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Severine Lopez, Peter D. Erskine, Yannick Cazes, Jean-Louis Morel, Gavin Lee, et al.. Biogeochemistry of the flora of Weda Bay, Halmahera Island (Indonesia) focusing on nickel hyperaccumulation. *Journal of Geochemical Exploration*, 2019, 202, pp.113-127. 10.1016/j.gexplo.2019.03.011 . hal-02624924

HAL Id: hal-02624924

<https://hal.inrae.fr/hal-02624924>

Submitted on 22 Oct 2021

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1 **Biogeochemistry of the flora of Weda Bay, Halmahera Island**
2 **(Indonesia) focusing on nickel hyperaccumulation**

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16

17 **ABSTRACT**

18 Indonesia has one of the largest surface expressions of ultramafic rocks on Earth and in parallel
19 hosts one of the most species-rich floras. Despite the extensive knowledge of the botanical diversity
20 and the chemistry of these substrates, until recently the records for nickel hyperaccumulators in the
21 region have been scant. Identification of native local hyperaccumulator species is the critical initial
22 step for phytomining as these species match ambient bioclimatic, geochemical and physiological
23 conditions. Prior to this research just 11 nickel hyperaccumulators were known from Indonesia.
24 This field-based investigation at Weda Bay revealed the existence of 13 nickel and two cobalt
25 hyperaccumulators. Phylogenetic affinity for nickel hyperaccumulation is diverse and spans several
26 orders but was most frequent in the Malpighiales as in other ultramafic regions of Southeast Asia.
27 In contrast to global patterns, hyperaccumulation was infrequent in the Phyllanthaceae.

28

29 **Keywords:** *biogeochemical cycling, hyperaccumulator, trace element, ultramafic, nickel*

30

31 1. INTRODUCTION

32

33 Ultramafic bedrock is part of the upper mantle (peridotite) obducted in continental margins (Searle
34 and Stevens, 1984). Such outcrops are widespread but relatively rare, covering > 3% of the surface
35 of the earth (Guillot and Hattori, 2013). Southeast Asia has some of the largest tropical outcrops in
36 the world with Borneo and Sulawesi together totalling over 23 000 km² (van der Ent et al., 2013b;
37 Galey et al., 2017). Ultramafic soils have high concentrations of iron (Fe) and magnesium (Mg), are
38 enriched in nickel (Ni), chromium (Cr) and cobalt (Co), and are phosphorus (P) and potassium (K)
39 deficient (Proctor, 2003). The atypical soil chemistry has caused the occurrence of distinct
40 vegetation types characterized by relatively low stature and high levels of endemism (Brooks,
41 1987; Proctor, 2003; Rajakaruna and Baker, 2004). Hyperaccumulators are unusual plants that
42 accumulate trace elements to exceptional concentrations in their living tissues at orders of
43 magnitude greater concentrations than 'normal' plants (Baker and Brooks, 1989; van der Ent et al.,
44 2013a). Some of these plants can reach up to 7.6% Ni in leaves (Mesjasz-Przybyłowicz et al., 2004)
45 and up to 16.9 dry Wt% the phloem sap (van der Ent and Mulligan, 2015). Hyperaccumulator plants
46 can achieve such extraordinary levels of accumulation due to enhanced uptake and translocation
47 mechanisms from the roots to the shoots (Baker, 1981; 1987). Trace element hyperaccumulation is
48 defined as foliar concentrations in excess >300 mg kg⁻¹ of Co, >1000 mg kg⁻¹ of Ni, >10 000 mg
49 kg⁻¹ of Mn when growing in natural habitats (Baker and Brooks, 1989; Reeves, 2003; van der Ent et
50 al., 2013a).

51

52 On a global scale, Ni hyperaccumulation is the most prevalent, with approximately 520 species
53 reported to date, of which just ~50 *hypernickelophores* (e.g. hyperaccumulator species with >1
54 Wt% shoot dry weight) are known globally (Reeves, 2003; Reeves et al., 2018a).
55 Hyperaccumulation is a rare phenomenon occurring in 0.2% of total angiosperms (Baker, 1981;
56 Baker and Brooks, 1989) and up to two percent of the ultramafic flora (van der Ent *et al.*, 2015b).
57 The greatest number of Ni hyperaccumulators has been reported from Cuba (130) and New
58 Caledonia (65) (Reeves et al., 2018b; Jaffré et al., 2013), and recently Sabah (Borneo Island) also
59 emerged as a hotspot for Ni hyperaccumulators with the recording of 25 species (van der Ent et al.,
60 2015b; 2016b). Nickel hyperaccumulators can be categorised in either obligate or facultative
61 species, the former restricted to ultramafic soils and displaying hyperaccumulation, the latter with
62 populations on non-ultramafic and ultramafic soils but only displaying hyperaccumulation on the
63 ultramafic soils (Pollard et al., 2014). The ecology and natural selection of hyperaccumulator plants
64 is an active field of inquiry, focussing on anti-herbivore defences, allelopathy and biotic interactions
65 (Martens and Boyd, 1994; Boyd and Martens, 1998; Jaffré et al., 2018). Nickel hyperaccumulator

66 plants have the potential to be used in phytomining, an environmentally sustainable technology to
67 produce Ni (Chaney, 1983; Chaney et al., 2007; van der Ent et al., 2015a). In a phytomining
68 operation, hyperaccumulator plants are grown on ultramafic soils, followed by harvesting and
69 incineration of the biomass to generate a commercial high-grade Ni bio-ore (Chaney et al., 2007;
70 Barbaroux et al., 2011; Van der Ent et al., 2015a).

71
72 Nickel hyperaccumulators have been recorded from at least 40 different plant families (Reeves,
73 2006), but are most prevalent in the order Brassicales (Brassicaceae, genera *Odontarrhena*
74 [synonym *Alyssum*], *Arabidopsis*, *Bornmuellera* [synonym *Leptoplax*], *Noccaea*) in temperate
75 regions and in the Asterales (*Berkheya*, *Pentacalia*, *Senecio*), the Buxales (Buxaceae; *Buxus*) and
76 the supraordinal COM clade (Celastrales, Oxalidales, Malpighiales, mainly Euphorbiaceae,
77 Phyllanthaceae, Salicaceae and Violaceae families) in tropical regions. In Southeast Asia, Ni
78 hyperaccumulator plants are predominantly from the Malpighiales order, and particularly the
79 Phyllanthaceae family (van der Ent et al., 2015b; Galey et al., 2017). The Malpighiales is one the
80 most diverse groups of flowering plants, comprising about 8% of all eudicots and 6% of all
81 angiosperms (Davis et al., 2005; Korotkova et al., 2009), and hyperaccumulators are mainly
82 represented in the Phyllanthaceae in the genera, *Actephila*, *Antidesma*, *Breynia*, *Cleistanthus*,
83 *Glochidion* and *Phyllanthus* (van der Ent et al., 2015b). The latter is cosmopolitan and the most
84 speciose genus with over 800 species globally, with major centres of diversity in New Caledonia
85 (113 species) and Cuba where Ni hyperaccumulators are numerous (Reeves et al., 1996; Reeves et
86 al., 1999). Limited systematic screening across phylogenetic lineages means that at present there is
87 no comprehensive understanding of the phenomenon, although such efforts are currently underway
88 using XRF devices (Gei et al., 2018) followed by detailed investigations of their ecophysiology
89 using advances techniques such as synchrotron-based X-ray Fluorescence Microscopy (van der Ent
90 et al., 2017a,b). Hyperaccumulator discoveries continue to be made in Southeast Asia, such as
91 *Antidesma montis-silam* from Sabah (Nkrumah et al., 2018), and even new species that are
92 hyperaccumulators, are described, such as *Actephila alanbakeri* (van der Ent et al., 2016b) and
93 *Phyllanthus rufuschaneyi* (Bouman et al., 2018) both from Sabah. The search for
94 hyperaccumulators has been limited to date in Indonesia. Analysis of herbarium specimens
95 originating from Indonesia led to the discovery of the following Ni hyperaccumulators: *Rinorea*
96 *bengalensis*, *R. javanica* (Violaceae), *Trichospermum kjellbergii* (Tiliaceae), *Planchonella oxyhedra*
97 (Sapotaceae), *Myristica laurifolia* var. *bifurcata* (Myristicaceae), *Brackenridgea palustris* subsp.
98 *kjellbergii* (Ochnaceae), *Psychotria* sp. (Rubiaceae), *Phyllanthus insulae-japen* and *Glochidion* aff.
99 *acustylum* (Phyllanthaceae) (Wither and Brooks, 1977; Reeves, 2003). More recently, fieldwork in

