Received: 15 April 2024 | Revised: 15 May 2024 | Accepted: 16 May 2024
DOI: 10.1111/1440-1703.12497

NOTES AND INSIGHTS

ECOLOGICAL RESEARCH WILEY

Ultramafic Ecology: Proceedings of the 10th International Conference on Serpentine Ecology

Metal hyperaccumulation in the Indonesian flora

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Abstract
In this review, I examined the number, distribution, and metal concentrations of all known metal hyperaccumulator plants from Indonesia. In total, 72 hyperaccumulator taxa were found: 19 accumulated Ni, 42 accumulated Al, 7 accumulated Cu, 2 accumulated Zn, and 2 accumulated Co in addition to Ni. There were six hypernickelophores with greater than 1% foliar nickel and with potential for agromining. Less than 10% of the hyperaccumulator species were single island endemics, and only one had an endangered status. Given that many species were only recorded from locations with mining activity, conservation assessments and actions should urgently be undertaken. There are undoubtedly many more hyperaccumulators to be found across Indonesia that will be discovered with further inter-disciplinary surveys.

KEYWORDS
COM clade, ecophysiology, mining, nickel, soils

1 | INTRODUCTION

Soil properties are important in influencing the distribution of tropical plant species (Davies et al., 2005; Sellan et al., 2019) with many species restricted to certain edaphic environments, such as naturally metal-rich ultramafic soils (Proctor, 2003; Galey et al., 2017). Unusual soil properties can also influence the evolution of populations and the physiological traits of plants growing on these soils (Rajakaruna, 2018). One example is the uptake and storage of metals from ultramafic soils into plant tissues, known as hyperaccumulation if the metal is above a given threshold (Reeves, 2024; Reeves et al., 2021; van der Ent et al., 2021; van der Ent, Baker, Reeves, et al., 2013). These thresholds are commonly 300 mg kg^{-1} for cobalt and copper, 1000 mg kg^{-1} for nickel; 10,000 mg kg^{-1} for manganese (van der Ent, Baker, Reeves, et al., 2013) and, in this review, I consider 10,000 mg kg^{-1} as a hyperaccumulation threshold for aluminium following Jansen, Watanabe, and Smets (2002) and Jansen et al. (2004) but acknowledge that different thresholds have been proposed (van der Ent et al., 2021). There are about 800 hyperaccumulator species (not including aluminium) described globally (Reeves et al., 2018, 2021), although this number is increasingly markedly with the use of handheld x-ray fluorescence (XRF) spectrometers to rapidly screen herbarium specimens in a non-destructive fashion (van der Ent et al., 2019). Hyperaccumulator plants are interesting from an ecological perspective due to their unusual ecophysiological characteristics, but also have value in prospecting for minerals as metal-rich deposits may be identified by the presence of high concentrations of metals in the leaves of plants growing over them (Brooks, Lee, et al., 1977). Similarly, hyperaccumulator plants can be used in the process of "agromining" whereby their ability to rapidly accumulate biomass with a high concentration of metals of interest may allow their subsequent harvest and processing into metal ores (van der Ent et al., 2015). Due to the old and highly weathered nature of many tropical soils, particularly Ultisols and Oxisols, soil aluminium concentrations are high, and thus aluminium hyperaccumulation has also evolved in a number of plant species. Among tropical species, aluminium accumulation is more common than accumulation of other metals and there are a number of studies with semi-quantitative analysis of a range of plant species from across the globe (Chenery, 1948; Jansen et al., 2000, 2004; Jansen, Watanabe, & Smets, 2002; Turner et al., 2021; Webb, 1954). The evolutionary reasons for metal hyperaccumulation have not yet been confirmed but many explanations focus on the potential defensive capabilities of having high metal concentrations in the leaves, the so-called "elemental defense" hypothesis (Boyd, 2007). South-east Asia is one of the hotspots for hyperaccumulator plants, with a large number of species described from Sabah (Malaysian Borneo) (van der Ent et al., 2019) but Indonesia, despite have a land area over 25 times larger, and extensive ultramafic outcrops, has been far less explored. The aim of this review paper is, therefore, to outline current knowledge on the presence and distribution of hyperaccumulator plants in the Indonesian flora and note possible future avenues for further discovery of these fascinating plant species.

