The Botanical Review
https://doi.org/10.1007/s12229-022-09278-2

Global Plant Ecology of Tropical Ultramafic Ecosystems

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Abstract

Ultramafic ecosystems are renowned for high endemism and habitat specialization. However, most of our understanding of ultramafic plant ecology comes from Mediterranean and temperate climes, raising questions about the generalizability of plant responses to ultramafic soils. This is especially apparent in tropical ultramafic ecosystems which exhibit a wide range of endemism and differentiation between ultramafic and adjacent non-ultramafic soils. Our objectives were two-fold: 1) synthesize our understanding of tropical ultramafic plant ecology, paying particular attention to generalities that may explain variation in endemism and habitat specialization among tropical ultramafic ecosystems; and 2) define an interdisciplinary research agenda using tropical ultramafic ecosystems as a macroecological model. We demonstrate that tropical ultramafic floras are diverse and variable in plant form and function due to the interactive effects of biogeography, climate, and edaphic properties. The variable rates of endemism, specialization, and stress tolerance traits across tropical ultramafic ecosystems have implications for the management and conservation of these diverse systems.

Resumen.

Los ecosistemas ultramáficos son reconocidos por su endemismo y especialización del hábitat. Sin embargo, la mayor parte de nuestra comprensión de la ecología vegetal ultramáfica proviene de climas mediterráneos y templados, lo que plantea dudas sobre la generalización de las respuestas de las plantas a los suelos ultramáficos. Esto es especialmente evidente en los ecosistemas tropicales ultramáficos que exhiben una amplia gama de endemismo y diferenciación entre suelos tropicales ultramáficos y no ultramáficos adyacentes. Nosotros teníamos dos objetivos: 1) sintetizar nuestra comprensión actual de la ecología de las plantas tropicales ultramáficas, prestando especial atención a las generalidades que pueden explicar la variación en el endemismo y la especialización del hábitat entre los ecosistemas tropicales ultramáficos; y 2) definir una agenda de investigación interdisciplinaria utilizando ecosistemas ultramáficos tropicales como modelo macroecológico. Las floras tropicales ultramáficas son diversas y variables en la forma y función de las plantas debido a los efectos interactivos de la biogeografía, el clima y las propiedades edáficas. Las tasas variables de endemismo, especialización y rasgos de tolerancia al estrés en los ecosistemas tropicales ultramáficos tienen implicaciones para el manejo y conservación de estos diversos sistemas.

Keywords Edaphic · Endemism · Hyperaccumulator · Metallophyte · Serpentine · Unusual soil

Introduction

Ultramafic (serpentine) soils have long attracted scientific attention due to their specialized flora and ecological and evolutionary implications. However, our understanding of ultramafic plant ecology remains dominated by research from temperate and Mediterranean ecosystems (e.g., Brady et al., 2005; Huenneke et al., 1990; Kazakou et al., 2008), raising questions about the generality of plant responses to ultramafic soils. Here, we review and synthesize our current understanding of tropical ultramafic ecosystems, highlighting significant gaps in our understanding to stimulate future research and collaboration across the tropics. We begin with a brief overview of shared characteristics of ultramafic soils and then describe how and why tropical ultramafic ecosystems may differ from ultramafic ecosystems in extra-tropical latitudes.

Ultramafic soils are globally distributed (Fig. 1) and derived from high iron and magnesium rocks which comprise Earth's mantle and most of its oceanic crust. Ultramafic rocks are hydrothermally altered (a process called serpentinization when that rock is peridotite), typically on the ocean floor, and can emerge due to the subduction of tectonic plates. As a result, ultramafic rocks and the soils derived from

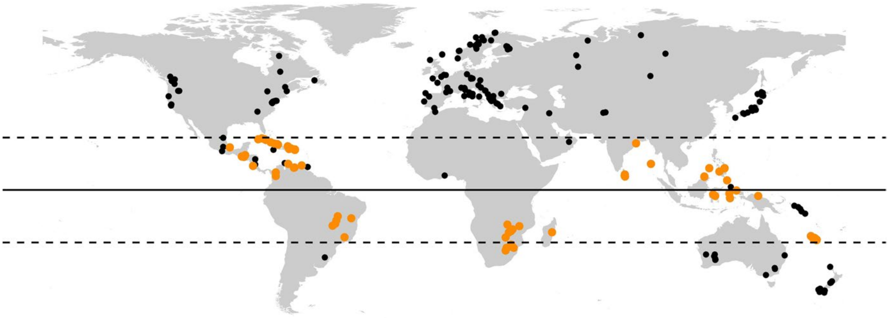

Fig. 1 The global distribution of ultramafic soils. Orange-filled points indicate major ultramafic formations reviewed in this study. Black-filled points indicate other ultramafic formations. Dashed lines indicate the Tropics of Cancer and Capricorn. Global ultramafic distribution data updated from Hulshof and Spasojevic (2021)

them are not randomly distributed; instead, they are often associated with active plate margins (Coleman & Jove, 1992; Moores, 2011). Because they form at seafloor spreading centers, ultramafic rocks played a prominent role in the development of plate tectonic theory, and serpentinization is considered an important analog for early ecosystems on both Earth and Mars (Moores, 2011). Variation in the structure and composition of ultramafic rocks due to processes occurring during their formation and weathering results in variation in the composition of soils derived from them which, in turn, influences the ecology of ultramafic plant communities.

In general, ultramafic soils tend to develop into Cambisols and Ferralsols (Echevarria et al., 2018) depending on underlying bedrock geochemistry and regional conditions (Proctor, 2003). Soils derived from ultramafic rocks are generally nutrient-poor, enriched in heavy metals and Mg, have low water-holding capacity, and are spatially patchy. The edaphic characteristics of ultramafic soils are known to negatively affect plant growth. Low P and K and low Ca/Mg ratios are key factors restricting plant development on ultramafic soils (Brady et al., 2005; Konečná et al., 2020; Kruckeberg, 1984; Palm & Volkenburgh 2014; Walker, 1954). Additionally, high concentrations of Ni, Mn, and Cr in the soils can lead to toxic concentrations in plant tissues (Brady et al., 2005; Seregin & Kozhevnikova, 2006). As a result, ultramafic soils are often inhabited by plants tolerant of low Ca and high concentrations of Ni (Isnard et al., 2016; Reeves et al., 1999) and plants with mechanisms to suppress heavy metal uptake (Oze et al., 2008). Together, these features often produce an unusual flora distinguishable in form, function, and species composition, characterized by high rates of endemism, high habitat specialization, slow plant growth rates, reduced leaf area, sclerophylly, and succulence (i.e., the serpentine syndrome) (Anacker et al., 2011; Brady et al., 2005; Jaffré, 1992; Jenny, 1980; Kazakou et al., 2008; Kruckeberg, 1984; Rajakaruna & Baker, 2004; Whittaker, 1954).

However, rates of endemism vary widely among tropical ultramafic outcrops; the degree of endemism in some areas is astounding (e.g., New Caledonia, Cuba, and Malaysia), yet limited or entirely lacking in others (e.g., Puerto Rico, Costa Rica, Sri Lanka). The age of tropical ultramafic soils may underlie differences in endemism, with more endemic species in older formations (Brooks, 1987; Reeves et al., 1983a). Alternatively, tropical ultramafic soils may not be as infertile as generally assumed based on work predominately in extra-tropical regions. The warmer temperatures and greater precipitation of tropical regions (Fig. 2) influence the geochemical composition of ultramafic soils (Lewis et al., 2006). Warmer temperatures and greater precipitation may increase decomposition and nutrient cycling (Austin & Vitousek, 1998) compared to extra-tropical regions, which could, in turn, counter the toxic effects caused by the excess of heavy metals (Stefanowicz et al., 2012). Faster decomposition and nutrient cycling could thus improve the low soil fertility of ultramafic soils in tropical areas; however, whether decomposition rates differ between tropical and extra-tropical ultramafic regions or between tropical ultramafic and adjacent non-ultramafic soils remains an open question. The montane rain forests that develop on ultramafic substrates (e.g., Aiba et al., 2015) provide some evidence of important climate-soil interactions and suggest that ultramafic soils may not be as infertile or harsh as is widely accepted. However, in other tropical areas with similar climates, the edaphic conditions of ultramafic soils promote similar flora in distant regions (Pillon et al., 2019), suggesting that the edaphic factor still plays a dominant role in determining plant composition, structure and function. Understanding the contrasting structure and function of tropical ultramafic plant communities at macroecological scales is thus warranted (Hulshof & Spasojevic, 2020).

Habitat specialization among tropical ultramafic and adjacent, non-ultramafic plant communities can also vary widely. Habitat specialization is caused

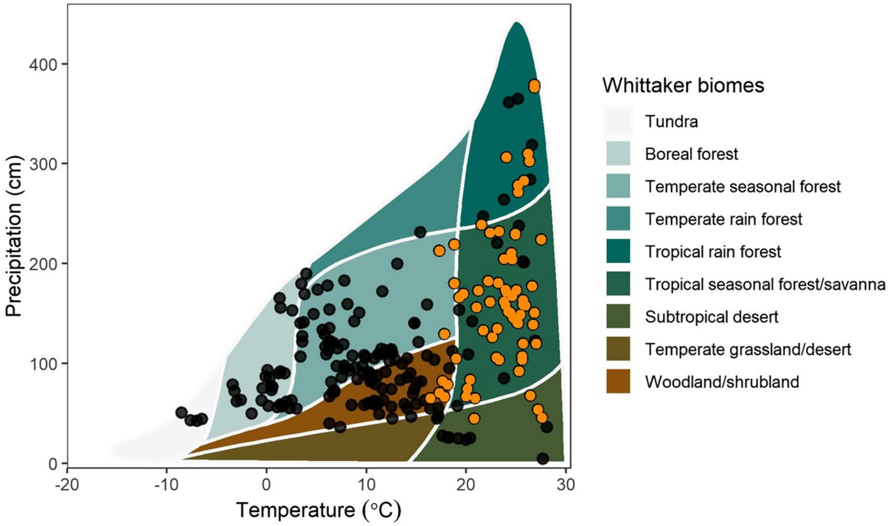

Fig. 2 Precipitation (cm) and temperature (°C) (known as a Whittaker biome plot) across ultramafic formations worldwide (global ultramafic outcrop distribution data updated from Hulshof and Spasojevic (2021), as shown in Fig. 1). Orange-filled data points indicate regions discussed in the present review. Tropical ultramafic formations occur across warmer temperatures and a broader range of precipitation than extra-tropical latitudes which may play important roles in determining patterns of plant diversity, form and function