100 Sulawesi recorded *Sarcotheca celebica* (Oxalidaceae) and *Knema matanensis* (Myristicaceae) as Ni
101 hyperaccumulators (Tjoa, pers. comm.; van der Ent et al., 2013b).
102 Ultramafic rock is serpentinised to varying degrees, and serpentinite is used to describe rocks
103 containing >50% serpentine group minerals in which the original mineralogy has been changed.
104 Ultramafic rock generally itself only contains 0.16–0.4% Ni (Butt and Cluzel, 2013) but this
105 increases significantly during surface weathering in humid tropical climates (Echevarria, 2018)
106 becomes atarget. Where they occur, ultramafic ecosystems are renowned for high levels of
107 endemism, especially in Southeast Asia (Galey et al., 2017). At the same time, ultramafic outcrops
108 holding Ni-rich laterites are Ni mining targets in the Indonesian region. That brings the minerals
109 industry capitalizing on Ni resources in direct conflict with biodiversity. The Weda Bay project in
110 Halmahera has a contract area of 54 874 ha with an estimated resource of 5.1 Mt of Ni and targeted
111 annual capacity of 65 kt yr⁻¹ in Ni. This study aims to provide baseline data on the biogeochemistry
112 of the ultramafic soils of Weda Bay Nickel (WBN) mine lease on Halmahera Island in Indonesia.
113 Specifically, the objectives of this research were to screen for the possible occurrence of
114 hyperaccumulator plants, to provide information on the foliar chemistry, and to provide an
115 indicative assessment of the potential for phytomining at Weda Bay Nickel.

116

117 **2. MATERIALS AND METHODS**

118

119 **2.1 Study area and sample collection**

120 During the fieldwork, a total of 21 non-permanent plots (see Figure 1 for locations and Table 1 for
121 site properties) were made in which 817 herbarium vouchers and associated foliar samples, in
122 addition to soil samples (totalling 85 samples), were collected for laboratory analysis. Plants were
123 screened in the field (>1000 specimens) for Ni hyperaccumulation using dimethylglyoxime
124 impregnated test paper, and after positive reaction detailed samples were collected for these
125 hyperaccumulator plants. This included samples of the rhizosphere soil, root, wood, branches and
126 leaves. In total 13 Ni hyperaccumulators species, 2 Co, 1 Mn and 10 Al hyperaccumulators were
127 discovered, and associated plant tissue samples totalling 316 samples with 46 matching rhizosphere
128 soil samples collected. The current work does not discuss the hyperaccumulator species from Weda
129 Bay, and we refer to Lopez *et al.* (2019a, b) for more information about the individual
130 hyperaccumulator species and the rhizosphere chemistry. Concentrations of Ni and other elements
131 were determined in the field with a handheld X-Ray Fluorescence (XRF) instrument. Fresh plant
132 leaves were put in paper bags to prevent decomposition before transport to the field station. Leaves
133 were dried at 70°C for five days in a dehydrating oven. Soil samples were collected from the centre
134 of 15 sites. After an elimination of the surface organic plant debris, organo-mineral horizons were

135 sampled at a depth between 0–5 cm below litter and mineral horizons were sampled at a depth of
136 10–25 cm depending on the soil type in order to avoid the organo-mineral horizon. In all cases,
137 except for Leptosols, it corresponded to either the Cambic horizon or the Ferralic horizon. The 30
138 soil samples were air-dried and then sieved to 2 mm before storage and analyses.

139

140 **2.2 Chemical analyses of plant tissue samples**

141 Foliar samples were crushed and ground, and a 500-mg subsample was digested in 3 mL
142 concentrated nitric acid (65%) and 1 mL hydrogen peroxide (30%) for 2 hours at 95°C. The digest
143 was diluted to 40 mL with ultra-pure water before analysis with ICP-AES (Liberty II, Varian).
144 Elements included in the analysis were Ni, Co, Cr, Cu, Zn, Mn, Fe, Mg, Ca, Na, K, S and P. The
145 potential for foliar contamination with soil particulates is a major risk for accurate analysis of foliar
146 elemental composition. This risk is highest in samples of ground-herbs, and lesser so for trees, but it
147 cannot be entirely avoided. Concomitantly high foliar concentrations of Fe (>2500 $\mu\text{g g}^{-1}$) and Cr
148 (>50 $\mu\text{g g}^{-1}$) are an indication for soil contamination as these elements are major constituents of
149 ultramafic soils.

150

151 **2.3 Chemical analyses of soil samples**

152 Soil samples (500 mg subsample) were acid-digested using freshly prepared Aqua Regia (6 mL
153 37% hydrochloric acid and 2 mL 70% nitric acid per sample) for a 2-hour program and diluted with
154 ultra-pure water to 50 mL before ICP-AES analysis of pseudo-total elements for Ni, Co, Cu, Zn,
155 Mn, Fe, Mg, Ca, Na, K, S and P. Soil pH was measured in a 1:5 soil : water mixture. Exchangeable
156 Ni, Co, Cr and Mn were extracted in 0.0166 M $[\text{Co}(\text{NH}_3)_6^{3+}, 3\text{Cl}^-]$ at a soil : solution ratio of 1:20
157 (2.5 g : 50 mL) and 1 hour shaking time according to international ISO standard 23470 (ISO
158 23470:2007). Extractable Ni, Cr and Mn in soil samples were obtained from a DTPA–TEA solution
159 (0.005 M diethylene triamine pentaacetic acid, 0.01 M calcium chloride, 0.1 M triethanolamine, pH
160 7.4) according to Lindsay and Norvell (1978) and concentrations in solutions were measured with
161 ICP-AES (Liberty II, Varian). Total C and N and organic C were quantified by combustion at 900
162 °C with a CHNS analyser (vario MICRO cube, Elementar Analysensysteme GmbH). Soil samples
163 were weighed using a four-decimal balance and weights recorded for correction of the precise
164 weights in the mass balance calculations. Samples were agitated for method-specific times using an
165 end-over-end shaker at 60 rpm and subsequently centrifuged (10 minutes at 4000 rpm). All soil
166 samples were analysed with ICP-AES (Liberty II, Varian) for Ni, Co, Cu, Zn, Mn, Fe, Mg, Ca, Na,
167 K, S and P. The ICP-AES instrument was calibrated using a multi-element standard prepared in
168 each extraction solution and internal standards were used to ensure of the reliability of ICP-AES
169 analysis.

170

171 **2.4 Mineralogical analyses of soil samples by X-Ray Diffraction (XRD)**

172 The dry samples from the soils from the 15 sites were ground and sieved to 80 µm for mineralogical
173 analysis by XRD. X-Ray diffraction (XRD) analysis was performed on the selected samples using a
174 D8 Bruker diffractometer with Co K_α¹ radiation (lambda = 1.7902 Å). The diffractometer is
175 equipped with a (θ, 2θ) goniometer and a position sensitive detector (PSD). X-ray diffractograms
176 were collected on powder samples at room atmosphere and temperature, within the 2theta range [3,
177 65°], with 0.035° step and 2s collecting time.

178

179 **2.5 Statistical analysis**

180 The ranges and means of the foliar and soil concentrations were calculated. Correlation coefficients
181 between the soil and plant chemistry data were also calculated. These analyses were undertaken
182 using the software packages STATISTICA Version 9.0 (StatSoft), Excel for Mac version 2011
183 (Microsoft) and R software (version 3.3.1).