2 | MATERIALS AND METHODS

A literature survey was conducted to identify hyperaccumulator plants growing under natural conditions in Indonesia. Their locations and maximum concentrations of metals (aluminium, cobalt, copper, nickel, and/or zinc) were recorded. Distributions were determined from Plants of the World Online (https://powo.science.kew.org) and Global Biodiversity Information Facility (https://www.gbif.org). All known Indonesian hyperaccumulators were checked for their Red List status (https://www.iucnredlist.org/). Additionally, hyperaccumulator species identified as growing in Brunei, Malaysia, Papua New Guinea or The Philippines (Do et al., 2020; Duddingan et al., 2023; Khairil & Burslem, 2018; Metali et al., 2015; van der Ent et al., 2019) were checked against the two databases above to determine if they were also found in Indonesia.

3 | RESULTS AND DISCUSSION

The first species recorded as a hyperaccumulator from Indonesia was *Rinorea bengalensis* (Wall.) Kuntze by Brooks and Wither (1977) with samples analyzed that were collected from Papua in a locality previously unknown to have ultramafic geology. Since then, a total of 72 taxa (in 33 families) have been found to hyperaccumulate metals across Indonesia (Table 1). Most of the taxa hyperaccumulate aluminium (42) or nickel (21) with two of these nickel hyperaccumulators also hyperaccumulating cobalt, there were also seven copper hyperaccumulators and two zinc hyperaccumulators. Hypernickelophores (i.e., >1% foliar Ni; Jaffré & Schmid, 1974) included *Phyllanthus insulae-japen* Airy Shaw, *Pouteria oxyedra* (Miq.) Baehni, and *Rinorea bengalensis* (Wall.) Kuntze—these species are particularly valuable as they may have potential for agromining in the region (van der Ent et al., 2015). There were 42 aluminium hyperaccumulators recorded—nearly one-quarter of which were in the genus *Symplocos* where this trait seems to be ubiquitous (Chenery, 1948). *Symplocos* is a well-known tree with its leaves used as a dye-fixative (mordant) by traditional cloth-workers where the high concentration of aluminium aids in fixing natural dyes to the fabrics (Cunningham et al., 2011). A total of seven copper hyperaccumulators were recorded, but from only one study (Brooks et al., 1978).

Aluminium accumulation (i.e., greater than 1000 mg kg^{-1}) is fairly common in tropical floras and different thresholds to define aluminium hyperaccumulation have been proposed (van der Ent et al., 2021). Jansen has used both 1000 and 10,000 mg kg^{-1} to define hyperaccumulation of this metal (Jansen, Broadley, et al., 2002 vs. Jansen, Watanabe, & Smets, 2002; Jansen et al., 2004) and Masunaga et al. (1998) noted differences in the relationship between foliar aluminium and calcium when aluminium concentrations were above 3000 mg kg^{-1} concurring with Metali et al. (2012) who noted a bi-modal distribution of foliar aluminium in tropical plants with a dip between 2300 and 3900 mg kg^{-1}. In this review, I opted to use the greatest value of 10,000 mg kg^{-1} as the cut-off for aluminium hyperaccumulation in order to emphasize the rarity of this phenomenon. It is important to consider a physiologically meaningful definition of hyperaccumulation where such high metal concentrations in plants are indicatative of physiological differences when compared with "normal" plants. It is also worth noting that there is little overlap between researchers who study nickel, cobalt, copper, and zinc hyperaccumulation and those who study aluminium hyperaccumulation, so the definitions and approaches need standardization and there is much opportunity for the cross-over of ideas and approaches.