by physiological adaptation to abiotic conditions at a cost to competitive ability (Anacker, 2014; Kruckeberg, 1951; Sianta & Kay, 2019). However, the competitive ability of tropical ultramafic plants compared to tropical non-ultramafic plants has not been studied. In addition, although herbivores affect tropical plant populations and their distributions across edaphic gradients (Fine et al., 2004), whether herbivores can reinforce or reduce differences between tropical ultramafic and non-ultramafic plant communities is not well known (e.g., Lau et al., 2008). Symbiotic rhizobia, mycorrhizal fungi, and other soil microorganisms may also increase soil nutrient availability or decrease soil metal concentrations, reducing differences between ultramafic and adjacent, non-ultramafic plant communities (e.g., Southworth et al., 2014). In tropical Brazil, for example, microbial decomposers were unaffected by ultramafic soils (Guimarães *unpublished data*). Serpentine soils also appear to promote ectomycorrhizal fungal diversity (Branco, 2010), which points to an important role of symbiosis in maintaining plant diversity in otherwise stressful habitats. Understanding the degree of habitat specialization in ultramafic and adjacent non-ultramafic soils has consequences for understanding other biotic interactions as well. The structure of pollinator networks, for example, may be influenced by high plant endemism or small floral size of highly specialized ultramafic flora (Alameda et al., 2020) which could have major implications for the maintenance of small, fragmented ultramafic plant populations as insect populations decline worldwide.

Although the tropical ultramafic plant ecology of some regions is well studied (e.g., New Caledonia: Jaffré et al., 2013; Pillon et al., 2010; Cuba: Areces-Berazaín et al., 2004; Borhidi, 1988a; Brooks, 1987), other regions, especially those with few to no endemic species or hyperaccumulators, remain understudied (Alexander et al., 2007; Rajakaruna & Boyd, 2009). Here, we argue that tropical ultramafic ecosystems are a unique macroecological model that can reveal fundamental interactions between climatic and edaphic properties underlying plant diversity patterns. Our objectives are two-fold. First, we synthesize our current understanding of tropical ultramafic plant ecology worldwide. We describe the ultramafic soils and vegetation within each region and then offer insight into drivers of plant form and function among tropical ultramafic plant communities (Table 1). Second, to guide future work, we outline a research agenda based on a macroecological approach. We describe how integrative research could help unify plant community ecology, plant physiology, geology, and soil biology to address critical questions in macroecology and macroevolution and promote the conservation of these globally distributed soils and their diverse biota.

We organize our synthesis by region, beginning with the Americas (Fig. 3). Except for Cuba, ultramafic ecosystems in the tropical Americas are poorly studied. We next traverse southern Africa, where ultramafic outcrops are widespread but, again, understudied. Finally, our synthesis ends in Asia and New Caledonia, global hotspots of ultramafic endemism and metal hyperaccumulation. In these regions, ultramafic endemism can reach 60% of the local flora, where complex biogeographical histories, diverse topography and climate, and geographic isolation have created an exceptionally diverse flora.

Table 1 Major tropical ultramafic ecosystems worldwide, including their approximate area as a percent of the total landmass of the larger geographic unit (region) and in square kilometers, elevational range, percent endemism, estimated geological age (MYA), range of mean annual precipitation (mm) and research priorities identified by regional experts

Region	Location	Area (%)	Area (km^2)	Elev. (masl)	Endemism (%)	Age (MYA)	Mean Annual Precipitation (mm)	Research priority
Puerto Rico	Sierra Bermeja; Susua; Maricao	1.5	135	250 – 900	4 island endemics	47–120	1200–2500	Interactions between climate, soil nutrient availability, and plant structure and function
Dominican Republic	Cordillera Central; Sierra de Yamasá; Cordillera Septentrional; Península de Samaná	2.54	475	5–380	54 sp	100–145	1318–1888	Plant conservation status and examining the potential for providing ecosystem services
Cuba	Throughout	7	5000 total (outcrops vary 61—1115)	70–380	3623 sp (57%)	1–30	1080–2140	Update of local inventories, floristic relationships between different outcrops, dispersal routes of the ultramafic flora, and a high-resolution national map of ultramafic plant formations

Table 1 (continued)

Region	Location	Area (%)	Area (km^2)	Elev. (masl)	Endemism (%)	Age (MYA)	Mean Annual Precipitation (mm)	Research priority
Guatemala	Sierra de Chaucas; Sierra de las Minas; Sierra Espiritu Santo; Sierra de Santa Cruz	2.04	2223	500– 2700	Unknown	85	10–2220	Compile plant composition data, including the degree of endemism and abundance data for each species
Costa Rica	Peninsula de Santa Elena	0.5	250	0–720	Unknown	85	800	The disappearance of clouds and associated cloud forested peaks and their associated fauna
Venezuela	Cerro Colorado, Falcon State; Loma de Hierro; Margarita Island	0.04	374	400– 700	Unknown	66–100	1230 (Loma de Hierro) 939 (Cerro Copey)	Physiological adaptation of species in ultramafic areas, geochemical research of plant material, and collection of seed material for experimental analysis

Table 1 (continued)

Region	Location	Area (%)	Area (km^2)	Elev. (masl)	Endemism (%)	Age (MYA)	Mean Annual Precipitation (mm)	Research priority
Brazil	Morro das Almas, Minas Gerais; various locations in Goiás, Bahia, and Pará	Unknown	8.17 (Morro das Almas)	950– 1785	5sp, but a few remain to be described	600–3000	1500	Understanding plant-soil microbial interactions and determining whether soil microorganisms play an active role in chelating heavy metals
South Africa & Eswatini	Barberton	0.04	500 (various outcrops)	750– 1800	~50 sp of 1600 sp (3.1%)	3500	750–1350	Detailed floristic surveys
South Africa	Sekhukhuneland	0.2	2400	900– 1900	~30 sp of 2200 sp (1.4%)	1950	650–950	Detailed floristic surveys
Zimbabwe	Great Dyke	0.64	2500	500– 1000	~30 sp of 1000 sp (3%)	2500	800–1200	Detailed floristic surveys
Sri Lanka	Along the boundary of the Vijayan and Highland Series	< 1	Six outcrops (less than 4 km^2 each)	11– 1000	No known ultramafic endemics. 3314 species of vascular plants are found in SL, of which 26.9% are endemic to the island	485	1000–3000	Detailed species surveys, including morphological and phenological observations to indicate ecotypic differences between ultramafic and non-ultramafic regions
Malaysia	Sabah, Borneo; Kinabalu Park	1.06	3500	180–2900	2542 sp (great part endemic?)	66–100	2000–3800 (Mt Kinabalu)	Detailed floristic surveys

Table 1 (continued)

Region	Location	Area (%)	Area (km^2)	Elev. (masl)	Endemism (%)	Age (MYA)	Mean Annual Precipitation (mm)	Research priority
Indonesia	Sulawesi and Halmahera Island	1.2	15,000 (sulawesi) + 8000 (Halmahera)	60–500	2225 species endemic to Sulawesi	66	Unknown	Detailed floristic surveys
Philippines	Palawan, Mindanao and Luzon Islands	Unknown	Unknown	50–1540	Unknown	23 to 33.9	1979–3175 (Mt Bloomfield)	Detailed floristic surveys
New Caledonia	Grande-Terre Island	28.8	5500	0–1618	2100 species in total (~ 60% are ultramafic obligates and > 80% are endemic)	37	850–4000 (Mt. Humboldt)	A complete mechanistic understanding of both maquis and ultramafic forest ecosystems, hyper-endemic species and their conservation, and an assessment of the potential effect of climate change
Madagascar	Ambatovy	0.02	90	1000	~ 34 sp of 1580 sp (2.2%)	90	900–2200	Detailed floristic surveys

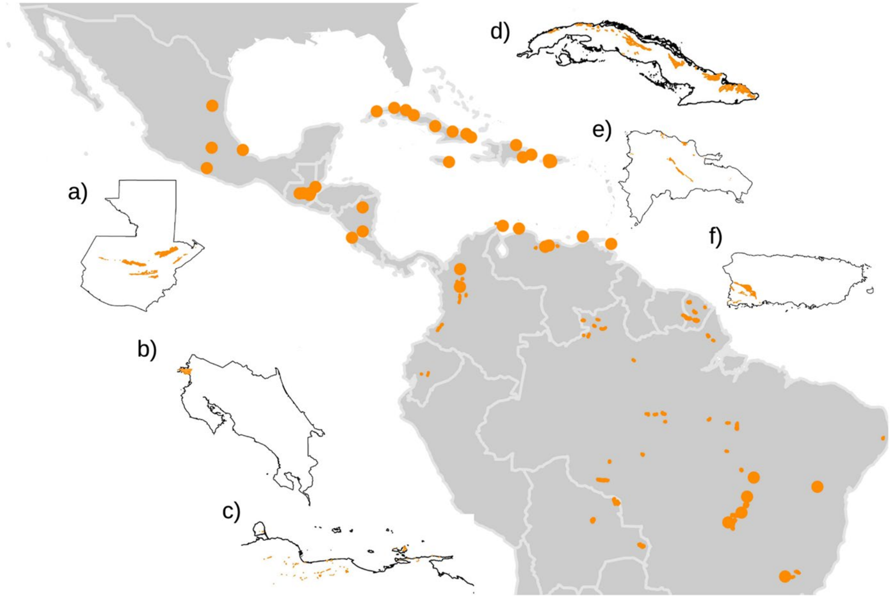

Fig. 3 Ultramafic outcrops (orange) of the Americas, including a) Guatemala; b) Costa Rica; c) northern Venezuela; d) Cuba; e) Dominican Republic; and f) Puerto Rico. Country insets are not drawn to scale. Orange-filled data points indicate regions discussed in the present review. Orange-filled polygons indicate other known, but poorly studied, ultramafic formations. Compiled geodatabase available through Dryad (upon publication)

