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Assessment of plant diversity and foliar chemistry on the Sri Lankan ultramafics reveals inconsistencies in the metal hyperaccumulator trait

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Abstract

Some of the largest expanses of ultramafic soils occur in South Asia, but knowledge of the plant diversity and biogeochemistry of these systems in Sri Lanka is very limited. This study aimed to assess the plant diversity and bedrock and foliar chemistry of all known Sri Lankan ultramafic outcrops. The field survey yielded a total of 132 plant taxa from 44 families. The enigmatic nickel hyperaccumulator *Rinorea bengalensis* (Violaceae), first reported in Sri Lanka over four decades ago, was rediscovered at a newly surveyed ultramafic site, however, it did not hyperaccumulate nickel. No new metal hyperaccumulator plants were identified, suggesting that *R. bengalensis* is a facultative nickel hyperaccumulator. This study is the first to highlight the floristic diversity of all known Sri Lankan ultramafic outcrops while revealing the facultative nature of nickel and copper hyperaccumulation among some of Sri Lanka's ultramafic plants.

KEYWORDS

Evolvulus alsinoides, Geobotany, *Hybanthus enneaspermus*, *Rinorea bengalensis*, serpentine plants

1 | INTRODUCTION

The inherent ability of terrestrial plants to sequester extraordinarily high metal or metalloid concentrations in their aerial organs is of great scientific interest, both for fundamental research and for applications in phytotechnologies, including phytomining/agromining (Baker et al., 2000; Brooks, 1998; Pollard et al., 2002). The hyperaccumulation trait has been reported from just <0.2% of all angiosperms globally (Baker, 1981; Whiting et al., 2004). It was originally described from plants from the Northern Hemisphere (Cesalpino, 1583; Minguzzi & Vergnano, 1948) and has since been reported from all continents, except for Antarctica, with new reports still emerging especially in the tropics (Do et al., 2020; McCartha et al., 2019; Navarrete Gutiérrez et al., 2021; Nkrumah et al., 2018). Hyperaccumulation in plants is recognized as the exceedance of metal(loid)-specific shoot concentrations, at least an order of magnitude higher compared to other plants growing on the same soil (Brooks, 1998). Several reviews have synthesized the current state of knowledge of metal(loid) hyperaccumulators from around the world and provided perspectives from foundational empirical studies (Ferrero et al., 2020; Galey et al., 2017; Rajakaruna et al., 2009; Teptina et al., 2018).

Hyperaccumulator plants are generally restricted to metalliferous soils (Baker & Brooks, 1989; Reeves et al., 2018), including so-called ultramafic soils derived from ultramafic bedrock which are characterized by high nickel (Ni), cobalt (Co) chromium (Cr), and manganese (Mn) concentrations, low potassium (K) status, and low calcium to magnesium (Ca:Mg) quotients (Baker et al., 1992; Harrison & Rajakaruna, 2011). The genetics of plant metal hyperaccumulation is such that it can vary between obligate, that is, species that constituently hyperaccumulate metals or metalloids when found on metalliferous soils, and facultative species that hyperaccumulate at some but not at all sites (Pollard et al., 2002). Established hypotheses about the adaptive significance of the trait (Boyd, 2004, 2012; Ferrero et al., 2020) focus on the Northern Hemisphere species, especially a number of species in Brassicaceae, such as *Noccaea caerulescens*, *Odontarrhena muralis*, and *Streptanthus polygaloides* (Macnair, 2003; Meindl & Ashman, 2015; Pope et al., 2013). Studies on Southern Hemisphere hyperaccumulators native to South America, the Western Pacific, primarily New Caledonia, Australia and Southeast Asia have revealed that many ultramafic outcrops are major centers for plant diversity and endemism, often rich in metal hyperaccumulator plant species (Galey et al., 2017; Jaffré et al., 2013; Proctor, 2003).

Ultramafic outcrops are fragments of the upper mantle and exposed at the Earth's surface due to tectonic plate interactions (Coleman & Jove, 1992). The adversity of the chemical properties of ultramafic soils pose edaphic stressors on the local vegetation which results in the evolution of adaptations to survive on these harsh sols (Proctor, 1971a, 1971b). Consequently, ultramafic ecosystems are unique natural laboratories for investigation of important biological questions across disciplines, including speciation, genetics, physiology, nutrition, cross-kingdom interactions, biogeography, plant–soil interactions, and conservation biology (Boyd, 2007; Harrison & Rajakaruna, 2011; Pollard et al., 2002; Whiting et al., 2004).

The future survival of ultramafic ecosystems is at risk from escalating anthropogenic impacts, including climate change, resource extraction, and land clearing (Gomez-Zotano et al., 2015; Kruckeberg, 2010; Weiss, 1999; Whiting et al., 2004; Wolf et al., 1999). Furthermore, economically valuable ore deposits (of Ni) occur in many ultramafic outcrops, which places the ecosystems in direct conflict with the resource industry (Erskine et al., 2021). Change in climate has wide-ranging and largely unpredictable impacts on many ecosystems globally (IPCC, 2014), yet investigations into the impact of climate change on ultramafic ecosystems, especially in the tropics, are virtually nonexistent (Corlett & Tomlinson, 2020; Damschen et al., 2012). An understanding of the complexity of the ecosystems on ultramafic outcrops is an essential foundation for basing more detailed ecological investigations.

