem productivity in the tropics [48].

Our data also shows that soil taxa across TDF ecoregions are diverse at the pantropical scale (Figure 3). Common soils include nutrient-poor soils that are either well-drained and have clay-enriched subsoils (Udults) or are iron and aluminum-rich and friable (Udox); soils with medium (Ustox and Ustults) or low capacity for water retention are considered sandy soils (Orthents), including those deposited by rivers on plains (Psamments). Additionally, TDF ecoregions include deep, organic-rich soils that are often highly fertile (Ustalfs and Ustolls), and rocky and shallow soils on slopes (Usterts). Our principal component analyses revealed global distributions of TDF soil depth and clay content, which influence water retention capacity across the soil profile as well as plant growth and nutrient availability [15,49,50]. Although the exhibited soil properties marked heterogeneity across biogeographic domains, with mean soil depth varying by an order of magnitude and total organic C, N, and P pools by threefold, our data indicate that TDF ecoregions are dominated by nutrient-poor soils with a medium capacity for retaining rainfall water.

4.2. Are Tropical Dry Forest Soils Fertile?

Our approach to classify soil suborders as belonging to three main fertility groups (according to Vitousek and Sanford [51]) allowed us to broadly assess the fertility of TDF [7,52]. We found that, globally, 29% of TDF soils would be characterized as fertile, whereas 53% would be described as nutrient-poor (Figure 3), aligning with analyses showing that about half of all TDFs occur on highly weathered soils [50,53]. The large proportion of infertile TDF soils have low nutrient, particularly P availability, which may constrain plant and microbial growth, as with heavily weathered soils in humid tropical forest biomes [54,55]. On the other hand, the frequent suggestion in the literature that TDFs are developed on fertile soil seems to be influenced by the soil properties of the Neotropical biogeographic domain, where TDF ecosystems have been extensively studied (see efforts of synthesis in [5,52,56–59]).

4.3. Vulnerability of Tropical Dry Forest Soils to Disturbances

We analyze the relative importance of twelve soil properties on the predictability of soils at the biogeographic domain scale. By analyzing this set of soil properties across major TDF ecoregions and biogeographic domains in a multivariate PCA (Figure 7), our study results show that the first and most important axis represents soil chemical and physical properties and is driven by total soil C and nutrients, soil bulk density, and soil depth. This analysis clearly separated the shallow and nutrient-rich soils of Oceania. The second axis, related to water retention capacity, was driven by clay content and related to soil weathering indicated by the CEC. This axis separated the highly weathered soils of African TDFs, which saw the lowest values of water retention capacity, from those of the Indo-Malayan region, which were characterized by high CEC and high water retention capacity. This differentiation in soil depth and nutrient content based on the Afrotropical

and Oceanian biogeographic domains highlights the importance of these multi-domain analyses, and the biases that can emerge from single domain analyses.

Oceania is the biogeographic domain that accounts for the largest C, N, and P stocks (Figure 6), a crude measure of soil fertility status [60]. The fertility observed in Oceanian soils is related to the high percent of volcanic parent material (90% of the area is covered by volcanic rocks) that, in combination with low precipitation, leads to moderate to high fertility soils. According to the conceptual model of the development of soils [61], these high values for total soil P are expected and are at least 50% greater than in other biogeographic domains; Ca, K, and Mg would be expected to follow similar patterns because base cations are also rock-derived elements [62,63]. In the Hawaiian portion of Oceania, recent volcanism has led to very young and minimally weathered soils. Across natural precipitation gradients in Hawai'i, island soil nutrient concentrations for N and the base cations decrease with large increases in the annual precipitation amount [64]. Although much of the available cations (e.g., Ca, Mg, and K) have been weathered from primary minerals, are highly leachable, and get lost rapidly, P is much less mobile and retained within the soil system [62], as has been shown in young volcanic TDF soils of Mexico [64,65].

In contrast, Afrotropical TDFs tend to develop on the least fertile soils and with the most severe conditions of aridity, including the hottest temperatures and the lowest rainfall amounts. These low fertility and low productivity conditions likely explain why, globally, African TDFs are among the lowest biomass forests in the TDF biome [66]. The deep and poor African soils may reflect a longer pedogenetic process in contrast to the those in other biogeographic domains; for example, soils of Africa, particularly those in the west of the continent are very weathered, representing among the oldest (100 s of millions to billions of years old) surface rocks on the planet [67,68]. Furthermore, parent material in this domain is often composed of granites and gneisses, which tend to lead to lower nutrient status soils [69]. These conditions likely explain the low CEC observed in our study. Finally, the low biomass of African TDFs may reflect a low availability of soil water, both because of low rainfall and high temperatures, but also because the biogeographic domain is associated with what is among the lowest mean values for clay content, which is a soil characteristic that drives soil water content [70] and a factor that modulates phenological patterns and biogeochemistry in TDF ecosystems [71,72].