Phyllanthus insulae-japen had the greatest recorded nickel concentrations at 38,720 mg kg^{-1}, which also seems to be the greatest foliar nickel concentration recorded from any species in South-east Asia (Galey

TABLE 1 Metal hyperaccumulator plants recorded from Indonesia with the maximum recorded concentrations (mg kg^{-1}) of five elements among the different plant species.

Species	Family	Al	Co	Cu	Ni	Zn	Location	Reference
Aporosa frutescens Blume	Phyllanthaceae	16,820	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Aporosa leytensis Merr.	Phyllanthaceae	13,379	-	-	-	-	Bualemo, Sulawesi	Trethowan, 2021a
Aporosa maingayi Hook.f.	Phyllanthaceae	19,950	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Aporosa nigricans Hook.f.	Phyllanthaceae	18,500	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Aporosa sp.	Phyllanthaceae	19,410	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Aristolochia sp.	Aristolochiaceae	-	-	-	2850	-	Weda Bay, Halmahera	Lopez, van der Ent, et al., 2019
Baccaurea bracteata Müll.Arg.	Phyllanthaceae	10,020	-	-	-	-	"Indonesia"	Watanabe et al., 2007
Baccaurea edulis Merr.[1]	Phyllanthaceae	16,400	-	-	-	-	"Indonesia"	Watanabe et al., 2007
Baccaurea javanica (Blume) Müll.Arg.[2]	Phyllanthaceae	22,900	-	-	-	-	"Indonesia"	Watanabe et al., 2007
Baccaurea motleyana (Müll. Arg.) Müll.Arg.	Phyllanthaceae	25,150	-	-	-	-	"Indonesia"	Watanabe et al., 2007
Baccaurea sp.	Phyllanthaceae	11,840	-	-	-	-	"Indonesia"	Watanabe et al., 2007
Brackenridgea palustris subsp. *kjellbergii* P.O.Karis[a]	Ochnaceae	-	-	-	1440	-	Malili, Sulawesi	Reeves, 2003
Casearia halmaherensis Slooten	Salicaceae	-	-	-	2800	-	Weda Bay, Halmahera	Hamdan et al., 2020
Coleus scutellarioides (L.) Benth.	Lamiaceae	-	-	500	-	-	Selayar	Brooks et al., 1978
Combretocarpus rotundatus (Miq.) Danser	Anisophylleaceae	10,019	-	-	-	-	Kalampangan, Kalimantan	Tuah et al., 2003
Cryptocarya sp.	Lauraceae	36,300	-	-	-	-	Weda Bay, Halmahera	Lopez, Benizri, et al., 2019
Cyathula prostrata (L.) Blume	Amaranthaceae	-	-	553	-	-	Selayar	Brooks et al., 1978
Dichapetalum gelonioides subsp. *sumatranum* Leenh.	Dichapetalaceae	-	-	-	-	15,000	Sarak Palembang, Sumatra	Baker et al., 1992
Dichapetalum gelonioides subsp. *tuberculatum* Leenh.	Dichapetalaceae	-	-	-	-	30,000	Padang Sidempuan, Sumatra	Baker et al., 1992
Diospyros sp.	Ebenaceae	15,270	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Elaeocarpus acronodia Mast.[3]	Elaeocarpaceae	38,400	-	-	-	-	Salak, Java	von Faber, 1925
Elaeocarpus aff. *culminicola* Warb.	Elaeocarpaceae	14,655	-	-	-	-	Wawonii	Trethowan, 2021a
Eurya acuminata DC.	Pentaphylacaceae	19,630	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Ficus trachypison K.Schum. & Lauterb.	Moraceae	-	-	-	1060	-	Weda Bay, Halmahera	Lopez, van der Ent, et al., 2019
Gironniera subaequalis Planch.	Cannabaceae	17,952	-	-	-	-	Wawonii	Trethowan, 2021a

(Continues)

TABLE 1 (Continued)