184

185 **3. RESULTS**

186

187 **3.1 Field survey and hyperaccumulator plant species**

188 The Weda Bay area consists largely of a ‘mosaic’ of secondary vegetation with patches of more
189 intact forest, and vegetation, which have experienced recurrent fires, particularly near the coast
190 (Figure 2). The highest plant diversity was encountered at the Casuarina site (secondary lowland
191 forest on serpentinite) and at Jira (secondary lowland forest on a laterite plateau). Prior to this field
192 survey no Ni hyperaccumulator plants were known from Halmahera Island, and just five
193 hyperaccumulators were known from Indonesia (van der Ent et al. 2013b). The fieldwork yielded
194 13 Ni hyperaccumulator plants from the locations survey (including Bukit Limber, Sake South,
195 Sake, Sake West, Uni-Uni, Casuarina) (Table 1). The hyperaccumulator plants originated from a
196 range of different families, and several records included families Anacardiaceae, Apocynaceae,
197 Aristolochiaceae, Moraceae, Piperaceae and Rosaceae that were not previously known to contain Ni
198 hyperaccumulating taxa. Several Ni hyperaccumulator species are locally common and occur
199 widespread at Weda Bay, namely *R. aff. bengalensis*, *Planchonella roxburghiana*, *F. trachypison*
200 and *T. morotaiense*. Burnt vegetation in the coastal areas was relatively species poor but hosted all
201 13 Ni discovered hyperaccumulator species including at Sake South and Casuarina. *Rinorea* aff.
202 *bengalensis* (Violaceae) is clearly closely-related to the widespread *R. bengalensis* (Sri Lanka to
203 Northeast Australia), but has morphological differences warranting typification as a distinct taxon
204 (J. DeMuria pers. comm.). It occurs as an under-storey shrub or small tree (up to 10 m tall and a

205 bole of 20 cm diameter) in dense secondary vegetation and short-statured forest on Cambisols.
206 *Ficus trachypison* is the sole Ni hyperaccumulating taxon from the genus *Ficus* and the family
207 Moraceae known globally. It is exceedingly common as a pioneer in degraded (burnt) scrub in the
208 coastal areas, such as at Sake River, and Location 2A–C on Hypereutric Cambisols. One of the
209 most interesting species, because it is a facultative Ni hyperaccumulator, is *Trichospermum*
210 *morotaiense* (Tiliaceae). This medium to large tree (up to 20 m tall and a bole of 40 cm diameter)
211 occurs mainly in riparian habitats on ultramafic soils (where it hyperaccumulates Ni) and on
212 limestone (where it does not hyperaccumulate Ni). The genus *Trichospermum* has 36 species
213 occurring predominantly in Malesia but distributed from Malaysia to the Solomon Islands and Fiji
214 and Samoa, with most species in New Guinea (Kostermans, 1972). *Trichospermum kjelbergii* from
215 Sulawesi was one of the first Ni hyperaccumulators to be discovered in Indonesia (Wither and
216 Brooks, 1977). *Planchonella roxburghiana* (Sapotaceae) is a medium-sized tree (up to 15 m tall and
217 with a bole of 25 cm diameter) that occurs in medium tall lowland forest (<20 m) on Hypereutric
218 Rhodic Cambisols. This species is slow-growing, judging by its hard timber, and closely related to
219 *Planchonella oxyhedra* recorded as a Ni hyperaccumulator from Central Sulawesi (Wither and
220 Brooks, 1977). No Ni hyperaccumulators were found at higher elevations (>500 m asl), such as at
221 Bukit Limber 900–1000 m asl, which has lower montane forest. This may be explained by the low
222 extractability of Ni and acidic pH in the Rhodic Plinthic Ferralsols of this site. Similarly, Ni
223 hyperaccumulators were absent from Uni-Uni, which has Geric Plinthic Rhodic Ferralsols, with the
224 exception of *Glochidion moluccanum* (Phyllanthaceae). The latter is a pioneer shrub (no more than
225 3 m tall) that is common in the graminoid scrub at Uni-Uni that has been repeatedly burnt. We refer
226 to Lopez *et al.* (2019a, b) for more detailed information about the individual hyperaccumulator
227 species.

228

229 **3.2 Soil mineralogy and soil types**

230 The diffractograms of the soils, both organo-mineral (0–5 cm layer) and mineral (10–25 cm layer)
231 horizons sampled on 15 sites (30 soil samples) were acquired to indicate the weathering status of
232 each pedon as well as the nature of the bedrock (*e.g.* degree of serpentinisation of the peridotite).
233 Diffractograms from organo-mineral horizons were usually less easily interpreted because of the
234 high background noise created by the high organic matter content. Therefore, the mineralogy of
235 mineral horizons was used to describe soils (Table 2) except for the soil on Limestone for which the
236 best diffractogram was from the organo-mineral horizon (lack of clay minerals in the mineral
237 horizon). Primary minerals derived from ultramafic soils were either from non-serpentinised
238 peridotite (*i.e.* diopside, enstatite, tremolite, fayalite) or from serpentinite (*i.e.* talc, serpentine,
239 magnetite). Secondary minerals were mainly clays (smectite group clays, probably montmorillonite

240 in all the cases) and iron oxides (*i.e.* goethite and hematite). None of the soils had pyroxenes or
241 olivines as major mineral constituents, although some soils contained traces of these minerals (Blue
242 Hill, Casuarina Plot 1, 2B and Woi Mioseng). One soil had tremolite as its major mineral
243 constituent (Casuarina Plot 2). Serpentine (mostly chrysotile and in one case clino-chrysotile: Bukit
244 Limber Plot 1) is the dominating mineral phase in the soils Blue Hill (co-dominating with
245 serpentine), Uni-Uni Plot 1 and Woi Mioseng). Secondary smectites dominate the mineralogy of
246 Blue Hill, and Location 2A, 2B and 2C. The mineralogy of the rest of ultramafic soils was
247 dominated by secondary goethite. Quartz can be considered as a secondary mineral in most of the
248 soils where it is present. Calcite was the only primary mineral detected for the Leptosol of
249 Doromesmesan and only some clays and traces of quartz could be detected in the organo-mineral
250 horizon. The mineral horizon was pure calcite on this soil. The variety of mineralogical profiles
251 (most representative profiles) is shown in Figure 5.

252

253 The soils, according to their morphology (field observations), chemistry and mineralogy could be
254 classified as the following types (Table 1): Rendzic Leptosol on Limestone; Hypereutric Leptosols
255 (Hypermagnesian) and Hypereutric Leptic Cambisols (Hypermagnesian) on Serpentinite; Ferralic
256 Rhodic Cambisols on poorly serpentinised Peridotite and Geric Plinthic Ferralsols on non-
257 serpentinised peridotites (including dunite). This variety of soils created a wide array of edaphic
258 conditions from low pH soils with no exchangeable cations, to neutral and high pH soils with a
259 CEC saturated with Mg. Also, the soils varied deeply from very shallow Leptosols (Blue Hill and
260 Doromesmesan) to very deep laterites (Bukit Limber Plots 1 & 2 and Uni-Uni Plot 1), thus
261 providing a wide array of physical properties for ecosystem processes (shallow *vs.* deep rooting).

262

263 **3.3 Soil chemical characteristics in the surveyed area**

264 Thirty soil samples were derived from (serpentinised) ultramafic bedrock and one was a Rendzic
265 Leptosol on Limestone (Doromesmesan). Chemical properties of mineral (10–25 cm layer) and
266 organo-mineral (0–5 cm layer) soil samples from each site are presented in Tables 3 to 8. These
267 mineral (Table 3) and organo-mineral (Table 4) horizons showed amounts of total Fe ranging from
268 1.5 to 39.8%, total Mg from 0.8 to 13.3%. They were all characterized by low concentrations of Ca,
269 P (less than 0.04%) and K (less than 0.03%) excepted for the site Location 2C with 0.05 and 0.08
270 for the mineral and organo-mineral horizons, respectively. These values and the high values of Ni,
271 which ranged from 87 to 13,587 mg kg⁻¹, confirmed the ultramafic origin of these different soil
272 samples.

273

274 The DTPA-extractable elements (such as Ca, Mg, and K) of the organo-mineral horizons (Table 6)
275 had the highest values in comparison to mineral horizons (Table 5), except for Fe and Mg. DTPA-
276 extractable Ni concentrations reached 772 mg kg⁻¹ in Sake South soil.

277

278 The pH ranged from 4.07 to 8.16 in the mineral horizons (Table 7) and from 4.65 to 8.07 in the
279 organo-mineral horizons (Table 8). Some Ferralsols or soils with Ferralic properties were present in
280 the collection (*e.g.* soils from Bukit Limber plot 2, Sake West, Uni-Uni plot 1) and their pH ranged
281 from 4.07 to 5.31 for mineral horizons and from 4.65 to 6.59 for organo-mineral horizons, in the
282 lower of the total range. Also, these soils had very low Cation Exchange Capacity (CEC), with
283 values ranging from 2.04 to 5.05 and from 4.32 to 8.66 cmol⁺ kg⁻¹, respectively for mineral and
284 organo-mineral horizons, compared to the whole collection (from 2.04 to 53.7 and from 4.32 to
285 64.3 cmol⁺ kg⁻¹, respectively for mineral and organo-mineral horizons). These soils were
286 characterized by low exchangeable Mg values compared to the whole range of soils: their Mg-CEC
287 ranged from 0.07 to 1.2 and from 0.38 to 4.1 cmol⁺ kg⁻¹, respectively for mineral and organo-
288 mineral soils. The other soils were (Hyper)Eutric Cambisols (Hyper)Magnesic and were also widely
289 present in the area. Their pH was higher in general (ranging from 6.06 to 8.16 and from 6.01 to
290 7.41, respectively for mineral and organo-mineral horizons) and so was their CEC (presence of
291 high-charge clays and higher organic matter contents) which ranged from 4.40 to 53.7 and from
292 7.49 to 64.3 cmol⁺ kg⁻¹, respectively for mineral and organo-mineral soils. Most of the CEC values
293 for these Cambisols were above 20.0 cmol⁺ kg⁻¹. The maximum reported values for Mg-CEC were
294 reported also for these soils and reached 50 and 40 cmol⁺ kg⁻¹, respectively for mineral and organo-
295 mineral horizons. The Rendzic Leptosol sampled from the site Doro Mesmesan Limestone Plot 1
296 showed particular values as it was not ultramafic with alkaline pH, high amount of total Ca and P
297 but low Fe and Mg concentration (Table 3 and 4), inducing a Ca/Mg ratio of 36–46. The CEC was
298 also greater in comparison with the other soils. The CEC in all soils was mostly influenced by the
299 organic matter content (Tables 7 and 8) and the amount of smectite-type clays in the mineral phases
300 (Table 2).