The Americas

A. Puerto Rico

In Puerto Rico, three small ultramafic outcrops occur across Sierra Bermeja, Monte del Estado, and Rio Guanajibo, with the latter two encompassed by Bosque Estatal de Susua and Bosque Estatal de Maricao (Fig. 4a–c), along an elevational (250–900 m) and precipitation gradient (1400–2520 mm) (Fig. 3d). Soil depth and forest structure are highly variable due to topography (Alvarez, 1983), and finely scaled topographic changes cause large variability in above-ground live biomass (Helmer et al., 2008). Forests range from evergreen montane forests with tall trees and lianas to shorter, dense, scrubby forests (Figueroa & Schmidt, 1981; Rivera et al., 1984; Fig. 4 a-c), atypical for the Subtropical Wet Forest Life Zone of this region (Ewel & Whitmore, 1973). Higher elevation forests are "almost all evergreen and sclerophyllous, giving the impression of an anomalous wet desert or dry rainforest" (Ewel & Whitmore, 1973, p. 72), primarily driven by the lower soil depth and water-holding capacity of ultramafic soils. Forests in this region include several species endemic to Puerto Rico (Cedeño-Maldonado & Breckon, 1996), a facultative hyperaccumulator (*Pyschotria grandis* (Rubiaceae); McAlister et al., 2015) and two strong Ni accumulators (Medina et al., 1994), endangered species (García, 1991), and newly described species (*Calliandra locoensis* (Fabaceae), García &

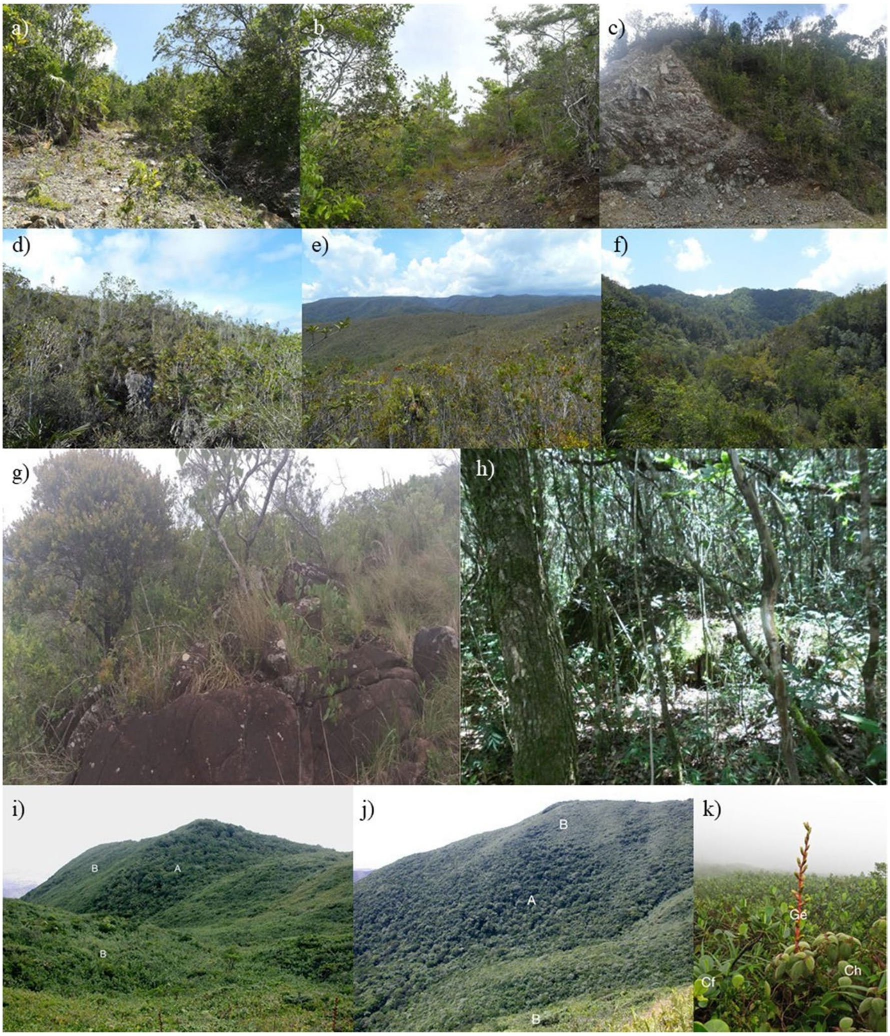

Fig. 4 Xeromorphic scrub in **a–b**) Susua; and **c**) Maricao, Puerto Rico, demonstrating exposed ultramafic rocks and xeromorphic vegetation (photos C. Garnica-Díaz); **d**) Thorny xeromorphic scrub, near Holguín, Holguín province, Cuba; **e**) subthorny xeromorphic scrub near Moa, Holguín province, Cuba; **f**) sclerophyllous rain forest, near Baracoa, Guantánamo province, Cuba (photos J. L. Gómez). Vegetation structure in Morro das Almas, Bom Sucesso, Brazil where **g**) vegetation is surrounded by native grasses, shallow soils with exposed rocks, a thin leaf litter layer, dominated by *Bromeliaceae* and *Bambusa* with an open canopy; and **h**) vegetation in the same area, near Rio das Mortes, with deeper soils, few exposed rocks, a thicker leaf litter layer and a closed canopy with abundant lianas (photos A. F. Guimaraes). Vegetation structure on Margarita Island, Venezuela: **i**) on wind-exposed areas, the vegetation is dominated by (A) palm forest and (B) *Clusia flava* (Clusiaceae); **j**) vegetation is dominated by (A) tall cloud forests in areas protected by the wind and (B) *Clusia flava* in wind-exposed areas; **k**) wet thicket with dominant *Clusia flava* (Cf), *Glomeropitcairnia erectiflora* (Ge, Bromeliaceae) and *Clidemia hirta* (Ch, Melastomataceae)

Kolterman, 1992) but few ultramafic restricted species (*C. locoensis* (Fabaceae), García & Kolterman, 1992; *Crescentia portoricensis* (Bignoniaceae), Cancel-Vélez, 2010). More broadly, tree species composition differs somewhat between ultramafic and nearby non-ultramafic substrates (Ewel & Whitmore, 1973), partly explained by less frequent disturbance (i.e., cultivation, deforestation) on infertile ultramafic soils resulting in more mature forests (Helmer et al., 2008).

B. Dominican Republic

Ultramafic outcrops in the Dominican Republic occur across the Cordillera Central, Sierra de Yamasá, Cordillera Septentrional and the Península de Samaná (García & Mejía, 1991; Haldeman et al., 1980). The Dominican Republic is also home to the only known exposed ultramafic formation resulting from ultra-high pressure between two convergent oceanic plate boundaries, the North American Plate, and the Caribbean Plate (Gazel et al., 2011). Despite many botanical and floristic surveys (e.g., García & Mejía, 2008; Veloz et al., 2011), research in ultramafic areas is far from complete. Ultramafic outcrops in the Dominican Republic contain several distinct vegetation types: humid broadleaf forest; gallery forests in stream and river margins; mixed forests dominated by *Pinus occidentalis* (Pinaceae); and xeromorphic shrubland (Cano et al., 2014). García & Mejía (2008) recorded 608 tree and shrub species, of which 89 are endemic to Hispaniola, and several are considered ultramafic endemics: *Calyptrogenia biflora* (Myrtaceae), *Calyptranthes garciae* (Myrtaceae), *Garcinia glaucescens* (Clusiaceae), *Leptogonum buchii* (Polygonaceae), *Piptocoma rufescens* (Asteraceae), *Tabebuia ophiolitica* (Bignoniaceae), and *Zombia antillarum* (Arecaceae). Thus, the ultramafic flora in the Dominican Republic is distinct from that of nearby Puerto Rico in both floristic composition, the presence of endemic species (in Puerto Rico, there are few ultramafic endemics), and vegetation dominated by *Pinus occidentalis*. In addition, many ultramafic areas are impacted by human activity, including agriculture and the extraction of materials for building roads (Veloz et al., 2011).

C. Cuba

Ultramafic outcrops are distributed throughout Cuba in a north-central band (Fig. 3a). Eleven outcrops, representing 7% of the island's surface, range in area from 61 to 1115 km^2 (González Torres, 2004) and occur across a range of climatic conditions (Table 1). With 3623 infrageneric taxa, the ultramafic flora represents approximately 57% of the 7000–7500 species that make up the Cuban vascular flora (González-Torres et al., 2016). About 1603 species are endemic to ultramafic soils (López, 2013). The most comprehensive information on floristic diversity and endemism in the eleven ultramafic outcrops is found in González Torres (2004). The ultramafic vegetation is characterized by woody xerophytic shrubs, palms, and trees. This vegetation is influenced by topography and precipitation. In the plains and low hills characterized by a summer dry season and a winter rainy season, thorny xeromorphic scrubs (Fig. 4d) are dominant. In the mountains, where precipitation occurs year-round, sub-thorny xeromorphic scrubs (Fig. 4e), pine forests, and sclerophyllous rainforests occur (Fig. 4f) (Capote & Berazaín, 1984; Borhidi, 1989, 1996). Regardless of climate, the effect of ultramafic soils on plants is equivalent to a reduction of at least 500 mm of annual precipitation (Borhidi, 1988a, 1996), reflected by xeromorphic plant traits (microphylly, sclerophylly, and spinescence). Fire and other anthropogenic disturbances convert thorny xeromorphic scrubs of the plains into tropical savannas with palms and a dense herbaceous cover (Borhidi, 1988b, 1996; Borhidi & Herrera, 1977; González-Torres, 2010).

The rich diversity and endemism found in Cuba can be explained by a long evolutionary period unaffected by glaciations (Brooks, 1987). Indeed, distinct ultramafic floras are less common in regions that were covered by ice caps during the Pleistocene (Reeves et al., 1983b). In Cuba, the alternation of marine maximums (interglacial period) of the Upper Pleistocene created isolated emergent land blocks. With the fall in sea level during glacial periods, blocks became connected through flat, newly emerged lands (Iturralde-Vinent, 2004). At high altitudes in mountainous regions at both ends of the Island, blocks remained above sea level, coinciding with "old" (10–30 million years) ultramafic areas. These older ultramafic blocks host 86% of the ultramafic endemism, whereas the "young" (1 million years) ultramafic sites host just 14% of the endemism (the remaining 5% of ultramafic endemics occur in both areas; Borhidi, 1988a, 1996; Reeves et al., 1996). The coupled processes of isolation and connection of stable emergent land facilitated evolution and subsequent speciation in ultramafic areas, giving rise to the high endemism and diversity that distinguishes the ultramafic plant communities of Cuba from other tropical regions in the Americas.