Species	Family	Al	Co	Cu	Ni	Zn	Location	Reference
Glochidion aff. *acustylum* Airy Shaw	Phyllanthaceae	-	-	-	6060	-	Soroako-Wasuponda, Sulawesi	Reeves, 2003
Glochidion moluccanum Blume[a]	Phyllanthaceae	-	-	-	10,700	-	Weda Bay, Halmahera	Lopez, van der Ent, et al., 2019
Hopea sp.	Dipterocarpaceae	13,110	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Knema matanensis W.J.de Wilde[a]	Myristicaceae	-	-	-	5000	-	Soroako, Sulawesi	van der Ent, Baker, van Balgooy, & Tjoa, 2013
Laportea ruderalis (G.Forst.) Chew	Urticaceae	-	-	600	-	-	Selayar	Brooks et al., 1978
Lasianthus sp.	Rubiaceae	10,285	-	-	-	-	Bualemo, Sulawesi	Trethowan, 2021a
Macaranga sp.	Euphorbiaceae	-	-	-	1060	-	Weda Bay, Halmahera	Lopez, van der Ent, et al., 2019
Melastoma malabathricum subsp. *malabathricum* Blume[4]	Melastomataceae	13,350	-	-	-	-	Salak, Java	von Faber, 1925
Memecylon oleifolium var. *laurinum* (Blume) Bakh.fil.[5]	Melastomataceae	12,710	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Memecylon paniculatum Jack	Melastomataceae	10,722	-	-	-	-	Wawonii	Trethowan, 2021a
Myristica bifurcata (J.Sinclair) W.J.de Wilde[6a]	Myristicaceae	-	-	-	1110	-	Jikodolong, Obi	Wither & Brooks, 1977
Ouret sanguinolenta (L.) Kuntze[7]	Amaranthaceae	-	-	393	-	-	Selayar	Brooks et al., 1978
Peperomia pellucida (L.) Kunth	Piperaceae	-	-	300	-	-	Selayar	Brooks et al., 1978
Phyllanthus insulae-japen Airy Shaw[a]	Phyllanthaceae	-	[200]	-	39,270	-	Woda, Yapen	Reeves, 2003; R. Reeves, pers. Comm.
Piper sp.	Piperaceae	-	-	-	2900	-	Weda Bay, Halmahera	Hamdan et al., 2020
Planchonella sp.[8]	Sapotaceae	-	-	-	18,800	-	Weda Bay, Halmahera	Lopez, van der Ent, et al., 2019
Polyspora excelsa (Blume) Orel, Peter G.Wilson, Curry & Luu[9]	Theaceae	11,280	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Polyosma integrifolia Blume	Escalloniaceae	15,011	-	-	-	-	Wawonii	Trethowan, 2021a
Polyosma sp.[10]	Escalloniaceae	11,130	-	-	-	-	Lore Lindu, Sulawesi	Schmitt et al., 2016
Pouteria oxyedra (Miq.) Baehni[11a]	Sapotaceae	-	-	-	27,500	-	Weda Bay, Halmahera	Hamdan et al., 2019
Psychotria sp.	Rubiaceae	-	-	-	1820	-	Danau Matano, Sulawesi	Reeves, 2003
Psychotria sp.	Rubiaceae	18,300	-	-	-	-	Weda Bay, Halmahera	Lopez, Benizri, et al., 2019
Pternandra coerulescens Jack	Melastomataceae	16,640	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998

TABLE 1 (Continued)