301

302 Soil weathering tends to favour Ca retention on the CEC and Mg leaching (Echevarria, 2018) and
303 exchangeable Ca was greater in organo-mineral horizons than in mineral horizons for all soils,
304 whereas it was the exact opposite for Mg. Therefore, most of the Ferralsols were not Magnesic,
305 whereas all Cambisols were Magnesic or Hypermagnesic.

306

307 The mean total Ni concentrations were 4.16 mg g⁻¹ (0.3–14.0 mg g⁻¹) and 3.77 mg g⁻¹ (0.1–
308 12.0 mg g⁻¹), respectively for mineral and organo-mineral soils. Exchangeable Ni (Ni-CEC) was

309 usually quite low compared to Mg or to Ca (being the major exchangeable cations) and ranged,
310 when detected, from 0.01 to 0.29 $\text{cmol}^+ \text{kg}^{-1}$ in mineral horizons and from 0.01 to 0.39 $\text{cmol}^+ \text{kg}^{-1}$ in
311 organo-mineral horizons. There is no clear contrast between the two horizons: in some soils it was
312 higher in the OM-rich horizons (mostly Ferralsols), whereas it was the opposite in some others
313 (mostly Cambisols). In the Ferralic Rhodic Eutric Cambisol (Magnesic) from Sake South, there was
314 an unusually high concentration of Ni-CEC in both horizons (1.2–1.4 $\text{cmol}^+ \text{kg}^{-1}$). In this soil, Ni
315 saturated 6.0 to 8.2 % of the total CEC. The DTPA-extractable Ni (Ni_{DTPA}) was moderate to high
316 with 4.0 to 704 and 0.1 to 773 $\mu\text{g g}^{-1}$, respectively for mineral and organo-mineral soils. Ferralsols
317 had Ni_{DTPA} values ranging from 4.0 to 17 $\mu\text{g g}^{-1}$ (with lower values in mineral soils), whereas
318 Cambisols had higher values ranging from 14 to 773 $\mu\text{g g}^{-1}$. Again, as for Ni-CEC, the greatest
319 values that were above 700 $\mu\text{g g}^{-1}$ also corresponded to the soil from Sake South, which is
320 somewhat an intergrade soil between Cambisols and Ferralsols.

321

322 **3.4 Plant foliar chemistry**

323 The 724 leaves from non-hyperaccumulator plants and the 93 leaves from Ni-hyperaccumulator
324 plants were sampled in 21 different ultramafic sites. Based on concentrations measured in soil and
325 foliar parts, the accumulation potential of different elements (Na, Mg, Al, P, S, K, Ca, Mn, Fe, Ni
326 and Zn) was presented for non-hyperaccumulator (Figure 6A) and Ni-hyperaccumulator (Figure
327 6B) plants. Based on a nonparametric Wilcoxon-Mann-Whitney statistical test, there were
328 significant differences between the ability of non-hyperaccumulator and hyperaccumulator plants to
329 extract all the elements considered.

330

331 For the three elements Ca, K and P, plants can be considered as accumulators, with a concentration
332 in their leaves greater than the concentration in soils. This observation was the same whatever the
333 plants; hyperaccumulators or non-hyperaccumulators. Indeed, the mean foliar concentrations were
334 around 15 g kg^{-1} for Ca, 7.9 g kg^{-1} for K and 530 mg kg^{-1} for P (Supplementary information,
335 Tables 1 and 3). These very low foliar P concentrations were typical for tropical rain forests plants,
336 as observed by many authors (Vitousek and Sanford, 1983; Kitayama et al., 2000; Vitousek et al.,
337 2010). Conversely, hyperaccumulator and non-hyperaccumulator plants here should be considered
338 as excluders for Mg and Mn; these elements showed lower concentrations in plant parts in
339 comparison with those measured in soils whatever the plant considered (Supplementary
340 information, Table 1 to 4). In total, 10 different Al hyperaccumulator plants were recorded (Table
341 10). There were 5 other Al hyperaccumulator records exceeding the nominal threshold ($>1000 \text{ mg}$
342 kg^{-1}), but these plants remain unidentified. The identified Al hyperaccumulators were
343 phylogenetically diverse (originating from 7 different families), although three species of

344 *Symplocos* (Symplocaceae) were prominent at higher altitudes in cloud forest on Bukit Limber. The
345 highest concentration was found in *Symplocos maliliensis* with 46 300 mg kg⁻¹ foliar Al. *Symplocos*
346 is a well-known genus of Al hyperaccumulators from Southeast Asia (Chenery, 1949; Schmitt et al.,
347 2016).

348
349 There were clear differences concerning foliar concentrations of the elements Al, Fe, Na, S, Zn and
350 Ni (Supplementary information, Tables 1 to 4), between the two plant types (*i.e.* Ni
351 hyperaccumulator and non-hyperaccumulator plants). For example, Al leaf concentrations for Ni
352 hyperaccumulator and non-hyperaccumulator plants were around 20 and 210 mg kg⁻¹, respectively,
353 with a concentration 10.5 times greater for non-hyperaccumulators. This is due to the fact that the
354 higher concentration for Ni hyperaccumulators was around 260 mg kg⁻¹ while it was around 35 000
355 mg kg⁻¹ for other plants, including Al hyperaccumulators obviously. All Al hyperaccumulators (that
356 did not accumulate Ni at all) were reported from sites with Ferralsols (Uni-Uni plot 2, Bukit Limber
357 plots 1 & 2 and Jira plot 1). Conversely, the foliar concentrations for Na and S were higher for
358 hyperaccumulator plants in comparison with non-hyperaccumulators: the concentrations were
359 around 1700 and 1300 mg kg⁻¹ for Na and 2300 and 1900 mg kg⁻¹ for S, respectively for
360 hyperaccumulator and non-hyperaccumulator plants, revealing a higher capability of the
361 hyperaccumulator plants to extract these elements (Na and S). The same trend was observed for Zn.
362 Indeed, we found a three-fold higher Zn concentration in Ni hyperaccumulators with approximately
363 70 mg kg⁻¹, while the concentration in other plants was around 25 mg kg⁻¹.

364
365 The most important difference was found in the foliar concentrations of Ni hyperaccumulators *vs.*
366 non-hyperaccumulators. The mean Ni concentration was ~5500 mg kg⁻¹ for the hyperaccumulators,
367 while it was ~230 mg kg⁻¹ for the non-hyperaccumulators. These important differences between
368 non-hyperaccumulator and hyperaccumulator samples were underlined by the distribution, based on
369 the Ni concentrations in leaves, of the number of non-hyperaccumulator samples and
370 hyperaccumulator samples (Figures 6 and 8). Moreover, a clear difference between these two types
371 of plants was highlighted, particularly for most of the measured elements in the leaves (Al, Ca, Fe,
372 K, Na, Co, S and Zn). Indeed, the distribution of leaves samples concerning the different elements,
373 such as Fe, Mn, Na and Zn, confirmed the trend that the Ni hyperaccumulator plants can extract
374 higher amounts of these elements, in comparison with the non-hyperaccumulators. The same trend
375 was observed for Co with concentrations around 35 and 2.5 mg kg⁻¹, respectively for
376 hyperaccumulator and non-hyperaccumulator plants, revealing a concentration 14 times greater for
377 hyperaccumulators.