Research in Cuba has focused on characterizing the flora and vegetation and local edaphic and climatic factors. Borhidi (1988a, 1996) analyzed the main ecological factors that determine ultramafic endemism in the flora and the marked xerophytism of the Cuban ultramafic vegetation. Subsequent work has focused on describing the diversity of ultramafic regions by correlating species diversity and endemism with spatial and climatic variables. These studies have shown that species diversity and endemism vary depending on the age and size of the ultramafic outcrop, elevation, habitat heterogeneity, and the distance to the evolutionary centers of the flora (Areces-Berazaín et al., 2004). Phylogenetic studies also demonstrate the role of ultramafic soils on the diversification of various endemic plant lineages (Jestrow et al., 2012). Population-level studies have been limited to the characterization of endemic ultramafic plant populations as a baseline for their conservation (Fiallo et al., 2020; Toledo et al., 2019) and the evaluation of germination strategies of pioneer endemic species (López et al., 2016). Community-level studies have described succession of plant communities from xeromorphic shrubs into savannas (Borhidi, 1988b; Borhidi & Herrera, 1977). Anthropogenic disturbances further alter vegetation structure and composition and soil biota (González-Torres, 2011; Lazcano et al., 1999; Matos & Bruzón, 2003; Matos & Torres, 2000; Rodríguez et al., 2004, 1987). These disturbances include fires (González-Torres, 2010, 2011; Matos & Torres, 2000), forest management (Lazcano et al., 1999), and mining (Matos & Bruzón, 2003; Rodríguez et al., 1987, 2004). Following disturbances, the secondary vegetation is floristically more deficient and physiognomically different from the vegetation that gave rise to them (Borhidi, 1992). Other studies have characterized the interactions between biotic components in ultramafic ecosystems, such as pollination networks (Alameda et al., 2020), seed predation (Sánchez et al., 2017), and plant facilitation (Gómez, 2020; Gómez et al., 2013; Oviedo et al., 2013).

D. Guatemala

Ultramafic rocks in Guatemala are associated with several sub-parallel mountain ranges oriented east to west (Fig. 3b) (Bonis, 1967; IGN et al. 1977; Upie-Maga & Maga-Bid, 2001). Detailed geologic mapping (Hughes et al., *unpublished*; Newcomb, 1975) and soil research (Rosito-Monzon, 1999) revealed additional, albeit smaller, areas of ultramafic rocks within this region. These mountain ranges have emerged through the activity of the Polochic and Motagua faults located at the contact zone between the North American and Caribbean Plates (Martens et al., 2012), and include the Sierra de Chuacus, the Sierra de las Minas, the Sierra Espiritu Santo, and the Sierra de Santa Cruz (Upie-Maga & Maga-Bid, 2001). A combination of steep regional (east to west direction) and local (within each mountain range) elevational gradients, together with the influence of regional climatic regimes (Magaña et al., 1999; Small et al., 2007), places these ultramafic outcrops in diverse climates, from low to high elevations, and dry to mesic and humid conditions.

These mountain ranges harbor unique and diverse plant communities (Rosito-Monzon, 1999; Veliz, 2008). However, to our knowledge, the plant ecology in this region is incomplete. In a first study conducted in the humid, warm easternmost region of the Sierra de Las Minas (Cerro Tipon), San Emeterio (2001) sampled vegetation in sixteen plots, three underlain by ultramafic rocks. Two plots (Juan de Paz at 100 m and Cerro Tipon at 500 m) were established in a broadleaf forest dominated by *Blepharidium guatemalens*e (Rubiaceae) and *Vitex gaumeri* (Lamiaceae) with a well-developed understory. In contrast, one plot (Cerro Tipon at 600 m) was established in a needle leaf forest dominated by *Pinus caribaea* (Pinaceae) with an understory composition consisting of several shrubs and herbs. In the humid, cold region in the eastern Sierra de Las Minas (2400–2810 m), Rosito-Monzon (1999) characterized three main forest types, two of these in areas underlain by ultramafic rocks. These forest types included conifer (2405 m, Cerro Pinalon) and mixed (2410–2700 m, Cerro Pinalon) forests. The canopy of the conifer forest was dominated by *Pinus tecunumanii* and *P. maximinoi* (Pinaceae) and a very diverse subcanopy that included a mixture of Nearctic and Neotropical species. The mixed forest had a canopy dominated by *P. ayacahuite*, *P. pseudostrobus*, *P. donnel-smithii* (Pinaceae), and *Cleyera theoides* (Pentaphylacaceae). The third forest type included broadleaf forests on soils underlain by granite, gneiss, and schists. Thus, the conifer and mixed forests likely occur due to the underlying ultramafic soils, and broadleaf species may be excluded from ultramafic soils in this region. Finally, in the westernmost region of the Sierra de Las Minas at Cerro Quisis and Cerro Carpintero (1500–2350 m), a cloud, broadleaf forest occurs on ultramafic soils (García -Lopez, 1998; Reiche-García, 2015). The forest has a mixture of Nearctic and Neotropical species, and dominant species in the canopy belong to the Chloranthaceae, Fagaceae, Juglandaceae, Myrtaceae, Phyllanthaceae, and Theaceae families.

E. Costa Rica

The Península de Santa Elena was formed as an island in the Pacific 85 million years ago before colliding with the Central American land bridge, making it one of the oldest landscapes in Central America (Janzen, 1998) (Fig. 3c). Active methane vents and carbonate deposits show active serpentinization (Sánchez-Murillo et al., 2014), and hyper-alkaline springs in this area have more Archaea and methanogens than has been detected in any terrestrial serpentinizing system (Crespo-Medina et al., 2017). Soils in Santa Elena are enriched in Mg and have exceptionally high Ni (Arguedas, 2019; Reeves et al., 2007a). The instability of ultramafic bedrock makes it susceptible to landslides, especially in steep terrain. Landslides down steep slopes of the Península de Santa Elena are visible on satellite images of Google Earth (Alexander, 2018), triggered by extreme weather events, like Hurricane Otto in November 2016 (Hulshof, *personal observation*).

The vegetation of Península de Santa Elena is well described (Alexander, 2018; Reeves et al., 2007a, b; Janzen, 1998). However, ecological studies describing species or vegetation dynamics are limited. A biogeochemical reconnaissance found no hyperaccumulators and few endemic species (Reeves et al., 2007a, b). Some species recorded in Santa Elena are new records for Costa Rica (Grayum, 2004). For example, *Piper flavidum* (Piperaceae), occurring only in this part of the country, is an ultramafic indicator (Grayum, 2004). Several studies provide a comprehensive evaluation of the ultramafic landscape of the Península de Santa Elena, including soils and plants (Alexander, 2018; Jiménez et al., 2016). Its location in the driest region of Costa Rica, together with its complex terrain, creates a mosaic of land cover types. In the eastern portion of the Península de Santa Elena, centuries of human-induced fire created a landscape characterized by semi-deciduous and deciduous vegetation dominated by plants like *Trachypogon plumosus* (Poaceae), the fire-adapted *Byrsonima crassifolia* (Malpighiaceae), and *Roupala montana* (Proteaceae) on moderate elevation hilltops (300 m). Evergreen dry forest species occur in patches along seasonal streams. In western Península de Santa Elena, the steeper terrain and orographic cloud formation create dense forest and scrub dominated by *Hematoxylon brasileto* (Fabaceae) below 500 m and above 500 m, dwarf cloud forests occur (Dauphin & Grayum, 2005; Hulshof et al., 2020). The characterization of plant taxonomic and functional diversity revealed dramatic turnover in plant composition and structure, primarily driven by cloudline (Hulshof et al., 2020). Rising cloudline and an increasing number of cloudless days make these cloud forests particularly vulnerable to climate change. The combination of ultramafic soils and aridity makes this an extreme environment; however, the topographical complexity and oceanic influence create diverse and unique habitat types in a relatively small area (250 km^2).

F. Colombia

In Colombia, ultramafic formations have been characterized and mapped at regional (Barbosa-Camacho, 2003; Nivia Guevara, 2001; Ortega-Montero, 1981–1982) and national (Gómez Tapias et al., 2017; Murcia, 1980) levels owing to their economic potential. One of Colombia's most extensive mining operations occurs at Cerro Matoso, located at the foothills of the northern Central Cordillera in Córdoba (Mejia & Durango, 1981–1982). A second well-known concentration of ultramafic rocks is found in Medellin, Antioquia, the second-largest city in Colombia (Álvarez Agudelo & Muñoz Arango, 1987), where the vegetation consists of ferns and small shrubs (Álvarez Agudelo & Muñoz Arango, 1987). Villegas (2000), working in Colombia's highly humid Choco region (mean annual precipitation ~ 5000 mm, one of the wettest regions on Earth), successfully identified ultramafic deposits based on the characteristic signature of the vegetation in Landsat images. In this area, gallery forests 25–30 m in height occur, with canopy emergent trees reaching 35 m. The reflectance signature of ultramafic vegetation was distinguishable due to the lower vegetation density of this substrate (Villegas, 2000). However, distinguishing substrate type using reflectance imagery was difficult in areas already altered by human activities (Vargas Cuervo & Rodríguez, 2008; Villegas, 2000), presumably because differences in vegetation density would be reduced. More recent hyperspectral techniques may be sensitive enough to distinguish differing leaf-level reflectances, potentially detecting more subtle differences between ultramafic and adjacent non-ultramafic vegetation.

G. Venezuela

Several ultramafic areas occur across the northern coast of Venezuela (Domenech et al., 2020; Lewis et al., 2006; Mendi et al., 2020; Sanz et al., 2011; Urbani, 2018) (Fig. 3e). Geological research has focused on three primary sites: Cerro Colorado (Paraguaná Peninsula, Falcón State), Loma de Hierro (Aragua State), where commercial Ni mining was recently active, and the ultramafic hills in Margarita Island (Nueva Esparta State). Plant ecological research has emphasized community structure and composition in Paraguaná (Matteucci, 1987) and Loma de Hierro (Monedero & González, 1994). The role of ultramafic soils in determining plant composition on Margarita Island has received the most attention (González, 2007; Sugden, 1986). The northeastern half of ultramafic outcrops in Margarita Island consists of "many irregular, elongate masses of highly serpentinized and deformed ultramafic rocks, from several meters to several kilometers in length" (Maresch, 1975, p. 847; Taylor, 1960). Substrate chemistry plays a prominent role in separating semi-deciduous shrublands and grasslands dominated by *Trachypogon spicatus* (Poaceae) (González, 2007). The shrub *Krameria ixine* (Krameriaceae), the herb *Evolvulus filipes* (Convolvulaceae), and the tree *Vitex capitata* (Lamiaceae) are restricted to ultramafic soils. However, several dominant semi-deciduous woodland species, including *Aspidosperma cuspa* (Apocynaceae), *Bourreria cumanensis* (Ehretiaceae), and *Ximenia americana* (Ximeniaceae), are substrate indifferent.