The paleo-history of the Indian subcontinent gave rise to ultramafic outcrops in the Himalayas, the Andaman and Nicobar Islands, and along the juncture of the Vijayan and Highland Complexes in Sri Lanka (Fernando et al., 2013; Pathirana, 1930; Radhakrishna et al., 1982; Thothathri, 1962) (Figure 1). In contrast to the breadth and depth of knowledge on European ultramafic ecosystems (Teptina et al., 2018), knowledge of these ecosystems in India and Sri Lanka is very rudimentary. To date, the entire literature on Sri Lankan ultramafic floras comprises two reviews (Galey et al., 2017; Rajakaruna & Baker, 2004) and six empirical studies (Chathuranga et al., 2015; Rajakaruna et al., 2002; Rajakaruna & Bohm, 2002; Samithri, 2015; Tennakone et al., 2007; Weerasinghe & Iqbal, 2011). Of the latter group, one provides preliminary floristic and leaf chemical data for 19 plants from Ginigalpellessa, 11 from Indikolapellessa, two from Yodhaganawa, and seven from Ussangoda (Rajakaruna & Bohm, 2002). Two additional studies detail floristic and plant chemical data for Ussangoda, the most significant of Sri Lankan ultramafic sites (Samithri, 2015; Weerasinghe & Iqbal, 2011), one examines Ni uptake by *Fimbristylis ovata* populations from Ussangoda (Chathuranga et al., 2015), while the others are about prospective Ni phytomining from Ussangoda via *Hybanthus enneaspermus* (now *Afrohybanthus enneaspermus*; Tennakone et al., 2007), and antimicrobial properties of 3–17 plant species each

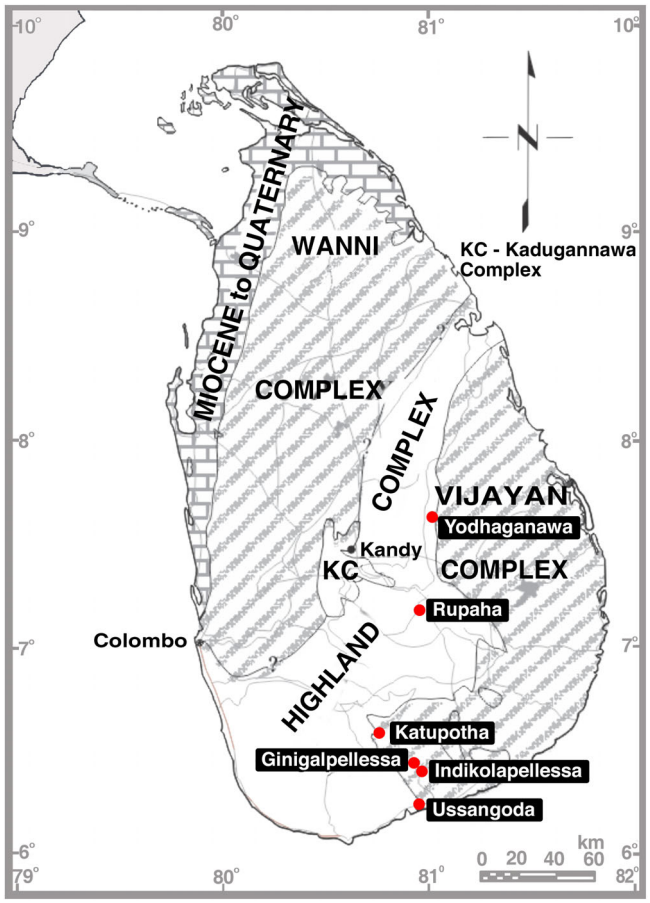

FIGURE 1 Map of Sri Lanka showing the serpentinite outcrops Ussangoda, Indikolapellessa, Ginigalpellessa, Rupaha, and Yodhaganawa, along the suture zone between the Vijayan and Highland complexes. The Katupotha site could not be located in this study [Color figure can be viewed at wileyonlinelibrary.com]

from Ginigalpellessa, Indikolapellessa, Yodhaganawa, and Ussangoda (Rajakaruna et al., 2002). Sri Lankan ultramafic flora originally came to attention in 1977 (Brooks, Lee, et al., 1977; Brooks, Wither, et al., 1977), when extreme Ni hyperaccumulation by the island's *R. bengalensis* (10,000 μg g^{-1} Ni) was reported after analysis of a herbarium specimen sourced from the central region, its exact location is still unknown despite subsequent efforts (Rajakaruna & Baker, 2004).

This study aimed to explore all known Sri Lankan ultramafic outcrops to further the state of knowledge on the plant diversity of these sites, with a particular focus on metal hyperaccumulator plants. Furthermore, this study aimed to compare new field survey data with published data on the only site (Ussangoda) that has been studied in some detail to date (Chathuranga et al., 2015; Rajakaruna & Baker, 2004; Rajakaruna & Bohm, 2002). To that end, the field surveys conducted in this study have generated a more complete inventory of the flora for accessible areas of the Ginigalpellessa, Indikolapellessa, Yodhaganawa, and Ussangoda outcrops, along with the first preliminary species list for Rupaha, an ultramafic outcrop that had not been surveyed previously.

2 | MATERIALS AND METHODS

2.1 | Field sites and sampling

Plant material samples were collected from the following documented ultramafic outcrops in Sri Lanka (Hewawasam et al., 2014) (Figures 1 and 2) as follows:

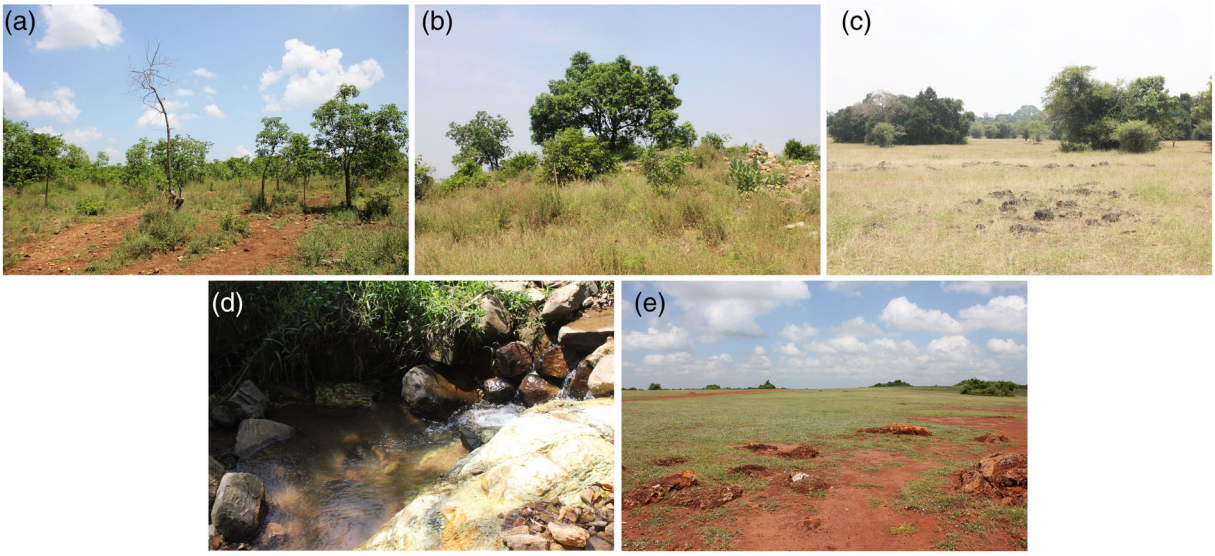

FIGURE 2 Study sites Ginigalpellessa (a), Indikolapellessa (b), Yodhaganawa (c), Rupaha (d), and Ussangoda (e) [Color figure can be viewed at wileyonlinelibrary.com]

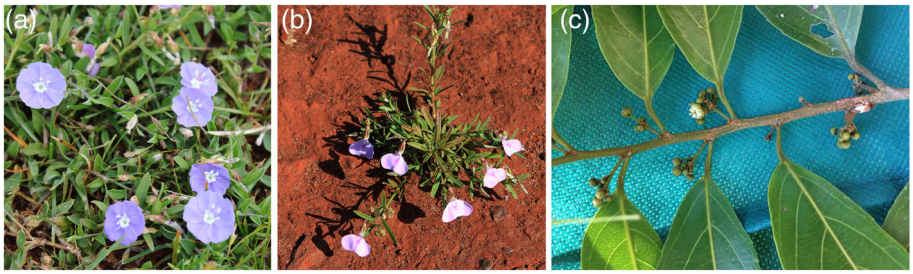

FIGURE 3 *Evolvulus alsinoides* (a), *Hybanthus enneaspermus* (b), and *Rinorea bengalensis* (c) [Color figure can be viewed at wileyonlinelibrary.com]

Ginigalpellessa (G) (6°22′56″N 80°53′30″E; outcrop size 100 ha), Indikolapellessa (I) (6°21′29"N 80°56′12″E; outcrop size 40 ha), Yodhaganawa (Y) (7°39′53″N 80°59′11″E; outcrop size 50 ha), Rupaha (R) (7°2′11″N 80°53′36″E; outcrop size 10 ha). The approximate areas sampled within each of these outcrops were 6 ha (G), 15 ha (I), 4 ha (Y), and 1 ha (R), representing 6%, 15%, 8%, 10% of the total exposed area of each outcrop, respectively. Plant collection for chemical analysis was made in triplicate per species, and once individually processed to the dry powdered state, pooled to a single sample representative of each species collected. We added published plant data for Ussangoda (U) (6°5′56″N 80°59′12″E; outcrop size 100 ha) (Rajakaruna & Bohm, 2002; Samithri, 2015; Weerasinghe & Iqbal, 2011) into the analysis. Katupotha, the sixth ultramafic outcrop we intended to study (Hewawasam et al., 2014), could not be located despite concerted efforts, suggesting it may have originally been incorrectly documented or has since been destroyed by land clearing. Bedrock samples from G, I, Y, R, and U were collected for X-ray fluorescence (XRF) analysis to determine their elemental composition. Soil elemental concentrations have already been published for all of the ultramafic outcrops (Chathuranga et al., 2015; Fernando et al., 2013; Hewawasam et al., 2014; Rajakaruna & Bohm, 2002; Rajapaksa et al., 2012; Vithanage et al., 2014). The G, I, Y, and U outcrops are semiarid and have a stunted sparse vegetation with highly sclerophyll life forms, while G, I, and Y outcrops have scattered trees and shrubs. In contrast, the R outcrops has dense tropical rainforest.

At all outcrops, plants were destructively sampled for analysis and photographed in the field, and herbarium specimens were made in situ for identification purposes. The samples collected for chemical analysis were mature leaves (10–20) from woody plants and large herbs, while for small-leaved low growing plants, entire shoots were harvested. The previously documented Ni hyperaccumulators *Evolvulus alsinoides* (Convolvulaceae) and *H. enneaspermus* (Violaceae; now *A. enneaspermus*) (Figures 3a,b) were also sampled, and attempts were made to relocate *R. bengalensis* (Violaceae) (Figure 3c) at Rupaha.

2.2 | Bed rock XRF analysis

Rock samples were analyzed by XRF at the GeoAnalytical Laboratory, Washington State University, as described by Rajakaruna et al. (2012). Major elements (Al–Ti) were reported as weight% expressed on oxide basis, and minor elements (Ba–Zr) as mg kg^{-1}.

2.3 | Plant identification

Photographs and herbarium specimens taken in the field, reference books, online resources, and botanical expertise of National Herbarium, Royal Botanic Garden, Peradeniya, Sri Lanka were used to determine the identification of the species. All voucher specimens were deposited at the National Herbarium.