Species	Family	Al	Co	Cu	Ni	Zn	Location	Reference
Rinorea bengalensis (Wall.) Kuntze	Violaceae	-	-	-	25,300	-	Weda Bay, Halmahera	Hamdan et al., 2019
Rinorea aff. *bengalensis* (Wall.) Kuntze	Violaceae	-	575	-	22,200	-	Weda Bay, Halmahera	Lopez, van der Ent, et al., 2019
Rinorea javanica (Blume) Kuntze	Violaceae	-	-	-	2170	-	Kalimantan	Brooks, Wither, & Zepernick, 1977 Brooks, 1987
Rinorea sp. nov.	Violaceae	-	-	-	1830	-	Gunung Piapi, Karekelong	Proctor et al., 1994
Sarcotheca celebica Veldkamp[a]	Oxalidaceae	-	-	-	1080	-	Morowali, Sulawesi	Trethowan, 2021a; Trethowan et al., 2021
Senna sophera L. (Roxb.)[12]	Fabaceae	-	-	333	-	-	Selayar	Brooks et al., 1978
Spathiostemon javensis Blume	Euphorbiaceae	16,290	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Symplocos acuminata (Blume) Miq.[13]	Symplocaceae	68,120	-	-	-	-	Kawak Manoek, Java	von Faber, 1925
Symplocos ambangensis Noot.[a]	Symplocaceae	23,690	-	-	-	-	Lore Lindu, Sulawesi	Schmitt et al., 2016
Symplocos henschelii (Moritzi) Benth. ex C.B.Clarke	Symplocaceae	31,200	-	-	-	-	Weda Bay, Halmahera	Lopez, Benizri, et al., 2019
Symplocos lucida Wall. ex G. Don	Symplocaceae	12,100	-	-	-	-	Weda Bay, Halmahera	Lopez, Benizri, et al., 2019
Symplocos maliliensis Noot.[a]	Symplocaceae	46,300	-	-	-	-	Weda Bay, Halmahera	Lopez, Benizri, et al., 2019
Symplocos odoratissima (Blume) Choisy ex Zoll.	Symplocaceae	49,104	-	-	-	-	Lore Lindu, Sulawesi	Schmitt et al., 2016
Symplocos ophirensis C.B. Clarke	Symplocaceae	32,220	-	-	-	-	Lore Lindu, Sulawesi	Schmitt et al., 2016
Symplocos sp. 1	Symplocaceae	36,642	-	-	-	-	Wawonii	Trethowan, 2021a; Trethowan et al., 2021
Symplocos sp. 2	Symplocaceae	31,357	-	-	-	-	Wawonii	Trethowan, 2021a; Trethowan et al., 2021
Syzygium sp.	Myrtaceae	12,800	-	-	-	-	Weda Bay, Halmahera	Lopez, Benizri, et al., 2019
Syzygium sp.[14]	Myrtaceae	22,750	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Trichospermum kjellbergii Burret[a]	Malvaceae	-	350	-	3770	-	Jikodolong, Obi	Wither & Brooks, 1977
Trichospermum morotaiense Kosterm.[a]	Malvaceae	-	-	-	5180	-	Weda Bay, Halmahera	Lopez, van der Ent, et al., 2019
Urophyllum corymbosum (Blume) Korth.[15]	Rubiaceae	44,500	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1997
Urophyllum macrophyllum (Blume) Koorth.	Rubiaceae	23,110	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998
Vernonia actaea J.Kost.[a]	Asteraceae	-	-	300	-	-	Selayar	Brooks et al., 1978

(Continues)

TABLE 1 (Continued)

Species	Family	Al	Co	Cu	Ni	Zn	Location	Reference
Xanthophyllum rufum A.W. Benn.	Polygalaceae	12,940	-	-	-	-	Ulu Gadut, Sumatra	Masunaga et al., 1998

Note: Names in the original publications: [1]*Baccaurea dulis*, [2]*Baccaurea minutiflora*, [3]*Elaeocarpus punctatus*, [4]*Melastoma setigerum*, [5]*Memecylon oleifolium* var. *laurinum*, [6]*Myristica laurifolia* var. *bifurcata*, [7]*Aerva scandens*, [8]*Planchonella roxburghioides*, [9]*Gordonia excelsa*, [10]*Polyosma celebica*, [11]*Planchonella oxyedra*, [12]*Cassia sophera*, [13]*Symplocos spicata*, [14]*Eugenia bisulea*, [15]*Maschalocorymbus corymbosus*.