In Margarita Island, humid forests, dry forests, and shrublands are found on ultramafic soils (Fig. 4i–k), whereas shrublands, cardonal (dominated by columnar cacti), and herbaceous cover dominate non-ultramafic soils. Sugden (1986) conducted analyses of the vegetation structure and composition in montane sites across Margarita Island, including Cerro Copey, one of the most prominent ultramafic outcrops on the island. Vegetation changes in coastal mountains (≤ 1000 m) are mainly determined by rapidly increasing levels of water availability with altitude, derived from higher precipitation, cloud cover (reducing evapotranspiration), and fog interception (Cavelier & Goldstein, 1989). In Cerro Copey, vegetation below 400 m on the windward face and below 500 m on the leeward face is dominated by deciduous and semi-deciduous forests and shrublands. Above those limits, water availability supports three types of evergreen vegetation dominated by woody plants, namely transition forests (~400–600 m on the windward and 600–700 m on the leeward sides), cloud forests above 500 and 700 m, respectively, and wet thickets (>800 m windward) (Sugden, 1986). Four species were restricted to cloud forests and tall woody wet thickets, and two species were restricted to transition forests. Both groups contain families belonging to ultramafic flora elsewhere in the tropics, such as Clusiaceae, Flacourtiaceae, Ochnaceae, and Rubiaceae. Altitudinal differentiation of vegetation is likely related to geochemical characteristics. Average soil pH and elemental concentrations differ markedly across elevation (Sugden, 1986), possibly due to considerable soil leaching in the cloud forest and wet thicket.

H. Brazil

Within Brazil, two ultramafic regions and their associated vegetation have been described: Morro das Almas in Minas Gerais State (Guimaraes et al., 2019), and various locations in Goiás State (Reeves et al., 2007b). There is also evidence of ultramafic outcrops in Bahia and Pará States (Reeves et al., 2007b), but to date, there are no published data regarding the flora of these regions (but see Group, 2020). Other ultramafic outcrops are patchily distributed across Brazil. Unfortunately, there are no laws specific to the conservation of ultramafic soils in the country, and as a result, metal-rich environments in Brazil remain among the most threatened (Jacobi et al., 2011).

The Morro das Almas (Bom Sucesso, Minas Gerais) is a complex of ultramafic soils in a relatively small area (8.17 km^2), located in the southernmost part of the Quadrilátero Ferrífero ('Iron Quadrangle'), an area well known for mining (Vilela et al., 2019). The local soil characteristics (Araujo et al., 2014; Vilela et al., 2019, 2020) and the flora (Guimaraes et al., 2019) of Morro das Almas were recently described. The area is in an ecotone between two distinct vegetation types: Brazilian savanna (Brazilian Cerrado) and Atlantic Forest, both considered biodiversity hotspots (Mittermeier et al., 2005). Vegetation types and species from both biomes occur in the area, with trees from the seasonal semi-deciduous forest, commonly found in montane areas in the Atlantic Forest, and shrubby vegetation typically found in Brazilian savannas. In addition, natural and semi-natural savannas dominated by *Kielmeyera speciosa* (Calophyllaceae) trees surround the Morro das Almas site. Ultramafic areas with shallow soils, a thin layer of leaf litter, and exposed soil and rocks are characterized by open savanna-like vegetation (Fig. 4g). Other areas with deeper soil, a thicker leaf litter layer, little exposed soil, and a few exposed rocks are occupied by closed-canopy forest-like vegetation (Fig. 4h). The most representative families are Fabaceae, Melastomataceae and Myrtaceae (Guimaraes et al., 2019), and two species are Endangered under the International Union for Conservation of Nature Red List (IUCN, 2015): *Trattinnickia ferruginea* (Burseraceae) and *Ocotea odorifer*a (Lauraceae). Tree species composition, structure, and species diversity are similar to nearby non-ultramafic forests (Guimaraes et al., *unpublished data*). To date, no endemic or new species have been described, but recent work to better understand soil–plant interactions in Morro das Almas is ongoing.

Research in Goiás State has been active since the 1980s (Brooks et al., 1988, 1992). Four large ultramafic complexes were identified: Barro Alto, Tocantins, Canabrava and Natividade (Berbert et al., 1981). The climate in the region is subtropical altitudinal (Kottek et al., 2006) with two distinct seasons: a wet season from October to April and a dry season from May to September (IBGE, 2012). To date, only two-thirds of the sampled specimens have been identified to species level (Reeves et al., 2007b) which includes the ultramafic endemic (and newly described species), *Pterolepis haplostemona* (Melastomataceae) (Almeda & Martins, 2015).

I. Other regions in the Americas (Mexico, Nicaragua, Jamaica, Guiana Shield)

In Mexico, ultramafic outcrops occur from Baja California Norte in the northwest to Chiapas in the southeast. The geological properties are well studied (e.g., Ortiz-Hernández et al., 2006), though the ultramafic vegetation is not (Navarrete Gutiérrez et al., 2018). Among three extensive outcrops, soil Ni concentrations vary from 200 to 2300 mg kg^{-1} (Navarrete Gutiérrez et al., 2018), and plant composition is dominated by species from the families Acanthaceae, Anacardiaceae, Asteraceae, Fabaceae, Sterculiaceae, and Verbenaceae. These plant families are shared across ultramafic outcrops in Africa, Brazil, Costa Rica, and Sri Lanka. Two ultramafic endemics are reported (*Plumbago pulchella* (Plumbaginaceae) and *Quercus conzattii* (Fagaceae)), but no hyperaccumulators have been found even among species reported as hyperaccumulators from other regions (Navarrete Gutiérrez et al., 2018). Given the broad distribution of ultramafic outcrops across Mexico, work on the structure and function of plant communities is likely to reveal important biogeographical trends and patterns in species distributions.

The Siuna Serpentinite Mélange in northeastern Nicaragua has received some geological attention (Escuder-Viruete et al., 2019; Flores et al., 2015), though, to our knowledge, the flora is not described. In Jamaica, ultramafic rocks are found in a small area near Arntully in the Blue Mountains and do not host a specialized flora (Draper, 1986), though the island-endemic shrub *Rondeletia brachyphylla* (Rubiaceae) appears restricted to this site (Adams, 1972). The trans-Amazonian greenstone belt extends across the northern Guiana Shield from Venezuela to the Amapá state in Brazil and is thought to share origins with the greenstone belt of Ghana in western Africa prior to continental drift (Naipal et al., 2019). In Guyana, ultramafic outcrops are primarily distributed in the northwest near Georgetown throughout the Kauramembo/Kauramembu Mountains (Wanamu-Blue Mountains), Barama River, Northwest District, where metamorphic rocks are intruded by ultramafic rocks (Kilpatrick, 1968). We could not locate publications describing the vegetation of this area. Ultramafic outcrops appear to occur extensively throughout French Guiana (Fig. 3), where tropical rain forest is the dominant vegetation type, and endemic species occur in small fragments (ter Steege et al., 2000). However, studies on ultramafic plant composition or structure could not be located.

Southern Africa

A. Zimbabwe

The Great Dyke of Zimbabwe was the first ultramafic region to garner global attention and was regarded as having a specifically adapted flora, albeit floristically poor (White, 1978; Wild, 1965; Prendergast, 2013). This ultramafic outcrop is remarkable as it is 530 km long and 5–11 km wide, stretching from north to south through the entire country. The predominant vegetation of this tropical region is miombo woodland (Proctor & Cole, 1992), but on the ultramafic substrates, the vegetation changes to open savanna and grassland (Werger et al., 1978). Given the more than 30 edaphic specialists restricted to the dyke, it is a principal site of plant endemism in southern Africa (Van Wyk & Smith, 2001). Important endemic flagship species include *Aloe ortholopha* (Asphodelaceae), *Euphorbia memoralis* (Euphorbiaceae), *Jamesbrittenia fodina* (Scrophulariaceae), and *Selago serpentina* (Scrophulariaceae) (Kunonga et al., 2019). Various Ni hyperaccumulators have been reported from this region (Brooks & Yang, 1984; van der Ent et al., 2020; Wild, 1968, and see Online Resource 1). Although Cu accumulators are not common in ultramafic floras, cuprophiles in Zimbabwe (and Botswana and Zambia) are commonly associated with Cu-enriched soils in this region (van der Ent et al., 2020; Wild, 1968).

B. South Africa (and Eswatini)

Within Africa, by far the most ultramafic research has been done in South Africa and Eswatini (De Ronde & De Wit, 1994; Scoon & Viljoen, 2019), with the focus on ultramafic intrusions around Barberton (Williamson & Balkwill, 2015), Sekhukhuneland (Siebert et al., 2001), Witwatersrand (Reddy et al., 2009), and Vredefort Dome (Boneschans et al., 2015). The metalliferous soil and associated flora along the Barberton Greenstone Belt in South Africa and Eswatini were brought to international attention by Morrey et al. (1989). Subsequently, this area received much attention through discoveries of new species (Balkwill et al., 2011), vegetation classification (Smith et al., 2001; Stalmans et al., 1999), Ni hyperaccumulation (Boyd et al., 2008), phytophage metal uptake (Migula et al., 2007), biological soil crusts (Venter et al., 2018), restoration of metalliferous soil (Morgenthal et al., 2004), and conservation ecology of threatened species (Witkowski et al., 2001). Various species are endemic to the Barberton Centre of Endemism (Van Wyk & Smith, 2001). The flagship species include *Berkheya coddii* (Asteraceae), *Dioscorea strydomiana* (Dioscoreaceae), *Ozoroa barbertonensis* (Anacardiaceae), *Protea curvata* (Proteaceae), and *Searsia pygmaea* (Anacardiaceae).