2.4 | Plant chemical analysis

Plants with a prostrate habitat (which are hence susceptible for contamination with soil particles) were quickly rinsed in water and air-dried after root material was removed. In the laboratory, plant samples were rapidly (~1 s) rinsed successively with water and 1 mM EDTA to remove residual surface contamination with soil particulates. Since prolonged wetting and/or soaking of leaf tissues risks leaching of tissue-bound metals, this process was necessarily very swift. It had previously been applied in other studies of Sri Lankan hyperaccumulators without confounding effects (Chathuranga et al., 2015). Post washing, the plant material was air-dried and placed in a 70°C oven for several days until fully dry. All samples were then finely ground either mechanically or manually, depending on the toughness of the particular sample. The subsequent processing and analyses of samples were based on established methodology (Chapman & Pratt, 1961; Kalra & Maynard, 1991). Approximately 1 g of ground dry foliar tissue was then dry-ashed in a muffle furnace (550°C, 6 h), the ash initially wetted with DI water, 5 ml 50% HCl and water added, and gently heated for 30 min, cooled, and brought up to 50 ml with DI water. Solutions

were finally analyzed by Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES) for Ca, K, Mg, K, P, Cu, Zn, Mn, B, Al, Fe, Ni, and Cr.

3 | RESULTS AND DISCUSSION

3.1 | Bedrock chemistry

The bedrock chemical data of each of the ultramafic outcrops (Table 1) conform with current knowledge of their ultramafic nature (Hewawasam et al., 2014; Proctor, 1971a, 1971b; Rajakaruna & Bohm, 2002), most notably, elevated Ni, Co, and Cr, low Ca:Mg quotients, high Fe, particularly at Ussangoda, high Mg at all sites except Ussangoda, and extremely low Ca, K, and P concentrations at all sites. The concentrations of Ni, Co, and Cr in the Rupaha rocks were clearly the lowest of all sites. Lowest concentrations of trace elements in Rupaha rocks (Table 1) suggest that its serpentinites were metamorphosized significantly later than those at other sites (Coleman & Jove, 1992).

TABLE 1 XRF (X-ray fluorescence) bulk chemistry of rocks expressed on oxide basis from Ginigalpelassa (G), Indikolapelassa (I), Yodhaganawa (Y), Rupaha (R), and Ussangoda (U)

Site	G	I	Y	R	U
Major elements (%)	(Weight %)				
SiO_2	35.9	40.5	42.0	42.1	46.7
TiO_2	0.03	0.01	0.002	0.01	0.26
Al_2O_3	0.55	0.27	0.29	0.14	3.82
FeO	6.73	7.13	7.40	1.03	31.2
MnO	0.11	0.09	0.11	0.03	0.35
MgO	36.7	35.8	39.7	41.2	0.47
CaO	0.20	0.11	0.08	0.21	0.03
Na_2O	0.09	0.10	0.10	0.12	0.04
K_2O	0.00	0.01	0.00	0.01	0.02
P_2O_5	0.003	0.004	0.01	0.014	0.05
Trace elements (mg kg^{-1})					
Ni	2356	3022	2724	4	4098
Cr	3071	2608	3251	10	17,582
Sc	3	6	5	1	22
V	25	22	13	3	214
Ba	15	17	15	18	130
Rb	1	1	1	1	2
Sr	4	2	0	7	3
Zr	9	8	9	6	205
Y	2	2	2	3	8
Nb	1.7	1.4	1.3	1.4	3.3
Ga	1	2	1	2	8
Cu	11	10	9	8	29
Zn	48	44	91	28	118
Pb	3	3	2	5	6
La	3	0	1	4	0
Ce	3	6	4	0	34
Th	1	0	0	1	3
Nd	1	0	2	1	6
U	1	0	1	0	5

Note: Major elements (Al–Ti), minor elements (Ba–Zr).

3.2 | Plant diversity of the ultramafic outcrops

These habitats ranged from coastal low-rainfall areas to moist, densely vegetated high-rainfall areas (Figure S1); a great majority of whose plants are not understood in terms of their adaptations to their nutritionally depauperate, metalliferous host substrates. The integrated list of plant taxa combining field identifications for the G, I, Y, R ultramafic outcrops, together with published taxa for the U site (Rajakaruna & Bohm, 2002; Samithri, 2015; Senevirathne et al., 2000; Weerasinghe & Iqbal, 2011) (Table S1) comprises 132 taxa from 44 families. The Fabaceae, Euphorbiaceae, and Asteraceae were the most species-rich families with 16, 10, and 10 species, respectively. Many taxa were restricted to 1–2 outcrops, with only 3 of the 132 taxa (*Carissa spinarum*, *Chromolaena odorata*, and *Euphorbia indica*) occurring on four of the five outcrops; surprisingly, none of the ultramafic-tolerant taxa were endemic to Sri Lanka. Why an island with 28% endemism among angiosperms (Wijesundara et al., 2020) has no ultramafic endemic taxa warrant further investigation. Factors that may contribute to this apparent anomaly may include the focus to date on collecting plants with floral or other reproductive structures and sampling that is carried out over a short period (i.e., 1–2 days) in mostly accessible areas within each outcrop. To date, less than 15% of each G, I, Y, and R outcrops has been surveyed. The U outcrop, on the other hand, has received much more attention, with at least four studies (Rajakaruna & Bohm, 2002; Samithri, 2015; Senevirathne et al., 2000; Weerasinghe & Iqbal, 2011) collectively surveying almost the entire outcrop. Lack of thorough and systematic survey of the ultramafic flora at G, I, Y, and R may have prevented the detection of any minor morphological features that may indicate taxonomically recognizable differences among the flora at each site. Additionally, whether any other historical (e.g., outcrop age, past land-use practices), climatic, ecological, or other physical (e.g., small and disjunct outcrops $<1\ km^2$ in area) factors also contribute to the lack of substrate-level endemism is also worthy of study. More detailed investigations are clearly needed to better document the geobotany of the ultramafic outcrops of Sri Lanka.