378

379 As shown in Figure 7, based on the DTPA-extractable metal concentrations measured in soils and
380 Ni concentrations in plant parts, Ni hyperaccumulator plants have a higher ability to extract other
381 strategic metals such as Mn, Co and Zn compared to non-hyperaccumulator plants. The difference
382 is not clear for Mn, with a ratio of DTPA-extractable metal present in the soil and leaf concentration
383 of 6.9 and 5.6 for hyperaccumulators and non-hyperaccumulators, respectively. Zn non-
384 hyperaccumulator plants were able to concentrate in their foliar parts 9.5-times the DTPA-
385 extractable Zn present in the soil, whereas the hyperaccumulator plants showed a ratio of 25.5, *i.e.*
386 2.7-times more in comparison with non-hyperaccumulator plants. For Co, the non-
387 hyperaccumulator plants showed a foliar concentration equivalent to that of the DTPA-extractable
388 Co concentrations found in the soil, but the hyperaccumulator plants were able to concentrate this
389 metal about 14-times more in comparison with non-hyperaccumulator plants. Based on the
390 comparison of foliar metal concentrations and DTPA metal concentrations present in the soil, the
391 best compartment appeared for Ni. Indeed, the non-hyperaccumulator plants concentrated this
392 element up to 1.5-times, while the concentrations in the areal parts of hyperaccumulator plants were
393 27.5-times higher than the DTPA concentrations in soils, that to say 19-times more than the non-
394 hyperaccumulator plants.

395

396 **3.5 Parasitic mistletoe on the Ni (hyper)accumulator *Ficus trachypison***

397 The mistletoe *Amyema cuernosensis* (Loranthaceae) was recorded parasitizing on the Ni
398 (hyper)accumulator *F. trachypison* near the Casuarina site (Figure 9, Table 11). It accumulated up
399 to 341 mg kg⁻¹ Ni which can only be acquired from the host since it is an obligate parasite with no
400 root system. The Ni concentrations in the stem and in the leaves of the host plant, *i.e.* *F.*
401 *trachypison*, were 3.0 and 217 mg kg⁻¹ Ni respectively.

402

403 **4. DISCUSSION**

404

405 The specific genesis and geochemistry of ultramafic soils is crucial to understand the occurrence of
406 hyperaccumulation and Ni hyperaccumulators (Echevarria, 2018; van der Ent et al., 2016a). It was
407 not always possible during this survey to access the bedrock at each location in order to describe it,
408 but when it was and described, it was clear that the soil characteristics (soil genesis and functioning)
409 was highly influenced by the degree of serpentinisation of the peridotite (van der Ent et al., 2018a).
410 The areas covered by strongly serpentinised peridotite or serpentinite always had Cambisols with
411 neutral pH and Mg as the main exchangeable cation in the CEC. These soils had very high level of
412 available Ni. These Hypereutric Cambisols (Hypermagnesian) are derived from strongly
413 serpentinised ultramafic bedrock in which the most important Ni-bearing phases are likely hydrous

414 and crystalline ferrous oxides and smectite minerals in which Ni is either sorbed or included in the
415 crystal lattice (Echevarria, 2018). Like other ultramafic soil covers in tropical areas (Proctor, 2003;
416 Echevarria, 2018), the mineralogy of Cambisols on serpentinite at Weda Bay was often dominated
417 by smectites in the weathered horizon (B_w). The Ferralsols presented several degrees of evolution,
418 probably because of the hilly landscape that induces soil erosion and rejuvenation (Echevarria,
419 2018). The most developed soil profiles were found at high altitude on the plateau at Bukit Limber
420 (ca. 1000 m asl.) and at Uni-Uni at a lower altitude (ca. 260 m asl.). The former had the deepest
421 profile development with a 30-m lateritic development in places (as was visible from a mining test
422 pit). The ultramafic region at Weda Bay has therefore a varied gradient of tropical ultramafic
423 pedogenesis.

424

425 One surprising finding was that the highest DTPA-extractable Ni concentration ever recorded in an
426 ultramafic soil (Echevarria, 2018; van der Ent et al., 2018a) was from a soil that was not a typical
427 Hypereutric Cambisol (Hypermagnesian). It was a Ferralic Cambisol (Magnesian), halfway between a
428 typical ultramafic Hypermagnesian Cambisol and a Geric Plinthic Rhodic Ferralsol. This soil was
429 very rich in total Ni (1.4 %) and had a pH of 5.92. The soil hosted strong Ni hyperaccumulators
430 (some displaying Ni concentrations in their leaves above 2.2 %) although a study in Sabah (Borneo
431 Island) showed that Ni hyperaccumulators are absent from acidic soils (*i.e.* soils with pH <6.3) and
432 consistently occur on soils with relatively high DTPA-extractable Ca, Mg and Ni concentrations
433 (van der et al., 2016c). It appears that the very high extractability of Ni in the soils were more
434 important than pH conditions for Ni hyperaccumulators. With the exception of the soil at Sake
435 South, the situation at Weda Bay was similar to that of Sabah, with all Ni hyperaccumulators
436 occurring on eroded hypermagnesian Cambisols with (extremely) high DTPA-extractable Ni
437 concentration. These shallow hypermagnesian Cambisols host a xerophytic adapted vegetation in
438 which Ni hyperaccumulators were common, and this aligns with reports from other tropical
439 ultramafic regions, for example in Cuba, New Caledonia, Sabah and the Philippines (van der Ent et
440 al., 2016a).

441

442 In contrast, Geric Ferralsols such as at Uni-Uni plot 2, or Bukit Limber plots 1 and 2 have no
443 occurrence of Ni hyperaccumulators and this may be explained by their physico-chemical
444 characteristics: these soils had low DTPA-extractable Ni concentration, acidic pH, and a
445 mineralogy dominated by goethite and hematite which resulted in a very low CEC. However, the
446 DTPA-extractable Al in these soils was high (up to 45 mg kg⁻¹) although ultramafic bedrocks are
447 relatively poor in Al, and these soils host Al hyperaccumulators from families or groups that were
448 previously known to contain Al hyperaccumulator taxa in nearby tropical regions: *e.g.* three

449 different species of *Symplocos* (Symplocaceae), one species of *Syzygium* (Myrtaceae), one species
450 of *Melastoma* (Melastomataceae), one species of *Psychotria* (Rubiaceae), and several species from
451 the Lauraceae, Theaceae and Cunoniaceae families. Therefore, Ni and Al hyperaccumulation were
452 found in contrasted edaphic situations which was confirmed by the foliar chemistry data from Weda
453 Bay, but also from nearby Sabah (van der Ent et al., 2018b).

454

455 Laboratory analysis with ICP-AES confirmed the indicative results achieved from the initial testing
456 in the field with DMG-test paper. Field-testing with DMG paper therefore remains a reliable and
457 quick method for Ni hyperaccumulator reconnaissance. After analysis, the highest Ni
458 concentrations in hyperaccumulator leaves were found in the shrub *R. aff. bengalensis* and in the
459 tree *P. roxburghiana*. Both species were hypernickelophores (with foliar Ni concentrations usually
460 above 1.0 %) and were only reported in soils with high DTPA-extractable Ni. In total four species
461 from the 18 hyperaccumulators reported could be considered as metal crops (high biomass, high Ni
462 accumulation), these were: *R. aff. bengalensis*, *F. trachypison*, *T. morotaiense* and *G. moluccanum*.
463 Of these species, *F. trachypison*, *T. morotaiense* and *G. moluccanum* appeared to be facultative Ni
464 hyperaccumulator species and pioneer species suitable for first-phase implementation on minerals
465 waste. *Rinorea aff. bengalensis*, is a strong Ni hyperaccumulator and could be cropped as an
466 understory shrub under the cover of species such as *T. morotaiense* in the second stage of
467 agromining and then coppiced for efficient Ni phytoextraction.

468

469 From the plants collected at Weda Bay, two specimens of *R. aff. bengalensis* showed Co
470 hyperaccumulation. Both were collected at the location 'Tanjung Ulie'. High foliar Co
471 concentrations had already been reported in the strong Ni hyperaccumulators *Rinorea javanica*
472 (Violaceae) with up to 670 $\mu\text{g g}^{-1}$ in natural conditions (Brooks et al., 1977; Lange et al., 2017). The
473 strong affinity of Mn-oxides for Co may explain the lower Co mobility in Mn-rich soils (Collins
474 and Kinsela, 2011). When soils are waterlogged, Co is associated mainly with amorphous Fe oxides
475 after the reduction of Mn and the dissolution of Mn-oxides, and thus becomes more available
476 (Lange et al., 2017). These conditions are also responsible for the high Co concentrations observed
477 in some *Rinorea* species as observed for other species, such as *Berkheya coddii* in South Africa
478 (Lange et al., 2017).