The Sekhukhuneland region is associated with the Cr- and Mg-rich ultramafic outcrops of the eastern Rustenburg Layered Suite of the Bushveld Igneous Complex (Siebert et al., 2002). The metal-enriched pyroxenite layers are renowned for their local plant endemism (Van Wyk & Smith, 2001), evidenced by the specific epithet *'sekhukhuniensis'* which commemorates this geographic area in the names of endemic species belonging to the Anacardiaceae, Ebenaceae, Euphorbiaceae, Fabaceae, Iridaceae, Polygalaceae and Vitaceae. No hyperaccumulators are found in the area, and studies have shown that species from this region have instead developed the ability to exclude metals (Adhikari et al., 2022). Nonetheless, strong associations exist between the vegetation and underlying metal-rich geological substrates (Siebert et al., 2002).

C. Other regions in Africa (Botswana, Madagascar, others)

The Archaean Tati Greenstone Belt in Botswana is known for its nickel-copper sulfide deposits. Ecological research has focused on several ultramafic formations with high Ni concentrations around Francistown, which lies in the east of the country near the border with Zimbabwe (Kausel, 1991; Ramotoroko et al., 2016). Limited floristic work has been done, but metal hyperaccumulation by indigenous plants has been investigated to identify mineral indicators (Koosaletse-Mswela et al., 2015; Nkoane et al., 2005). In Madagascar, ultramafic soils are rare, with the most prominent outcrop being the lateritic Ni deposit of the Antampombato-Ambatovy Complex. It is about 80 km^2 in area and is found at 1000 m above sea level along the eastern escarpment (Melluso et al., 2005) near Ambatovy. Minimal research has been done on the soil and plants of this region but there have been attempts to compile lists of endemic species (Phillipson et al., 2010). The ultramafic flora of Madagascar shares a number of plant families (the Celastrales, Oxalidales, and Malpighiales clade) with the ultramafic flora of Cuba and New Caledonia (Pillon et al., 2019). Other ultramafic outcrops occur in Cameroon, Angola, and Zambia but floristic information is lacking.

South and Southeast Asia

A. Sri Lanka

In Sri Lanka, six small ultramafic outcrops, each less than 4 km^2, are located along a Precambrian suture zone along the boundary of the Vijayan and Highland Series (see Fig. 4 in Kumarathilaka et al., 2016), metamorphic remnants of two ancient tectonic plates (Dissanayaka, 1982; Munasinghe & Dissanayake, 1980). The geochemistry of five of the six outcrops has been well-documented (Fernando et al., 2013;

Hewawasam et al., 2014; Rajapaksa et al., 2012; Vithanage et al., 2014). Despite recent extensive field explorations (Fernando et al., 2022), the sixth outcrop (Katupotha) has not been located, suggesting it may have been erroneously documented in previous reports or has since been altered beyond recognition by intense anthropogenic activity. The floristic diversity and plant-soil ionic relations of Sri Lanka's ultramafic outcrops, especially Ussangoda along the southern coast (Fig. 5f–h), have received some attention (Chathuranga et al., 2015; Samithri, 2015; Weerasinghe & Iqbal, 2011). To date, less than 100 species have been reported (Galey et al., 2017), compared to the many-fold more documented from other sites in Southeast Asia (van der Ent et al., 2015a). More detailed floristic surveys of the outcrops will likely yield previously undescribed species, rare and endemic species, or cryptic ecotypes (Chathuranga et al., 2015) worthy of further study and conservation (Galey et al., 2017). Surprisingly, of the species documented from Sri Lanka's ultramafic soils,

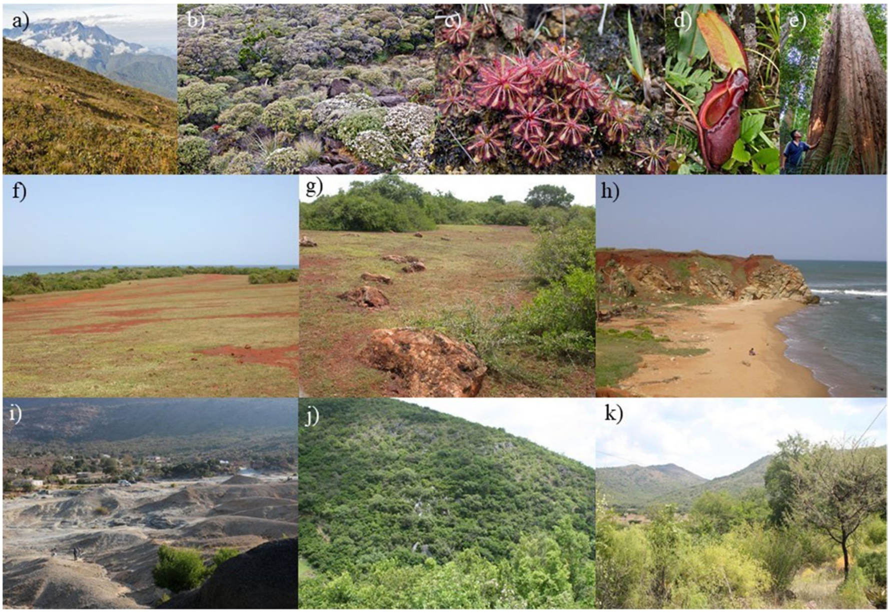

Fig. 5 In Sabah, Malaysia: **a**) stunted graminoid scrub on the summit of Mount Tambuyukon; **b**) extremely short vegetation on high altitude ultramafics on Mount Kinabalu; **c**) *Drosera ultramafica* (Droseraceae) on Mt. Tambuyukon, an ultramafic endemic; **d**) the famous *Nepenthes rajah* (Nepenthaceae) from Mount Kinabalu, a carnivorous pitcher plant endemic to Kinabalu Park; **e**) lowland forest on ultramafic Ferralsols in Sabah can have very high stature (with trees up to 50 m) dominated by Dipterocarps (Dipterocarpaceae) (photos A. Van der Ent). Sri Lanka's most studied outcrop, Ussangoda, is located on India's extreme southern coast overlooking the Indian Ocean: **f**) The soils are hematite-rich and clayey sand. Soils are poorly developed, except in the shrub islands in the background; **g**) shallow soils and exposed rock in the ultramafic barren and shrub islands; **h**) edge of Ussangoda demonstrating its proximity to the Indian Ocean. Coastal ultramafic areas, like Ussangoda, are likely more influenced by coastal fog and sea spray than inland sites (photos N. Rajakaruna). In southern Africa: **i**) plains bushveld in Sekhukhuneland, South Africa; **j**) serpentine savanna in Eswatini; and **k**) serpentine sourveld in Barberton (photos S. Siebert)

only *Vernonia zeylanica* (Asteraceae) is endemic to Sri Lanka (Ministry of Environment and Renewable Energy, 2012), although this taxon is not restricted to the substrate.

Although Sri Lanka's ultramafic flora appears to be depauperate with respect to endemism and metal hyperaccumulators (but see Rajakaruna & Bohm, 2002), the outcrops harbor several taxa worthy of conservation. These include four near-threatened species (*Striga angustifolia* (Orobanchaceae), *Maerua arenaria* (Capparaceae), *Salvadora percia* (Salvadoraceae), and *Olax imbricata* (Olacaceae)), and several vulnerable or data-deficient species (Galey et al., 2017; Ministry of Environment and Renewable Energy, 2012). Additionally, the well-known Ni hyperaccumulator *Rinorea bengalensis* (Violaceae) of southeast Asia (van der Ent & Mulligan, 2015), which was presumed extinct in Sri Lanka (Ministry of Environment and Renewable Energy, 2012), was recently discovered in non-ultramafic soils in southwestern Sri Lanka and the ultramafic outcrop at Rupaha (Fernando et al., 2022).

B. India

Similar to Sri Lanka, research on the ultramafic ecology of neighboring India is preliminary. There is extensive research on the petrogenesis, mineralogy and geochemistry of the Naga Hills Ophiolite Complex in the northeast Indian states of Manipur, Nagaland, parts of Arunachal Pradesh and the adjoining areas of western Myanmar (Ghose et al., 2014, 2021; Dey et al., 2018). Despite the detailed geologic studies, there is no published information on the plant diversity of the region, except for a reference to palms, pines and spear grass (likely, *Heteropogon contortus*), growing on the serpentinites of the Naga Hills Ophiolite Complex. The only published botanical study is of the Sukinda chromite mines in the Jajpur district, Odisha, recording 113 plant species belonging to 51 families (Samantaray et al., 2001), including species that show the capacity to accumulate Ni and Cr (Samantaray et al., 1999). At least eight Ni hyperaccumulator plant species belonging to eight genera and seven families also occur on India's Andaman Islands (Datta et al., 2015; Pal et al., 2004). Of these, *Dichapetalum gelonioides* subsp. *andamanicum* (Dichapetalaceae) and *Rinorea bengalensis* (Violaceae) accumulate up to 30,000 µg g − 1 Ni. Remote sensing tools can examine vegetation communities on the ultramafics of the Andaman Islands, where outcrops are mostly inaccessible, and the vegetation deserves more intensive exploration (Chaudhury et al., 2015).

C. Other regions in Southeast Asia (Malaysia, Indonesia, Philippines)

The vegetation on ultramafic soils on Southeast Asia are highly varied and range from tall forests (trees > 50 m) in lowlands to short graminoid communities in upper montane to sub-alpine zones at high altitude (Fig. 5a–e) (van der Ent et al., 2016). The biogeographical affinities are complex, reflecting the paleo-history, isolation of islands, diversity of climates and local geology (Proctor, 2003; Galey et al., 2017). Consequently, endemicity is generally very high at the landscape scale (van der Ent et al., 2015a). For example, montane forest on Mount Tambuyukon (Sabah, Malaysia) had 132 species in 250 m^2 plots, some of the most biodiverse vegetation communities globally (van der Ent et al., 2016). The Malaysian state of Sabah on the island of Borneo has over 3500 km^2 of ultramafic outcrops, from which 4252 plant species have been recorded (van der Ent et al., 2015a). Kinabalu Park is world-renowned for its biodiversity, with over 5800 plant species in an area of just 1200 km^2 (Beaman, 2005; van der Ent et al., 2016). The ultramafic outcrops in Kinabalu Park have over 2542 plant species, of which a large percentage is endemic to either Kinabalu Park or Borneo Island (van der Ent et al., 2016).