3.3 | Foliar chemistry of plant species from the ultramafic outcrops

Plant foliar elemental concentrations (Tables 2 and 3), expressed as $\mu g\ g^{-1}$ dry tissue weight, did not reveal any hyperaccumulator plants, even for species that have previously been recognized as Ni hyperaccumulators, including *E. alsinoides* and *H. enneaspermus* (now *A. enneaspermus*; Rajakaruna & Bohm, 2002) and *R. bengalensis* (Brooks, Wither, et al., 1977), that were sampled in this study. Nickel hyperaccumulation is defined as $>1000\ \mu g\ g^{-1}$, whereas respective foliar Ni concentrations for these three species were ~68, 90, and 39 $\mu g\ g^{-1}$ (Table 3). Foliage Ni concentrations varied overall between 1 and 163 $\mu g\ g^{-1}$, Mn varied between 11 and 418 $\mu g\ g^{-1}$, with the highest value observed in *R. bengalensis* at the Rupaha site, where foliar Al in *Achyranthes aspera* was 1515 $\mu g\ g^{-1}$ (Table 3). Foliage concentration-ratios of Ca/Mg varied by as much as 36-fold, from 0.13 to 4.73 across all taxa analyzed chemically (Table 2).

This study targeted all known Sri Lankan ultramafic outcrops. No hyperaccumulator plants were recorded, despite *E. alsinoides* and *H. enneaspermus* (now, *A. enneaspermus*) reported previously as strong Ni hyperaccumulators from the Ussangoda ultramafic outcrop (Rajakaruna & Bohm, 2002; Samithri, 2015; Senevirathne et al., 2000; Weerasinghe & Iqbal, 2011). Interestingly, analyses of these two species from Ginigalpellessa and Indikolapellessa did not reveal any Ni hyperaccumulator plants. These findings warrant follow-up growth experiments on plants of varying provenance to examine differences in the Ni hyperaccumulation trait, as it is likely these species could be facultative hyperaccumulators. Similarly, while *Toddalia asiatica* (Rutaceae; now *Zanthoxylum asiaticum*) and *Crotalaria* spp. from Ussangoda were reported as Ni hyperaccumulators previously (Rajakaruna & Bohm, 2002; Samithri, 2015), the samples collected from Indikolapellessa and Yodhaganawa in the current study were not hyperaccumulating Ni. In a wide-ranging review of the ecology and biogeochemistry of South and Southeast Asian ultramafic outcrops, Galey et al. (2017) report on Cu hyperaccumulator plants from Sri Lankan ultramafic soils based on the study by Rajakaruna et al. (2002), on the basis of revision of the Cu hyperaccumulation threshold to 300 $\mu g\ g^{-1}$ (van der Ent et al., 2013). Species common to this current field study and that earlier study (Rajakaruna & Bohm, 2002) are *Calotropis gigantea* (Apocynaceae), *Carissa spinarum* (Apocynaceae), and *Phyllanthus* sp. (Phyllanthaceae). On that basis, comparison of foliar Cu concentrations of these species between published data (Rajakaruna & Bohm, 2002) and present data here show that the species hyperaccumulate Cu on the Ginigalpellessa site, but not on the Indikolapellessa and Yodhaganawa sites, again pointing to the plastic or facultative nature of metal hyperaccumulation. A study on some extremely Cu-enriched ultramafic soils in Brazil and Malaysia revealed that all plants restrict Cu uptake and act as excluders, with no more than 298 $\mu g\ g^{-1}$ foliar Cu recorded (van der Ent & Reeves, 2015).

TABLE 2 Foliar elemental macronutrient concentrations (μg g^{-1}) and Ca/Mg concentration-ratios for Ginigalpelassa (G), Indikolapelassa (I), Yodhaganawa (Y), Rupaha (R), and Ussangoda (U)