Note that although the Co concentration for *Phyllanthus insulae-yapen* does not fall above the hyperaccumulation threshold for this species, it is nevertheless presented for interest.

[a]Indicates species found only in Indonesia.

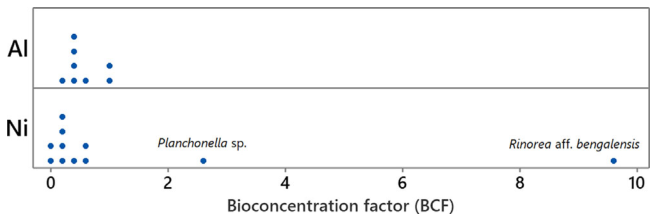

FIGURE 1 Metal (aluminium and nickel) bioconcentration factors (quotient of foliar metal concentration to soil metal concentration) for Indonesian hyperaccumulator plants. Each point indicates a single species mean.

et al., 2017; van der Ent et al., 2019) The Celastrales-Oxalidales-Malpighiales (COM) clade, which includes *Phyllanthus*, is well known for having a number hyperaccumulator species (Jaffré et al., 2013) and, although four of the six hypernickelophores were in this clade, the median foliar nickel concentrations of all 21 nickel hyperaccumulators were not significantly greater in this clade than all the other clades combined (3335 vs. 2800 mg kg^{-1}; Mann–Whitney, $p = 0.94$). The majority of the aluminium hyperaccumulators were in the Phyllanthaceae, Rubiaceae or Symplocaceae, but there was no clear phylogenetic pattern for copper hyperaccumulators.

Much of the data on hyperaccumulator plants is from analysis of historical herbarium specimens by researchers who did not conduct fieldwork in Indonesia, so there is little analysis of metal concentrations in soils or other plant tissues. For the species where both leaves and soil have been examined (van der Ent, Baker, van Balgooy, & Tjoa, 2013; Netty et al., 2012; Lopez, van der Ent, et al., 2019; Trethowan, 2021a, 2021b; Trethowan et al., 2021), bioconcentration factors (i.e., the quotient of foliar metal concentration to soil metal concentration) for nickel ranged over two orders of magnitude from 0.03 to 9.6 with a median of 0.23 whereas those for aluminium were more constrained with a median of 0.43 (Figure 1). However, apart from the two outlying taxa for nickel (*Planchonella* sp. and *Rinorea* aff. *bengalensis*), the distribution of the two elements are similar (Mann–Whitney, $p = 0.30$). This variability is mostly due to variation in plant uptake rather than differences in soil metal concentrations. The data suggest that hyperaccumulators of aluminium appears to be the upper end of a normal/lognormal distribution whereas strong nickel hyperaccumulators (hypernickelophores) are distinctly different, possibly due to different physiological mechanisms of metal uptake. Most of the nickel and aluminium hyperaccumulators were trees, whereas copper hyperaccumulators were mostly herbs and shrubs which might influence the physiological transfer processes as copper concentrations are often greater in below-ground than above-ground plant organs (Duddingan et al., 2023).