479

480 The occurrence of parasitic mistletoes on hyperaccumulator plants is a very rare phenomenon, and
481 has not previously been reported in tropical species or woody hyperaccumulator plants/mistletoes.
482 The herbaceous *Orobanche nowackiana* parasitizes the Ni hyperaccumulator *Alyssum murale* in
483 Albania while accumulating up to 299 mg kg^{-1} in its leaves (Bani et al., 2018). Similarly, Reeves

484 (1992) reported *O. rechingeri* parasitizing *Alyssum lesbiacum* while accumulating more than 600
485 mg kg⁻¹ Ni. The only other now example is the American *Cuscuta californica* parasitizing the
486 herbaceous Ni hyperaccumulator *Streptanthus polygaloides* reaching up to 800 mg kg⁻¹ Ni (Boyd et
487 al., 1999).

488

489 With only a small portion of the ultramafic flora of Indonesia screened for Ni hyperaccumulation,
490 this field survey considerably extends the list of Indonesian Ni hyperaccumulators. It is expected
491 that more Ni hyperaccumulators will be discovered in the near future in this country because it has
492 the largest ultramafic extension worldwide with a highly diverse flora (van der Ent et al., 2013b).
493 Many hyperaccumulator plants are rare, with restricted ranges on ultramafic soils, making them
494 sensitive to destructive forces of mining and forest fires (Whiting et al., 2004; Erskine et al., 2012),
495 and this adds to the urgency for screening to avoid this valuable biological resource from being lost
496 before its known.

497

498 **ACKNOWLEDGEMENTS**

499 We acknowledge the financial and operational support from Eramet and PT Weda Bay Nickel to
500 conduct this research. The French National Research Agency through the national “Investissements
501 d’avenir” program (ANR-10-LABX-21, LABEX RESSOURCES21) and through the ANR-14-
502 CE04-0005 Project “Agromine” is acknowledged for funding support. PT Weda Bay Nickel were
503 responsible for all relevant permits in Indonesia and for transporting the plant and soil samples for
504 chemical analysis in France. A. van der Ent is the recipient of a Discovery Early Career Researcher
505 Award (DE160100429) from the Australian Research Council.

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724 **FIGURE CAPTIONS**

725

726 **Figure 1.** Map of the field sampling sites and the location of Weda Bay on Halmahera Island,
727 Indonesia.

728

729 **Figure 2.** Aerial views of the landscapes at Weda Bay, Halmahera, Indonesia. Panel **A** shows
730 exposed serpentinite bedrock in a rock fall near Jira with forest dominated by Casuarinaceae; panel
731 **B** showing a riverbed upstream of the site of panel A with serpentinite bedrock and a short scrubby
732 vegetation; Panel **C** shows mature riverine further downstream; panel **D** shows burnt vegetation on
733 Plinthic Geric Rhodic Ferralsols near Uni-Uni.

734

735 **Figure 3.** Ground-level views of vegetation types at Weda Bay, Halmahera, Indonesia. Panel **A**
736 shows mature riverine forest at the site “Serpentinite River”; panel **B** shows mature forest near site
737 Casuarina’ panel **C** shows burnt ‘maquis-type’ vegetation characterised by sedges (Cyperaceae) on
738 Geric Plinthic Rhodic Ferralsols at Uni-Uni, and panel **D** shows young forest dominated by
739 *Macaranga* spp. (Euphorbiaceae) on Ferralic Rhodic Hypereutric Cambisols (Hypermagnesian) at
740 Sake River.

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742 **Figure 4.** Soil profiles at key localities at Weda Bay, Halmahera, Indonesia. Panel **A** shows
743 Hypereutric Cambic Skeletic Leptosols (Hypermagnesian) at the site “Blue Hill”; panel **B** shows
744 Geric Plinthic Rhodic Ferralsols; panel **C** shows ferrocrete with plinthic nodules consisting mainly
745 of hematite; panels **D** and **E** show Hypereutric Cambisols (Hypermagnesian) at the sites Casuarina
746 and Sake West; panel **F** shows Geric Plinthic Rhodic Ferralsols at Uni-Uni.

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748 **Figure 5.** X-Ray Diffractograms of the fine earth fraction (< 50 μ m) of the B horizons of 5
749 representative profiles on ultramafic bedrock and of the A-organo-mineral horizon of the Rendzic
750 Leptosol on Limestone. CALC=Calcite; DIOP=Diopside; ENST=Enstatite; GIBBS=Gibbsite;
751 GOET=Goethite; HEM=Hematite; MAGN=Magnetite; QUARTZ=Quartz; TREM=Tremolite;
752 SERP=Serpentine.

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754 **Figure 6.** Plant part and soil total concentrations of different elements for non-hyperaccumulator
755 plants (**A**) and hyperaccumulator plants (**B**). All concentrations are expressed as mg kg^{-1} dry mass.

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757 **Figure 7.** Correlations between element concentrations in plant parts (natural logarithm scale) and
758 number of hyperaccumulator (93 samples) and non-hyperaccumulator (724 samples) plants.

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760 **Figure 8.** Plant foliar and soil bioavailable concentrations with DTPA extractions of different
761 elements for non-hyperaccumulator plants and hyperaccumulator plants. All concentrations are
762 expressed as mg kg^{-1} dry mass.

763

764 **Figure 9.** The mistletoe *Amyema cuernosensis* parasitizing the Ni hyperaccumulator *Ficus*
765 *trachypison* near the Casuarina site. Panel **A** shows the white mistletoe plant attached to the host;
766 panel **B** shows the inflorescences of *Amyema cuernosensis*; and Panel **C** shows a section of woody
767 stem of *Ficus trachypison* with the mistletoe stems attached with haustoria.

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770 **TABLE CAPTIONS**

771

772 **Table 1.** Sites properties showing plot enumeration, location, soil class and dominant vegetation
773 type.

774

775 **Table 2.** Mineralogy of the soils (Mineral horizons – 10–25 cm layer) sampled at each site. For the
776 soil in Doromesmesan, the mineralogy was based on the organo-mineral Horizon (0-5 cm layer).
777 +++ (most abundant mineral); ++ (abundant mineral); + (frequent mineral); (+) (detectable traces).

778

779 **Table 3.** Total elements for mineral soil (10–25 cm layer) samples from each site.

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781 **Table 4.** Total elements for organo-mineral soil (0–5 cm layer) samples from each site.

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783 **Table 5.** DTPA-extractable elements for mineral soil (10–25 cm layer) samples from each site.

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785 **Table 6.** DTPA-extractable elements for organo-mineral soil (0–5 cm layer) samples from each site.

786

787 **Table 7.** pH, exchangeable cations ($\text{cmol}^+ \text{kg}^{-1}$) and nitrogen and carbon content for mineral soil
788 (10–25 cm layer) samples from each site. Abbreviations: Cation Exchange Capacity (CEC), % of
789 soil total nitrogen (%N), % of soil total carbon (%C), % of soil organic carbon (%Corg).

790

791 **Table 8.** pH, exchangeable cations ($\text{cmol}^+ \text{kg}^{-1}$) and nitrogen and carbon content for organo-mineral
792 soil (0–5 cm layer) samples from each site. Abbreviations: Cation Exchange Capacity (CEC), % of
793 soil total nitrogen (%N), % of soil total carbon (%C), % of soil organic carbon (%Corg).

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795 **Table 9.** Ni distribution in leaf samples (mg kg^{-1}) and soil samples for each site. Abbreviations:
796 Extractable Ni (Ni-DTPA, mg kg^{-1}), Exchangeable Ni (Ni-CEC, $\text{cmol}^+ \text{kg}^{-1}$) and Ni total (Ni-T, g
797 kg^{-1}), no data (n.d).

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799 **Table 10.** Aluminium (mg kg^{-1}) hyperaccumulator plant records (identified and unidentified
800 specimens) from the Weda Bay area.

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802 **Table 11.** Elemental concentrations (mg kg^{-1}) in the mistletoe *Amyema cuernosensis*
803 (Loranthaceae) and the host *Ficus trachypison* (Moraceae).

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806 **SUPPLEMENTARY INFORMATION**

807

808 **Table S1.** Macronutrients (g kg^{-1}) of non-hyperaccumulator leaves (number of samples are
809 indicated, means and ranges are provided).

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811 **Table S2.** Micronutrients (mg kg^{-1}) of non-hyperaccumulator leaves (number of samples are
812 indicated, means and ranges are provided).