Taxon	Habit	Site	Ca	Mg	Ca/Mg ratio	K	P
Acacia auriculiformis	Tree	G	5.34	11.4	0.47	4.17	1.19
Acanthospermum hispidum	Herb	I	5.05	12.3	0.41	9.6	1.63
Achyranthes aspera	Herb	R	12	10.5	1.14	55	3.9
Acronychia pedunculata	Tree	R	6.65	7.62	0.87	13.8	1460
Afrohybanthus enneaspermus (*Hybanthus enneaspermus*)	Herb	G	2.77	9.21	0.3	4.94	3444
Afrohybanthus enneaspermus (*Hybanthus enneaspermus*)	Herb	I	11.6	11.1	1.05	13.8	2538
Allophylus cobbe	Shrub	R	6.6	9.17	0.72	6.12	1520
Atalantia ceylanica	Shrub	Y	9.11	6.92	1.32	7.82	1400
Azadirachta indica	Tree	I	9.59	7.16	1.34	12.9	1.67
Azadirachta indica	Tree	Y	6.89	5.64	1.22	21	1.76
Bauhinia racemosa	Tree	Y	4.23	7.06	0.6	8.32	1.36
Calotropis gigantea	Shrub	I	7.96	13.4	0.59	36	4.01
Carissa spinarum	Shrub	I	20.2	5.65	3.58	5.57	2.94
Carissa spinarum	Shrub	Y	5.66	2.71	2.09	4.52	1.36
Catunaregam spinosa	Shrub	Y	2.88	10.9	0.27	2.19	0.72
Cestrum nocturnum	Shrub	R	2.5	5.77	0.43	44.9	5176
Cestrum nocturnum	Shrub	R	5.54	10.9	0.51	28.5	3323
Cestrum nocturnum	Shrub	R	38.1	13.7	2.77	24.4	1893
Cestrum nocturnum	Shrub	R	8.24	7.52	1.1	26.2	2695
Chromolaena odorata	Herb	G	6.33	10.9	0.58	9.43	1.94
Chromolaena odorata	Herb	Y	2.65	10.3	0.26	17.9	3.75
Clinopodium umbrosum	Herb	G	2.34	17.5	0.13	12.5	2.13
Crassocephalum crepidioides	Herb	R	7	8.1	0.87	29.9	1.31
Crotalaria pallida	Herb	I	9.1	10.5	0.87	6.18	2.3
Crotalaria verrucosa	Herb	Y	2.24	7.23	0.31	19.9	2.42
Croton laccifer	Shrub	G	6.83	12.9	0.53	4.23	1.53
Croton aromaticus	Shrub	G	4.12	14.2	0.29	9.61	2.58
Cyanotis pilosa	Herb	G	14.8	14.1	1.05	4.9	1.01
Dimorphocalyx glabellus	Shrub	Y	9.24	11.4	0.81	13.5	1.17
Eugenia uniflora (*Eugenia willdenowii*)	Shrub	G	3.17	3.79	0.84	8.82	0.82
Euphorbia indica	Herb	G	1.41	6.69	0.21	19.9	1.1
Euphorbia indica	Herb	I	3.54	7.07	0.5	13.8	3.48
Euphorbia indica	Herb	Y	4.4	10.5	0.42	9.4	1.77
Euphorbia rosea	Herb	G	3.41	10.8	0.32	4.11	2.17
Evolvulus alsinoides	Herb	I	4.29	10	0.43	14.2	2.91
Evolvulus alsinoides	Herb	I	3.68	6.45	0.57	13.1	1.33
Evolvulus alsinoides	Herb	G	3.69	8.45	0.44	12.9	0.88
Falconeria insignis (*Sapium insigne*)	Tree	Y	5.54	9.41	0.59	12.9	0.8
Fimbristylis cymosa	Herb	G	1.31	5.43	0.24	12.3	0.68

(Continues)

TABLE 2 (Continued)

Taxon	Habit	Site	Ca	Mg	Ca/Mg ratio	K	P
Fimbristylis dichotoma	Herb	G	1.43	8.02	0.18	17	1.31
Flueggea leucopyrus	Shrub	Y	11	12.7	0.87	2.75	1.16
Garcinia spicata	Tree	Y	6.27	6.97	0.9	4.8	0.781
Garcinia spicata	Tree	Y	6.01	5.84	1.03	6.9	0.988
Gymnostachyum hirsutum	Herb	R	17.5	12.8	1.37	39.7	1.49
Ixora pavetta	Shrub	I	7.97	6.56	1.22	6.9	0.9
Ixora pavetta	Shrub	Y	7.43	9.72	0.76	8.3	1.1
Leucas zeylanica	Herb	G	8.51	6.87	1.24	23.5	3.31
Leucas biflora	Herb	R	7.93	8.93	0.89	40.8	2.87
Morinda coreia	Tree	G	15.4	10.9	1.41	5.81	1.04
Oldenlandia umbellata	Herb	I	9.84	6.83	1.44	11.3	1.91
Pavatta zeylanica	Shrub	R	12.8	6.64	1.93	7.61	1.09
Phyllanthus debilis	herb	I	13.6	10.1	1.36	13.6	2
Phyllanthus maderaspatensis	Shrub	I	9.59	6.4	1.49	14.1	2.01
Phyllanthus myrtifolius	Shrub	I	6.21	3.93	1.58	8.65	0.96
Polycarpon prostatum	Herb	Y	1.86	12.4	0.15	9.3	0.75
Polygala glaucoides	Herb	Y	3.11	9.84	0.32	10	0.88
Polygonum chinensis	Herb	R	12.7	11.7	1.09	29.3	2.44
Pterospermum suberifolium	Tree	G	3.97	4.41	0.9	6.17	1.29
Rinorea bengalensis	Shrub	R	14	3.36	4.73	13.5	1121
Senegalia caesia (*Acacia caesia*)	Vine	R	11.7	5.99	2.35	7.57	1.32
Striga angustifolia	Herb	G	2.45	9.82	0.25	15.2	3280
Syzygium cumini	Tree	Y	2.87	6.31	0.45	3.75	0.67
Tephrosia pumila	Herb	Y	3.91	9.74	0.4	6.86	1.43
Vicoa indica	Herb	I	5.04	9.19	0.55	12.9	2.28
Zanthoxylum asiaticum (*Toddalia asiatica*)	Vine	Y	5.76	9.48	0.61	16.8	0.81
Ziziphus oenoplia	Shrub	Y	4.85	8.71	0.56	8.94	0.83

Note: Names within parentheses for some taxa are nomenclature used in previous studies of Sri Lankan serpentine plants (Rajakaruna & Bohm, 2002; Samithri, 2015; Senevirathne et al., 2000; Weerasinghe & Iqbal, 2011).