All of the cobalt, copper and nickel hyperaccumulators were found in eastern Indonesia (mostly Sulawesi and Maluku). Aluminium hyperaccumulators were found more broadly (Kalimantan, Mukulu, Sumatra, Sulawesi) and were found on ultramafic soils in addition to non-ultramafic soils (Halmahera, Wawonii). Overall, 12 of the species had the entirely of their range in Indonesia (Table 1) and half of those were single island endemics (according to GBIF records), namely: *Brackenridgea palustris* subsp. *kjellbergii* P.O.Karis, *Glochidion moluccanum* Blume, *Knema matanensis* W.J.de Wilde, *Symplocos ambangensis* Noot., and *Symplocos maliliensis* Noot. found only on Sulawesi, and *Phyllanthus insulae-japen* found only on Yapen. Eighteen of the species in Table 1 have been assessed for their Red List status and all except one were Least Concern. Only *Knema matanensis* has a threat status, being considered Endangered, as it is known from just three localities in Sulawesi (Junaedi, 2023). Given that the majority of the nickel hyperaccumulators have been recorded from known nickel mining areas such as Jikodolong (Obi), Soroako (Sulawesi) and, particularly, Weda Bay (Halmahera) we might expect a greater number of species to be under threat from mining activities and thus performing formal conservation assessments would be prudent. It is however, pleasing to note that Yapen island, the only collection location for *Phyllanthus insulae-japen*, which appears to be known from only one collection in 1961, is still largely forested (Diamond & Bishop, 2020). Of the hyperaccumulators recorded from other insular South-east Asian regions, over ninety were also recorded from Indonesia, potentially more than doubling the number of putative hyperaccumulators from the country.

Around half of Indonesia still remains forested (Margono et al., 2014) and has nearly 40,000 plant species (Budiharta et al., 2011) so extensive tracts of "typical" lowland forest where aluminium accumulators are most common (Metali et al., 2015) are still present. Aluminium hyperaccumulation is broadly distributed geographically and there are numerous historical records of hyperaccumulating genera noted by Chenery (1948), Jansen et al. (2000, 2004); Jansen, Watanabe, and Smets (2002) and Webb (1954) that are worth surveying. Additionally, Indonesia hosts some of the most extensive outcrops of ultramafic soils in the world, yet the prevalence of nickel hyperaccumulators is low so far and further exploration would undoubtedly reveal further species. In Sabah, there are 91 hyperaccumulators (van der Ent et al., 2019) and there are 28 in the Philippines (Duddingan et al., 2023) outlining the potential for the Indonesian flora to host a greater number of hyperaccumulators. Focussing on the analysis of plant species in clades where hyperaccumulation is known to be more common would be a suitable first step in future analyses, or targeting the species known to hyperaccumulate metals in other South-east Asian countries. However, there are more recent reports of a number of species hyperaccumulating metals that are not in families traditionally considered to contain hyperaccumulators so analysis of additional families should not be ignored. The use of handheld XRF spectrometers would be valuable to screen for new hyperaccumulator species. For example, screening of target families in the Sabah Forest Research Centre's herbarium more than doubled the number of hyperaccumulators from Sabah among the 7300 specimens scanned (van der Ent et al., 2019). Cutting edge techniques can also be complemented by indigenous knowledge; for example, a number of plant species are known as traditionally-used mordants (Cunningham et al., 2011) and, because of the role of aluminium in this process, analyzing these species would be fruitful first steps in the search for additional aluminium hyperaccumulators. Nickel hyperaccumulators are found on nickel-rich ultramafic soils, most commonly on circum-neutral soils with high concentrations of available nickel (van der Ent et al., 2016) so these soil types should be targeted for further exploration. In contrast, manganese hyperaccumulators are not restricted to ultramafic soils but a survey of five locations in Sulawesi only found foliar manganese greater than 5000 mg kg^{-1} in five species, and none had more than 10,0000 mg kg^{-1} although *Stemonurus celebicus* Valeton had the greatest concentration at 8640 mg kg^{-1} (Trethowan, 2021a; Trethowan et al., 2021). There are still many areas of Indonesia where traditional botanical surveys and plant collections are rare, so collection and analysis of more specimens will be fruitful. In conclusion, combinations of anthropology, botanical surveys, soil science and fluorescence spectrometry, will allow further discovery of the metal-loving botanical riches of Indonesia – one of the most biodiverse countries in the world.

ACKNOWLEDGMENTS

Thanks to Roger Reeves for additional information on *Phyllanthus insulae-yapen*.

CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

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How to cite this article: Brearley, F. Q. (2024). Metal hyperaccumulation in the Indonesian flora. *Ecological Research*, 1–9. https://doi.org/10.1111/1440-1703.12497