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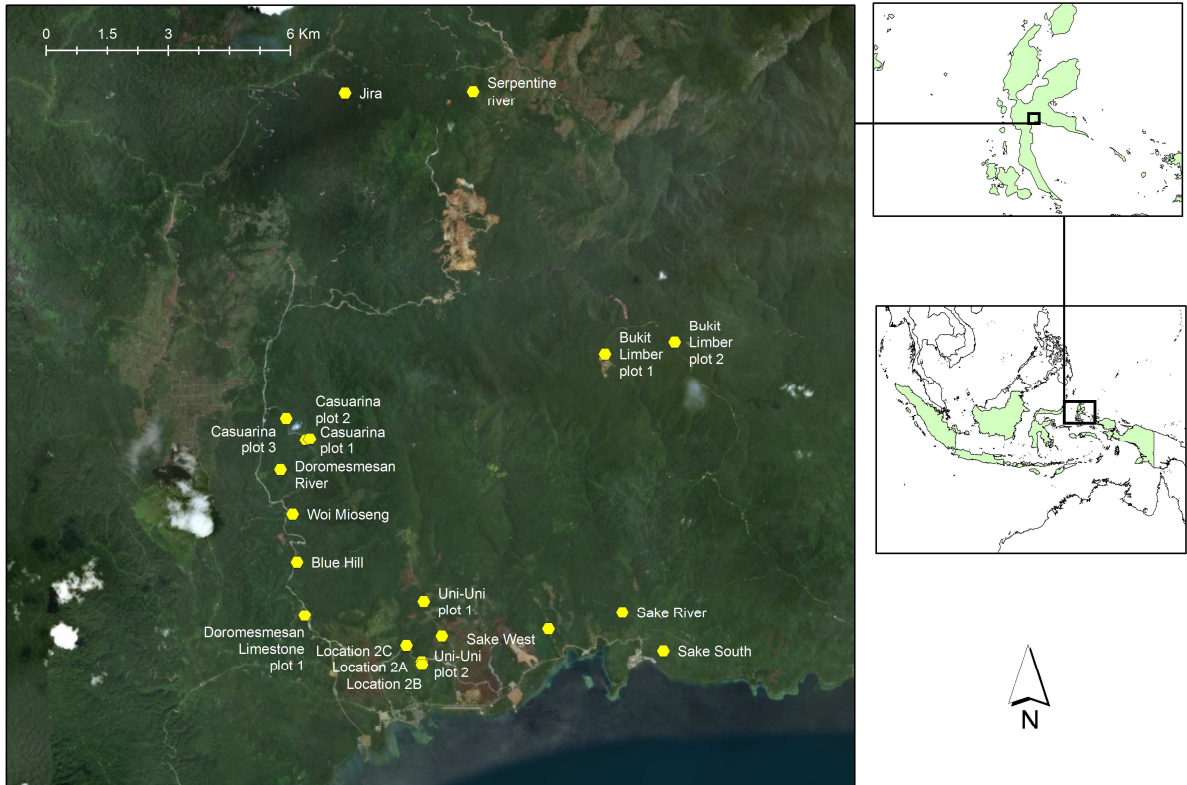
814 **Table S3.** Macronutrients (g kg^{-1}) of hyperaccumulator leaves (number of samples are indicated,
815 means and ranges are provided).

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817 **Table S4.** Micronutrients (mg kg^{-1}) of hyperaccumulator leaves (number of samples are indicated,
818 means and ranges are provided).

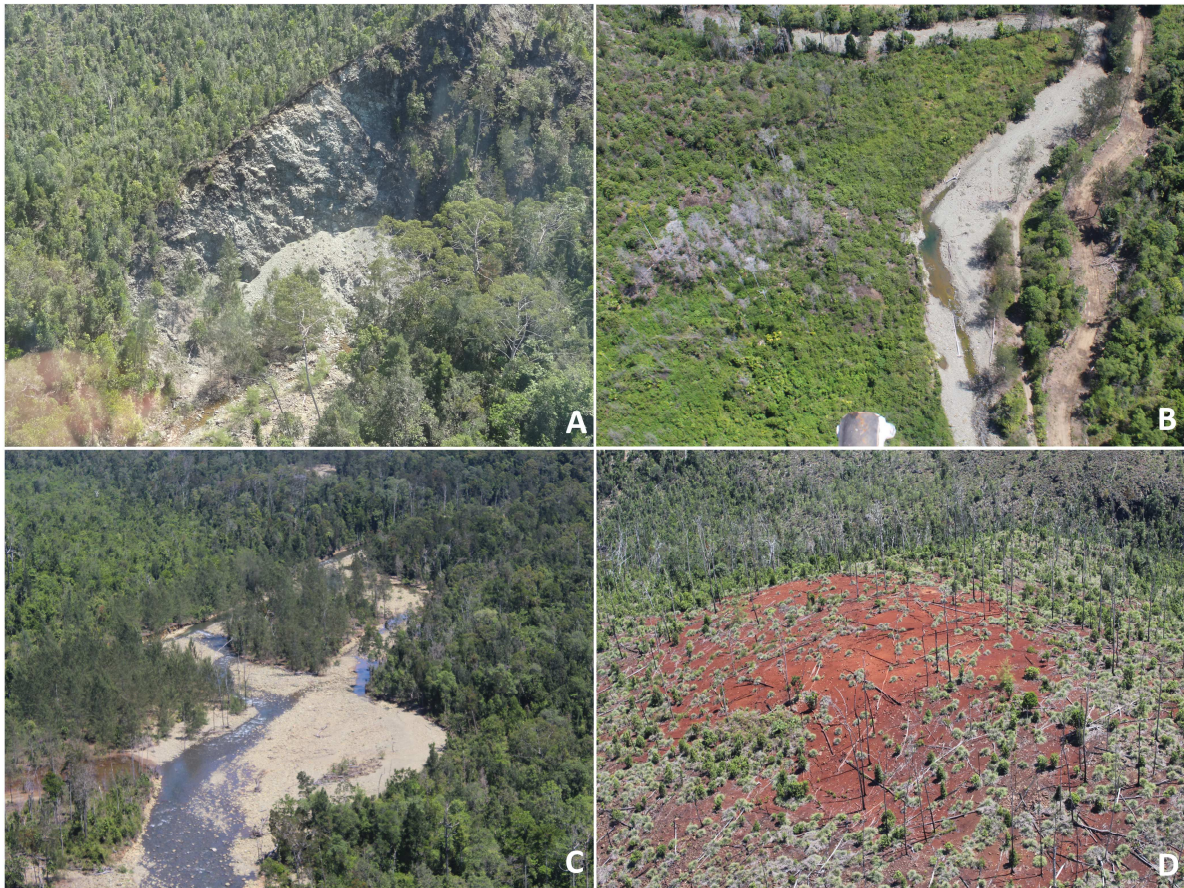
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Figure 1. Map of the field sampling sites and the location of Weda Bay on Halmahera Island, Indonesia.