3.4 | Outlook for conservation and research

The high levels of plant diversity (132 species in 44 families) so far documented on outcrops that have only been partially (<15%) surveyed reaffirm the importance of Sri Lanka's ultramafic outcrops on the island's plant diversity. Ussangoda is the most species-rich site; however, it is plausible that the dense tropical rainforest habitat of the Rupaha site previously never studied is in fact the most species-rich. The easily accessible Ussangoda is more conducive to research than the Rupaha site, which has limited access, mostly due to steep terrain and private land ownership (Figure 2). Further, the area sampled in the previous vegetation surveys (Rajakaruna & Bohm, 2002; Samithri, 2015; Senevirathne et al., 2000; Weerasinghe & Iqbal, 2011) at the Ussangoda site is much larger (almost the entire outcrop of 100 ha), compared to the area we sampled at Rupaha (1 ha out of the total of 10 ha). Of the 11 species at Rupaha, there was no overlap with the other ultramafic outcrops, except for *Acacia caesia* (Fabaceae; now, *Senegalia caesia*), non-native to Sri Lanka, and *Allophylus cobbe* (Sapindaceae), both also recorded at Ussangoda. The rediscovery of *R. bengalensis* at the Rupaha site in this study is significant, given that it was only known from herbarium specimens (Brooks, Lee, et al., 1977; Brooks, Wither, et al., 1977). This species is a facultative Ni hyperaccumulator (van der Ent et al., 2020), and the

TABLE 3 Foliar elemental micronutrient and additional metal concentrations (μg g^{-1}) for Ginigalpelassa (G), Indikolapelassa (I), Yodhaganawa (Y), Rupaha (R), and Ussangoda (U)

Taxon	Habit	Site	Cu	Zn	Mn	B	Al	Fe	Ni	Cr
Acacia auriculiformis	Tree	G	4.14	12.3	48.3	13.4	42.0	112	2.76	<1.03
Acanthospermum hispidum	Herb	I	2.65	18.3	68.8	28.3	138	290	28.8	2.93
Achyranthes aspera	Herb	R	4.88	17.9	55.4	46.6	1515	758	1.60	3.04
Acronychia pedunculata	Tree	R	5.28	28.0	161	28.3	96.2	80.8	1.85	1.11
Afrohybanthus enneaspermus (*Hybanthus enneaspermus*)	Herb	G	11.0	26.9	47.1	22.1	317	1867	66.9	14.7
Afrohybanthus enneaspermus (*Hybanthus enneaspermus*)	Herb	I	4.80	57.8	93.6	40.9	804	1897	89.5	27.9
Atalantia ceylanica	Shrub	Y	2.55	7.18	17.9	48.1	89.6	171	79.3	2.85
Azadirachta indica	Tree	I	1.91	18.3	28.1	77.2	120	171	33.2	2.65
Azadirachta indica	Tree	Y	4.87	23.7	37.5	17.7	25.9	26.3	3.74	<<1.01
Bauhinia racemosa	Tree	Y	2.04	17.6	33.0	26.1	86.5	147	38.8	2.62
Calotropis gigantea	Shrub	I	1.48	21.3	141	51.7	32.9	41.4	17.5	<0.1
Carissa spinarum	Shrub	I	5.32	35.6	186	205	50.1	67.6	31.3	1.11
Carissa spinarum	Shrub	Y	3.12	29.3	64.5	55.8	91.2	64.0	16.7	2.12
Catunaregam spinosa	Shrub	Y	4.03	7.45	13.4	32.6	95.7	55.7	25.4	1.54
Cestrum nocturnum	Shrub	R	16.2	72.0	22.8	33.0	46.0	58.6	1.16	<1.07
Cestrum nocturnum	Shrub	R	10.1	48.4	54.0	38.7	86.1	50.5	<1.16	<1.16
Cestrum nocturnum	Shrub	R	6.48	36.5	40.4	31.9	831	443	1.88	2.01
Cestrum nocturnum	Shrub	R	12.0	57.3	29.6	63.2	109	56.2	<1.59	<1.59
Chromolaena odorata	Herb	G	14.2	42.9	38.1	74.0	73.2	123	22.0	1.33
Chromolaena odorata	Herb	Y	5.06	34.7	23.9	47.4	54.9	108	51.1	2.10
Clinopodium umbrosum	Herb	G	9.42	13.1	26.3	32.4	110	157	10.9	<3.50
Crassocephalum crepidioides	Herb	R	7.65	16.3	30.0	33.4	479	341	4.29	6.11
Crotalaria pallida	Herb	I	8.25	25.9	151	26.8	33.8	18.6	25.2	<1.13
Crotalaria verrucosa	Herb	Y	3.20	33.6	32.5	17.6	55.5	45.1	38.3	1.80
Croton laccifer	Shrub	G	1.63	9.65	83.8	66.8	176	208	35.4	2.48
Croton aromaticus	Shrub	G	4.28	11.5	145	58.6	123	137	32.0	4.53
Cyanotis pilosa	Herb	G	5.27	51.3	96.9	23.4	114	94.9	61.0	<2.36
Dimorphocalyx glabellus	Shrub	Y	6.71	31.9	82.5	70.5	119	588	112	9.70
Eugenia uniflora (*Eugenia willdenowii*)	Shrub	G	4.87	11.3	12.0	4.3	40.1	10.9	20.1	1.35
Euphorbia indica	Herb	G	4.47	11.2	54.2	4.98	134	379	17.4	4.65
Euphorbia indica	Herb	I	9.05	15.5	70.9	22.7	171	988	41.0	6.93
Euphorbia indica	Herb	Y	6.76	31.7	28.8	25.2	65.2	238	20.1	2.25
Euphorbia rosea	Herb	G	11.1	54.4	27.1	40.5	57.6	92.9	32.7	3.51
Evolvulus alsinoides	Herb	I	2.58	29.3	55.0	24.0	153	1313	67.8	11.6
Evolvulus alsinoides	Herb	I	4.02	22.9	55.7	29.3	464	1985	163	15.1
Evolvulus alsinoides	Herb	G	11.7	25.6	78.0	22.0	121	1047	88.4	9.60
Falconeria insignis (*Sapium insigne*)	Tree	Y	4.88	3.97	11.3	12.2	37.0	9.59	72.7	<1.06
Fimbristylis cymosa	Herb	G	1.05	10.7	110	4.54	86.6	999	71.6	9.14
Fimbristylis dichotoma	Herb	G	<2.30	8.33	101	3.96	133	407	15.6	3.46