Despite the uncertainties related to global land cover data [73], the deep, nutrient-poor Afrotropical soils and shallow, nutrient-rich soils of Oceania constitute TDF extremes on a complex TDF gradient of conditions, with implications for soil conservation management and the practice of restoration of TDF landscapes. On the one hand, the shallow soils of Oceania are very sensitive to land-use and land-cover change-driven erosion. A total of 35% of this domain is in a degraded state, which is the largest among global TDFs [74], and soil conservation represents a significant priority for stewardship organizations in the domain. In the Afrotropical domain, very low water retention capacity, high temperatures, and low rainfall make it the most arid among global TDFs. Compounding these problems, this domain is among the largest in deforestation rates across continents, including a continuous increase in the rate of deforestation in the last 30 years (1990–2020) [74]. Where the nutrient capital of a forest is distributed more heavily in live biomass, land-conversion-related loss of nutrients may represent another set of constraints on effective restoration for the domain. In the case of both the Oceanian and Afrotropical realms, soil resources represent important limitations for the success of TDF restoration plans, highlighting, for example, the importance of selecting species with root systems, nutrient use efficiencies, and water-use strategies that are mostly likely to drive restoration success.

4.4. Vulnerability of Soil C, N, and P to Ongoing Climate Change: Some Clues Derived from the Relationship between Soil Fertility and Climate in TDF Ecoregions

Our analyses provide a novel pantropical overview of climatic and geological variation, which combine to influence soil fertility and water availability in the TDF biome. Aridity

captured in this study from the Lang aridity index positively correlated with total soil C and nutrients (Figure 9), reflecting the effects of precipitation amounts in the driest month rather than precipitation in the wettest month or rainy season precipitation (Table S8). This C pattern in soils across TDF landscapes is consistent with the observed sensitivity of ecosystem function to precipitation amount in the dry season [15,75–77]. This result also highlights the sensitivity of C and nutrient stocks in these TDF ecosystems to droughts and long-term drying; for example, when baseline changes drive longer and more severe dry seasons. While change is likely, rates of change in total soil C and nutrients cannot be inferred from our spatial analyses.

Our analysis also suggests complex effects of temperature on total soil C and N (Figure 9). The sensitivity of total soil C to temperature related primarily to a positive relationship with maximum temperature and, to a lesser extent, a positive relationship with minimum temperature (Table S8). However, these strong relationships across TDF ecoregions involved variation in precipitation regime, which can have important interacting effects on ecosystem productivity and biogeochemistry [78]. Moreover, in a recent pantropical study of TDF fires, Corona-Núñez and Campo [79] found that the most extensive fires and highest biomass consumption rates during 1997–2020 were driven by climate, particularly related to high water stress, itself driven by low precipitation, high temperature, and an increase in aridity. The worst fire conditions were associated with years seeing the strongest El Niño events. Given future warming and increased variability in precipitation [28], understanding both short-term and long-term impacts of climate change on this biome will require a new generation of observational, experimental manipulation-based, and modeling-based studies.

5. Conclusions

The results summarized here highlight the remarkable diversity of TDF soils, as well as that this diversity is not evenly distributed across the TDF biome. At various ecoregional and biogeographic domain scales, variation in climatic and geological properties of TDF systems resulted in strong consequences for soil physical and biogeochemical properties, with implications for productivity and ecosystem recovery [14,80]. Our analyses also show how strongly soil fertility varies across biogeographic domains, with complex drivers for this variation, defying efforts to generalize about this global biome. We also conclude that a detailed understanding of soil diversity at all spatial scales and their relationship with the climate may be required to accurately predict the impact of global warming on forest C, improve restoration of tropical dry forest ecosystems, and improve the sustainable soil management in future scenarios.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/su14116803/s1>, Table S1. Biogeographic domains and ecoregions included in this study, their surfaces, and centroids. Number of ecoregions within each biogeographic domain in parentheses; Table S2. Statistical metrics of climate and soil variables selected for this study; Tables S3–S7. Statistical metrics of climate and soil variables selected for biogeographic domains; Table S8. Correlates of spatial variation in soil fertility properties with climate in tropical dry forest ecoregions; Figure S1. Variation in soil physical properties within and amongst biogeographic domains; Figure S2. Variation in soil water retention properties within and amongst biogeographic domains; Figure S3. Variation in soil fertility properties within and amongst biogeographic domains.

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Data Availability Statement: Data supporting the reported results and datasets generated during the study are available upon request.

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Abbreviations

CEC	cation exchange capacity
MAP	mean annual precipitation
MAT	mean annual temperature
PC	principal component
PCA	principal component analysis
TDF	tropical dry forest

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