Indonesia has some of the most extensive surface exposures of ultramafic bedrock globally, with over 15,000 km^2 on Sulawesi Island and over 8,000 km^2 on Halmahera Island (van der Ent et al., 2013). As a result, Indonesia hosts one of the most species-rich floras, but the records for Ni hyperaccumulator plant species in the region have been scant until recently (Lopez et al., 2019a, b). The extremely high levels of plant diversity of Sulawesi Island (of 5972 plant species, 2225 are endemic; Middleton et al., 2019), coupled with the low state of knowledge on biodiversity (Cannon et al., 2007), severely hampers conservation efforts. The Philippines has extensive ultramafic outcrops on numerous islands, notably in Palawan and Mindanao, but compared to studies of the plant diversity of the ultramafic outcrops of Malaysia, knowledge of the flora is extremely limited (Proctor et al., 2000; Proctor, 2003).

Geological sources indicate that ultramafic rocks outcrop widely on the Island of New Guinea (Indonesian West Papua and Papua New Guinea), but there is a genuine gap in the knowledge about the vegetation of these ecosystems in this part of the world. This is despite the exceptional richness of the New Guinean flora, which is now known to have the world's richest island flora (Cámara-Leret et al., 2020). There is a report on vegetation mapping of the Raja Ampat Islands, which mentions the distinctive 'ultrabasic scrubland' of Waigeo and Kawe Islands (Webb, 2005), but other information is scant. This further points to the importance of stimulating basic taxonomic inventories of vegetation in numerous ultramafic outcrops across the Malesian Region that remain unexplored.

Hyperaccumulator plants (either of Ni, Co, or Mn) of Southeast Asia have been described in Sabah (101 species), Indonesia (26 species, including two species in Sulawesi Island and 16 on the Island of Halmahera), and the Philippines (three species; Quimado et al., 2015) (Online Resource 1). Sabah has become especially well-known for the array of hyperaccumulator plant species discovered there over the last decade. This now includes 28 Ni-hyperaccumulator species, 12 cobalt hyperaccumulator species, and 51 manganese hyperaccumulator species (van der Ent et al. 2015a; 2019). Of those, 10 species are classified as 'hypernickelophores' (i.e., plants with > 10,000 µg Ni g-1), belonging to Dichapetalaceae, Phyllanthaceae, Violaceae and Rubiaceae and Salicaceae. Noteworthy is the tree *Phyllanthus balgooyi* (Phyllanthaceae) which has a bright green phloem sap with 20 wt% Ni (Mesjasz-Przybylowicz et al., 2015), and the tree *Antidesma montis-silam* (Phyllanthaceae) with 32,700 µg Ni g-1 in its leaves (Nkrumah et al., 2018) (and see Online Resource 1 for more detailed species accounts). The prevalence of hyperaccumulator species in this region is likely a consequence of its complex geological history, including tectonic events resulting in submergence and emergence, the complex terrain resulting in climatic variability, geographic isolation due to the insular nature of the Malay Archipelago, and its exceptional biodiversity with over 40,000 plant species.

New Caledonia

New Caledonia is an archipelago of five larger islands and many smaller outlying islands located 1200 km off the eastern coast of Australia (Maurizot et al., 2020). It is globally recognized as a biodiversity hotspot with remarkable plant diversity and high endemism resulting from biotic interactions, climate, topography, and soil types (Grandcolas et al., 2008; Jaffré, 1992; Pillon et al., 2010). New Caledonia has an estimated 3400 plant species, including ~ 2560 endemics, despite the absence or underrepresentation of typical pantropical families, such as Araceae, Bignoniaceae, or Dichapetalaceae (Munzinger et al., 2021). Ultramafic endemism is a key factor driving New Caledonia floral diversity as ultramafic soils cover a third (~ 5500 km^2) of Grande-Terre (Isnard et al., 2016; Jaffré, 1980), the largest island of New Caledonia. Grande-Terre has a complex terrain assembled during two major tectonic events that ultimately resulted in the overthrust of one of the largest ophiolitic nappes (a mass of rock forced over another), in the world (Pelletier, 2006). Once weathered, two major types of soils emerged: (i) the "Brown Hypermagnesian" soils or magnesic Cambisols found over ultramafic bedrock (or highly serpentinized peridotite) in geological contact areas (between ultramafic and non-ultramafic); and (ii) the "Ferritic Ferralitic" or Ferralsols, which cover most of the southeastern part of the island (Grand Massif du Sud) and often develop a hematite hardpan locally called cuirasse (Fritsch, 2012; Jaffré & Latham, 1974; Latham et al., 1978; Losfeld et al., 2015). On these soils, two highly discernable vegetation types occur – the maquis, a low sclerophyll evergreen scrubland, and various rainforests (Isnard et al., 2016; Jaffré, 1980).

The maquis covers approximately 80% of ultramafic soils from sea level to the highest elevations of ultramafic massifs (~ 1600 m) and primarily forms after forest fires (Morat, 1993). There are three types of maquis: (1) "ligno-herbaceous" maquis, consisting of a dense herbaceous layer dominated by tall Cyperaceae with a fragmented shrubby layer common on Ferralsols; (2) "bushy" maquis, characterized by a dense, bushy layer, the absence of a herbaceous layer and the presence of small groups of ramified shrubs found on Ferralsols rich in gravel or cuirasses > 200 m in elevation; and (3) "shrubby" maquis, found on magnesic Cambisol consisting of ramified shrubs with a thin herbaceous layer (short Cyperaceae) (Isnard et al., 2016; Jaffré, 1980). The maquis varies significantly depending on soil type and altitude, which influence the dominance of species and vegetation type, stature, and layering (i.e., height or density) (Jaffré, 1980).

Unlike the maquis, which is distinctive from secondary vegetation on non-ultramafic soils (i.e., savanna and thicket), rainforests on non-ultramafic substrates are relatively similar to those on ultramafic soils because these forests evolved on deeper soils and, as a result, are less edaphically limited (Isnard et al., 2016; McCoy et al., 1999). There are two major types of rainforests: (i) wet evergreen forests of low and medium altitudes, found between 500 and 1000 m, or in areas with annual precipitation between 1500 and 3500 mm; these forests primarily occur on steep terrain on Ferralsols or Magnesic Cambisols and are usually dominated by species of the genus *Araucaria* or by *Agathis ovata* (Araucariaceae); and the (ii) wet evergreen forests of high altitude, which are found above 1000 m in areas with annual precipitation greater than 3500 mm on Ferralsols (Jaffré, 1980).

In all, ultramafic outcrops host over 2100 plant species and therefore a significant fraction of the total New Caledonian flora, despite covering only a third of the main island. More than 60% of these species are ultramafic obligates, and more than 95% are endemic (Isnard et al., 2016; Gâteblé et al., 2019). In addition, common tropical families such as Dilleniaceae and Ericaceae are almost found exclusively on ultramafic substrates (Isnard et al., 2016). Although phylogenetic studies often demonstrate that oceanic island ecosystems promote adaptive radiations, adaptive radiations are rare in New Caledonia (Losos & Ricklefs, 2009; Barrabé et al., 2019). *Oxera* (Lamiaceae) and *Diospyros* (Ebenaceae) are the only two genera that fully satisfy the criteria (Givnish, 2015; Paun et al., 2016; Barrabé et al., 2019). Current thinking argues that the archipelago's old age and limited environmental gradients (excluding diversity of soils) are the leading factors explaining the lack of adaptive radiations in New Caledonia (Pillon et al., 2017).

Regardless, remarkable endemism is observed at the genus level, suggesting selective pressure for plant adaptation on ultramafic soils (Anacker, 2014). It also ostensibly promotes the occurrence of specific traits such as hyperaccumulation, which has evolved several times independently (Jaffré et al., 2013). To date, over 180 hyperaccumulators (Co, Mn, Ni, and Zn) have been recorded, including the endemic tree *Pycnandra acuminata* (Sapotaceae), which accumulates up to 25% Ni in its blue-green latex, the highest known Ni concentration found in any living tissue (Gei et al., 2020; Jaffré et al., 1976) and *Diospyros calciphila*, the only known hyperaccumulator to arise from adaptive radiation in the archipelago (Gei et al., 2020; Jaffré et al., 1976).

An Interdisciplinary Research Agenda for Tropical Ultramafic Plant Ecology

Tropical ultramafic plant communities are diverse and variable in plant form and function due to the interactive effects of biogeography and climatic and edaphic properties. Environmental gradients across tropical ultramafic soils, predominantly due to precipitation and elevation, make these systems an appealing macroecological model. The susceptibility of tropical ultramafic ecosystems to human-induced climate change, land-use change, and other anthropogenic threats creates additional urgency for further research. We encourage future work to bridge disciplines including genetics, ecology, physiology, and soil biology to better understand the mechanisms driving speciation, specialization, and hyperaccumulation in these systems. An interdisciplinary approach would help us to better understand: 1) variable rates of endemism and habitat specialization; 2) climatic and edaphic interactions; 3) soil microbial functioning; 4) genetic mechanisms of hyperaccumulation, and 5) the role of hyperaccumulators in habitat restoration.