(Continues)

TABLE 3 (Continued)

Taxon	Habit	Site	Cu	Zn	Mn	B	Al	Fe	Ni	Cr
Flueggea leucopyrus	Shrub	Y	1.56	6.84	28.2	75.0	91.0	23.0	52.1	2.12
Garcinia spicata	Tree	Y	2.92	22.9	24.1	22.8	44.8	8.55	23.5	1.74
Garcinia spicata	Tree	Y	3.20	17.2	21.7	16.3	45.8	<5.0	9.67	<1.08
Gymnostachyum hirsutum	Herb	R	7.88	62.7	92.2	33.1	88.2	142	<2.48	<2.48
Ixora pavetta	Shrub	I	3.87	14.5	18.5	16.1	32.4	1.3	16.8	<1.06
Ixora pavetta	Shrub	Y	0.920	11.2	19.0	40.4	60.7	60.9	26.9	2.75
Leucas zeylanica	Herb	G	8.91	42.8	65.2	31.9	291	608	34.0	6.24
Leucas biflora	Herb	R	11.0	22.7	32.4	38.9	286	216	2.87	3.74
Morinda coreia	Tree	G	5.56	51.7	99.5	23.1	111	56.6	57.2	1.21
Oldenlandia umbellata	Herb	I	21.8	38.8	91.0	24.4	765	1614	76.2	11.7
Pavatta zeylanica	Shrub	R	4.34	10.3	43.8	37.3	156	66.3	2.17	1.25
Phyllanthus debilis	herb	I	6.31	20.6	79.9	36.8	189	272	54.8	2.59
Phyllanthus maderaspatensis	Shrub	I	6.95	26.1	57.8	48.1	81.3	135	22.4	1.25
Phyllanthus myrtifolius	Shrub	I	8.13	26.6	67.1	23.1	271	591	38.4	5.88
Polycarpon prostatum	Herb	Y	8.63	40.1	58.9	21.6	192	1040	163	21.4
Polygala glaucoides	Herb	Y	8.27	29.4	47.0	20.0	140	1024	87.0	19.5
Polygonum chinensis	Herb	R	7.61	19.3	47.6	30.9	54.3	42.4	<1.14	<1.14
Pterospermum suberifolium	Tree	G	4.36	23.4	63.3	38.2	64.8	120	15.1	<2.36
Rinorea bengalensis	Shrub	R	3.48	297	418	28.8	156	135	39.1	6.31
Senegalia caesia (*Acacia caesia*)	Vine	R	5.87	16.1	87.5	25.6	349	1218	51.8	11.1
Striga angustifolia	Herb	G	7.02	38.4	30.8	11.6	44.3	151	55.5	<2.44
Syzygium cumini	Tree	Y	4.10	9.21	40.4	29.5	60.8	57.1	22.6	13.7
Tephrosia pumila	Herb	Y	12.7	52.8	73.8	15.3	82.8	146	47.1	2.75
Vicoa indica	Herb	I	10.1	26.1	31.7	25.2	121	179	44.8	3.78
Zanthoxylum asiaticum (*Toddalia asiatica*)	Vine	Y	2.06	20.1	38.3	26.5	53.1	70.7	21.6	<1.89
Ziziphus oenoplia	Shrub	Y	2.41	15.9	219	37.5	102	143	28.1	2.36

Note: Names within parentheses for some taxa are nomenclature used in previous studies of Sri Lankan ultramafic plants (Rajakaruna & Bohm, 2002; Samithri, 2015; Senevirathne et al., 2000; Weerasinghe & Iqbal, 2011).

samples analyzed from Rupaha were not above the Ni hyperaccumulation threshold. The paucity of ultramafic ecosystems on the entire Indian subcontinent (Galey et al., 2017) is in itself a strong impetus for furthering investigations on the disjunct outcrops in Sri Lanka. It is clear from the current study that there is also a need to investigate intraspecific variation in Ni and Cu hyperaccumulation among ultramafic plants (Reeves et al., 2015). Furthermore, the little known Rupaha outcrop, which is strikingly different from the much-studied Ussangoda site, should be further explored as the current survey was limited to 1 day and focused mostly on collecting taxa with taxonomically distinguishable features, including reproductive organs, within easily accessible areas of steep terrain characterizing this site. Exhaustive and systematic surveys at all five sites, covering the entirety of the exposed outcrop at each site, may reveal additional taxa of taxonomic interest, including those that may hyperaccumulate metals. Katupotha, the sixth ultramafic outcrop (Hewawasam et al., 2014), now being unlocatable as natural habitat, provides a case in point as to why the ultramafic outcrops in Sri Lanka must be protected from degradation as a matter of urgency, so that they can be the focus of more rigorous geobotanical studies.

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

Denise R. M. Fernando and Nishanta Rajakaruna coordinated the project, conducted fieldwork, and contributed to manuscript preparation. Douglas Siril A. Wijesundara, Mohamed C. M. Iqbal, Asiri S. Weerasinghe, Gunawarna W. A. Rohan Fernando, and Anthony E. Fernando contributed field expertise and to the preparation of the manuscript. Charlotte H. Miranda and Jordan M. Gosse checked and prepared all data, including the tables. Sadhana Samithri contributed expert taxonomical advice and floristic data on the Ussangoda site. Antony van der Ent advised on aspects of ultramafic ecology and had major input into manuscript preparation. All authors contributed to manuscript preparation.

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SUPPORTING INFORMATION

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