Endemism and habitat specialization are defining characteristics of ultramafic ecosystems. However, endemism and habitat specialization are highly variable across the tropics, driven by large- (e.g., biogeography) (Heads, 2008) and small- (e.g., soil microbial activity) scale processes. At biogeographical scales, age, area, and the degree of isolation appear to be key drivers of rates of endemism and specialization across tropical ultramafic ecosystems. The influence of geological age on the degree of endemism is especially apparent in Cuba, where older blocks remaining above sea level during glacial maximums (10–30 million years) host 86% of the ultramafic endemism on the island, whereas younger blocks (1 million years) host just 14% (Borhidi, 1988a, 1996; Reeves et al., 1996). However, age alone cannot explain variable rates of endemism across tropical ultramafic ecosystems. Ultramafic ecosystems of Central and South America and parts of southern Africa range from several hundred million to several billion years old, yet the degree of endemism is relatively low. Patch size and precipitation may largely explain these differences. Ultramafic outcrops are often small, patchy, and spatially isolated. Thus, it is reasonable to expect that ultramafic outcrops should be subject to the selective pressures defined by island biogeography theory (Heads, 2008; Kruckeberg, 1991). However, small ultramafic areas may be more influenced by surrounding areas than are large ones. As a result, endemism should be lower on small and isolated outcrops compared to larger or less isolated ones (MacArthur & Wilson, 1967). This is certainly true among tropical islands, including Cuba, New Caledonia, and southeast Asia. Although island biogeography theory is untested across the tropical ultramafic ecosystems reviewed here, research suggests the spatial structure may determine the distribution of ultramafic plant endemism and diversity (Harrison, 2011) yet may only be important under certain conditions (Grace et al., 2007; Harrison, 2011), such as when dispersal abilities and substrate area are intermediate. The small patch size of ultramafic outcrops in Brazil and Sri Lanka, for example, may help explain why the vegetation appears undifferentiated between ultramafic and adjacent non-ultramafic soils. In addition to patch size, precipitation appears to affect endemism positively (Harrison et al., 2006). Indeed, endemism peaks at high precipitation in California (Fernandez-Going et al., 2013) and globally (Anacker, 2011). Mean annual precipitation also determines the degree of differentiation between ultramafic and non-ultramafic plant community composition across California (Fernandez-Going et al., 2013), suggesting the differentiation between tropical ultramafic and non-ultramafic plant communities may be driven by precipitation too—more specifically, greater precipitation may reduce the serpentine syndrome, reducing compositional and structural differences between ultramafic and adjacent non-ultramafic soils. Together, these seemingly contradictory patterns in some tropical ultramafic ecosystems—high endemism but low compositional or structural differentiation between ultramafic and non-ultramafic soils at high precipitation—raise many ecological and evolutionary questions. Testing these and other ideas related to broad scale patterns of plant diversity and species distributions would require extensive spatial data through, for example, the creation of a georeferenced database of ultramafic flora based on herbarium collections (e.g., Birnbaum et al., 2015). High resolution maps of ultramafic outcrops and remote or hyperspectral imagery of ultramafic flora would also facilitate other spatially explicit analyses including spectral characterizations, historical trends, and monitoring of anthropogenic impacts (Vega-Nieva et al., 2019).

Precipitation gradients across ultramafic soils (as in Costa Rica, Puerto Rico, Venezuela, Guatemala, New Caledonia, and Malaysia) provide additional platforms for disentangling the roles of climatic and edaphic variation on plant composition. Weathering patterns of ultramafic rocks vary according to their age, climate (precipitation and temperature), and drainage and geochemical analyses (e.g., Paul et al., 2021, 2022) may largely explain variation in plant composition. On the other hand, in different biogeographical regions with similar climates (e.g., Cuba, Madagascar, and New Caledonia), ultramafic soils are a selective filter for similarly specialized plant lineages (Pillon et al., 2019). The selection of similar plant lineages in similar environments, or ecological sorting, results from phylogenetic niche conservatism (Ackerly, 2003), suggesting that plants adapted to ultramafic soils may have descended from an evolutionary precursor with traits conferring greater success on ultramafic substrates. Further, species adapted to ultramafic and other low-productivity environments tend to share a suite of traits including low photosynthetic rates, low nutrient uptake, high leaf longevity, high root:shoot ratios, increased ability to accumulate nutrient reserves, small and thick leaves, and increased investments in secondary defense compounds (the stress resistance syndrome) (Chapin III et al., 1993; Rajakaruna, 2018; von Wettberg et al., 2014). However, the traits that confer increased plant success on ultramafic substrates are not fully known (see O'Dell & Rajakaruna, 2011), especially in the tropics, and experimental analyses or the measurement of plant functional, anatomical, or physiological traits (e.g., Garnica-Díaz, 2020; Hulshof et al., 2020; Quintela-Sabarís et al., 2020; Trethowan et al., 2021) would be worthy pursuits. Specifically, measuring and including plant functional traits in a global database of ultramafic endemics or metal hyperaccumulators (e.g., Reeves et al., 2018) could provide global comparisons of plant functional strategies in extreme environments.

In many other understudied tropical ultramafic areas, such as in Guatemala, the extent to which plant species or lineages are restricted to ultramafic soils is challenging to assess, given the paucity of data. Plant composition and abundance data would likely reveal relationships between habitat specialization across different biogeographical regions and varying climate and underlying soil geochemistry. In still other tropical ultramafic areas, plant communities are indistinguishable from adjacent, non-ultramafic plant communities. In addition to the effects of patch size, isolation, and geological age, the differentiation of ultramafic plant communities may be reduced or reinforced by soil microbiota. For example, the high concentration of heavy metals in ultramafic soils has dramatic consequences for soil biota and some studies report inhibited microbial growth (Oijagbe et al., 2019), lower soil microbial biomass (Giller et al., 2009; Pal et al., 2005), lower enzyme activity, reduction of soil microbial diversity, and slower decomposition and respiration rates (Gall et al., 2015), perhaps reinforcing differences between ultramafic and non-ultramafic flora. In contrast, microbes from ultramafic soils can exhibit genes related to heavy metal tolerance (Porter et al., 2017), and may play a role in reducing metal toxicity in plants (Benizri & Kidd, 2018; Pal et al., 2006; 2007; Pal & Paul, 2012). Other studies have shown that arbuscular mycorrhizal fungi contribute to plant growth, root colonization and nutrient uptake in ultramafic soils (Doubková et al., 2011) and ultramafic soils appear to be associated with specific microbial strands, including a predominance of actinomycetes and actinobacteria (Costa et al., 2019; Degrood et al., 2005). Soil microbiological functioning was also unaffected by high heavy metal concentrations of ultramafic soils (Costa et al., 2019; Pessoa-Filho et al., 2015). In Brazil (Morro Das Almas, Minas Gerais State), there seems to be little influence of ultramafic soils on gram negative bacteria and fungi when compared to non-ultramafic soils (Guimaraes, 2022, unpublished data), which may, in part, underlie the similarity of plant composition between ultramafic and non-ultramafic flora in this area (Guimaraes et al., 2019). Thus, while some studies point to depauperate ultramafic soil microbiota (Branco, 2010; Visioli et al., 2018), others indicate high biodiversity of soil organisms. Thus, a clear research priority is to disentangle the conditions by which ultramafic soils reduce or promote soil microbial diversity (Vilela et al., 2019) and how microbial diversity, in turn, influences plant life.

Although many tropical ultramafic regions are centers of hyperaccumulation (Reeves, 2003), little is known about the genetic and biochemical aspects that govern this phenomenon or the adaptive significance of metal hyperaccumulation. Likely, genes involved in nutrient (Ca, Mg, K) and metal (e.g., Fe, Ni) transport characterize the evolutionary precursors of adaptation to ultramafic substrates. However, most of what is known about ultramafic adaptation and metal hyperaccumulation is derived from Brassicaceae, which are mostly temperate and herbaceous species (Pillon et al., 2019). Work from Mediterranean climates suggests that metal hyperaccumulation is a chemical defense against herbivores and pathogens, otherwise known as the “elemental defense hypothesis” (Martens & Boyd, 1994). Whether this is true for tropical hyperaccumulators, many of which are trees and shrubs, is unknown. Given the longstanding view that biotic interactions are more important in the tropics (Schemske et al., 2009), metal hyperaccumulation in tropical ecosystems could provide new insights into plant–herbivore and plant-pathogen coevolution. In addition, intraspecific variation in hyperaccumulation or facultative hyperaccumulation (Goolsby and Mason, 2015; Pollard et al., 2014; Reeves et al. 2018), as seen in tropical *Rinorea bengalensis* (Brooks et al., 1977; Fernando et al., 2022) and *Psychotria grandis* (Campbell et al., 2013), for example, suggests environmental and genetic factors contribute to variation in the hyperaccumulation trait.

The study of the molecular mechanisms (e.g., Verbruggen et al., 2009) involved in metal hyperaccumulation is also valuable for the ecological restoration of disturbed ecosystems (Merlot et al., 2015). Phytoremediation and agro-mining are novel technologies that use hyperaccumulating plants as an alternative way to extract metals from the soil (e.g., Rue et al., 2020), mitigate environmental damage, and conserve plant genetic resources in mining areas (e.g., Mohanty et al., 2012; van der Ent et al., 2015b). For example, Sri Lanka’s ultramafic outcrops have attracted much attention from environmental chemists, with greenhouse studies focusing on using biochar and microbial inoculation to reduce metal toxicity on crops growing on ultramafic soils (Bandara et al. 2017; Herath et al., 2014). We hope such studies will not lead to the conversion of pristine ultramafic habitats for agricultural purposes but rather the restoration of ultramafic outcrops degraded by anthropogenic activities.

Conclusions

In summary, we have synthesized our current understanding of the ecology of tropical ultramafic ecosystems, a system that has long been studied for its ecological and evolutionary implications, albeit mostly in extra-tropical latitudes. Our comprehensive approach reveals important generalities among tropical ultramafic ecosystems, including the effect of soil-climate interactions and biogeography. In addition, we have identified many tropical ultramafic ecosystems that remain understudied, and for which, disentangling the interacting effects of historical, climatic, and edaphic factors would be feasible and productive. In doing so, we hope to inspire collaboration among plant community ecologists, physiologists, geologists, and soil biologists to address novel tests of macroecological and macroevolutionary theories.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12229-022-09278-2.

Acknowledgements *A. Funding*: This material is based upon work supported by the National Science Foundation under Grant No. NSF MSB-ECA #1833358 and NSF CAREER #2042453 to CMH. The authors thank two anonymous reviewers for their thoughtful comments. We also thank Jon Walters for help with the geospatial database and documentation and José Ramón Martínez Batlle for help accessing the geological map of the Dominican Republic.

Author Contribution CMH and CGD planned the manuscript; CMH edited and organized the first draft. The following authors wrote and edited specific sections: Puerto Rico: CGD and CMH; Cuba: RBI, FLFT, JLGH; Dominican Republic BC and RC; Costa Rica: ECM and CMH; Brazil: AFG and EVDB; Venezuela: EM and GV; New Caledonia: ALDP; Sri Lanka and India: NR; Guatemala and Colombia: CR; southern Africa: SJS; Malaysia, Indonesia, Philippines: AVDE. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement All data is archived in Dryad (https://doi.org/10.5061/dryad.0zpc8670p), including an updated georeferenced list of prominent ultramafic outcrops worldwide, a region-specific bibliography, and a georeferenced database of ultramafic outcrops in the Americas.

Declarations

Conflicts of Interest The authors declare no conflicts of interest.

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