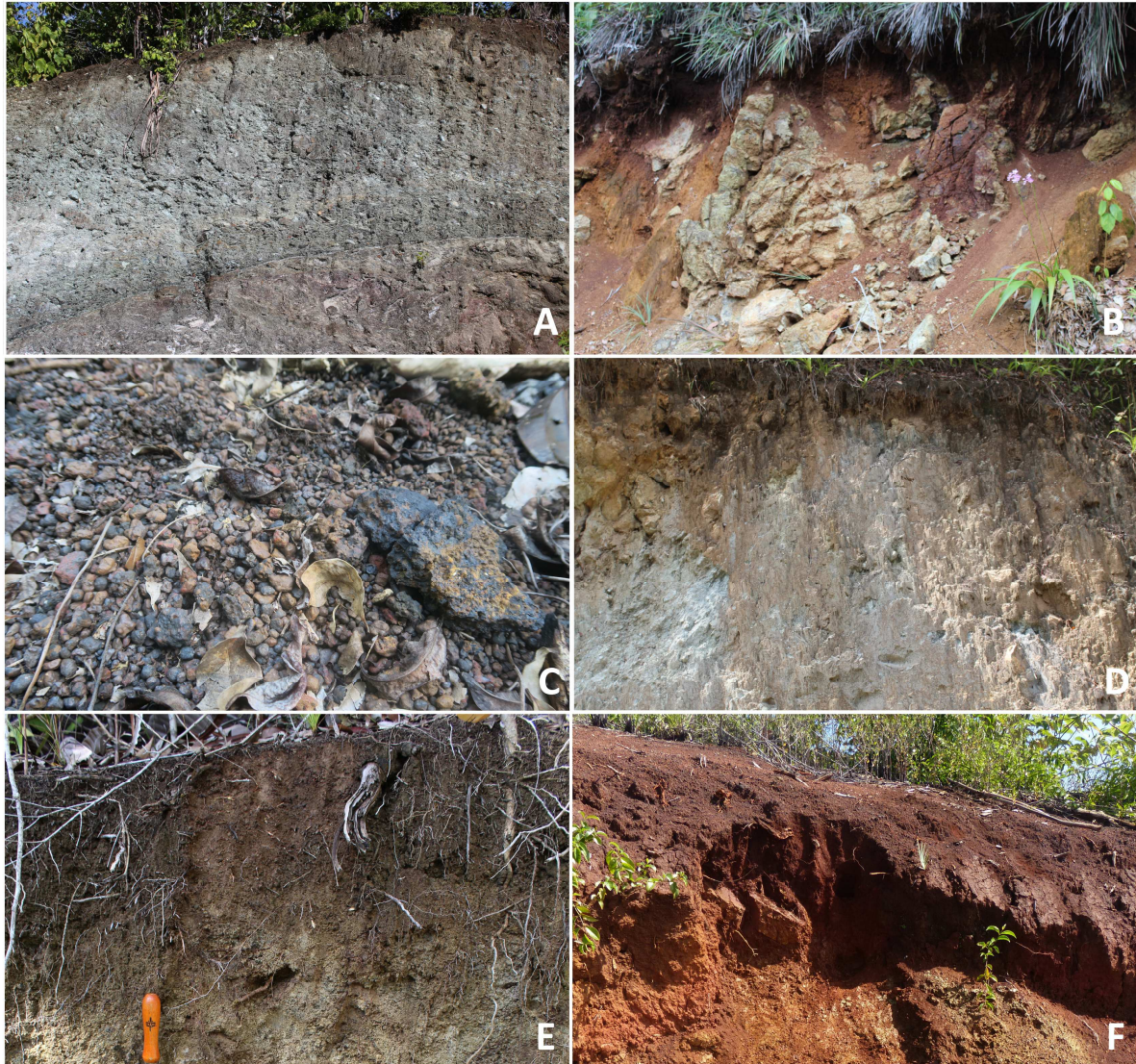
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Figure 2. Aerial views of the landscapes at Weda Bay, Halmahera, Indonesia. Panel **A** shows exposed serpentinite bedrock in a rock fall near Jira with forest dominated by Casuarinaceae; panel **B** showing a riverbed upstream of the site of panel A with serpentinite bedrock and a short scrubby vegetation; Panel **C** shows mature riverine further downstream; panel **D** shows burnt vegetation on Plinthic Geric Rhodic Ferralsols near Uni-Uni.



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Figure 3. Ground-level views of vegetation types at Weda Bay, Halmahera, Indonesia. Panel **A** shows mature riverine forest at the site “Serpentine River”; panel **B** shows mature forest near site Casuarina’ panel **C** shows burnt ‘maquis-type’ vegetation characterised by sedges (Cyperaceae) on Geric Plinthic Rhodic Ferralsols at Uni-Uni, and panel **D** shows young forest dominated by *Macaranga* spp. (Euphorbiaceae) on Ferralic Rhodic Hypereutric Cambisols (Hypermagnesian) at Sake River.

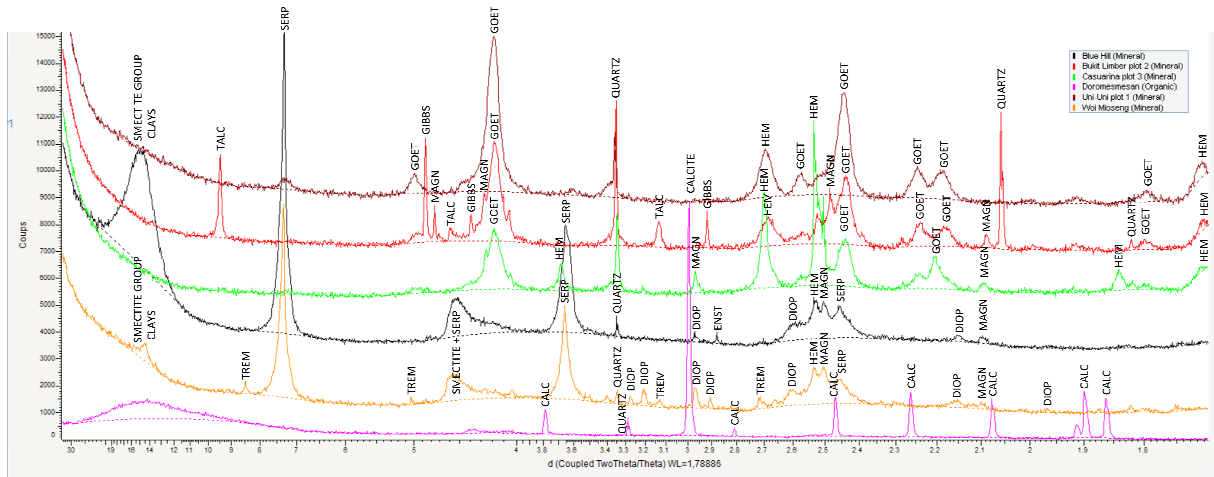


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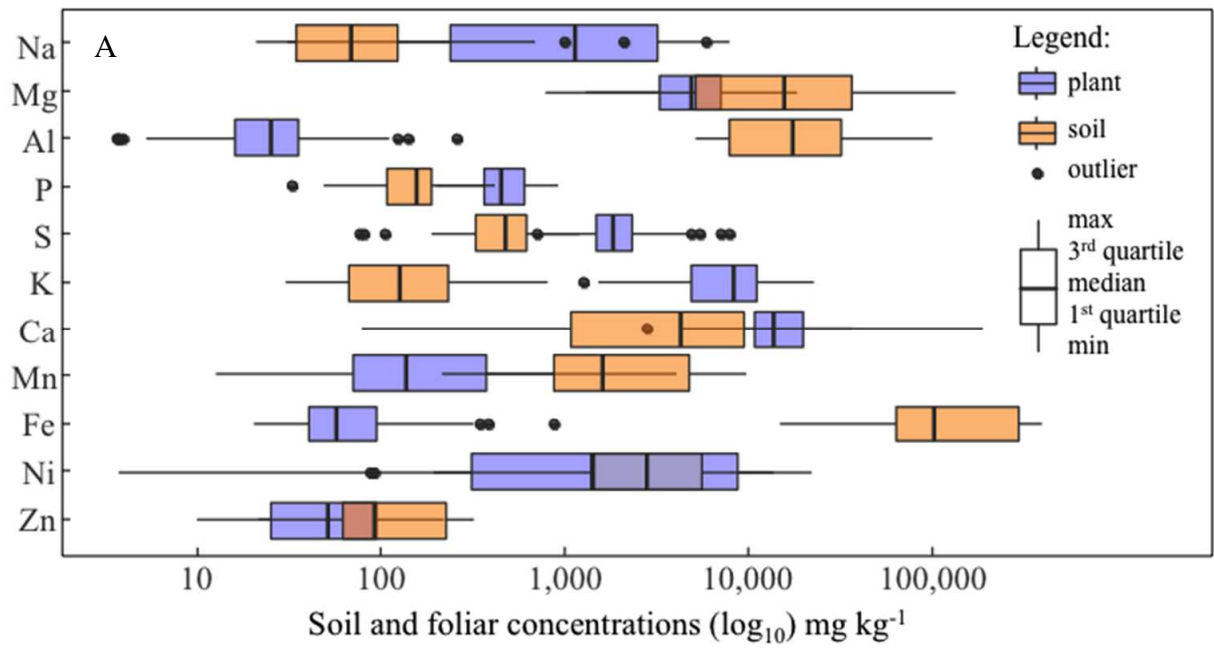
25 **Figure 4.** Soil profiles at key localities at Weda Bay, Halmahera, Indonesia. Panel **A** shows
 26 Hypereutric Cambic Skeletic Leptosols (Hypermagnesian) at the site “Blue Hill”; panel **B** shows
 27 Geric Plinthic Rhodic Ferralsols; panel **C** shows ferrocrete with plinthic nodules consisting
 28 mainly of hematite; panels **D** and **E** show Hypereutric Cambisols (Hypermagnesian) at the sites
 29 Casuarina and Sake West; panel **F** shows Geric Plinthic Rhodic Ferralsols at Uni-Uni.

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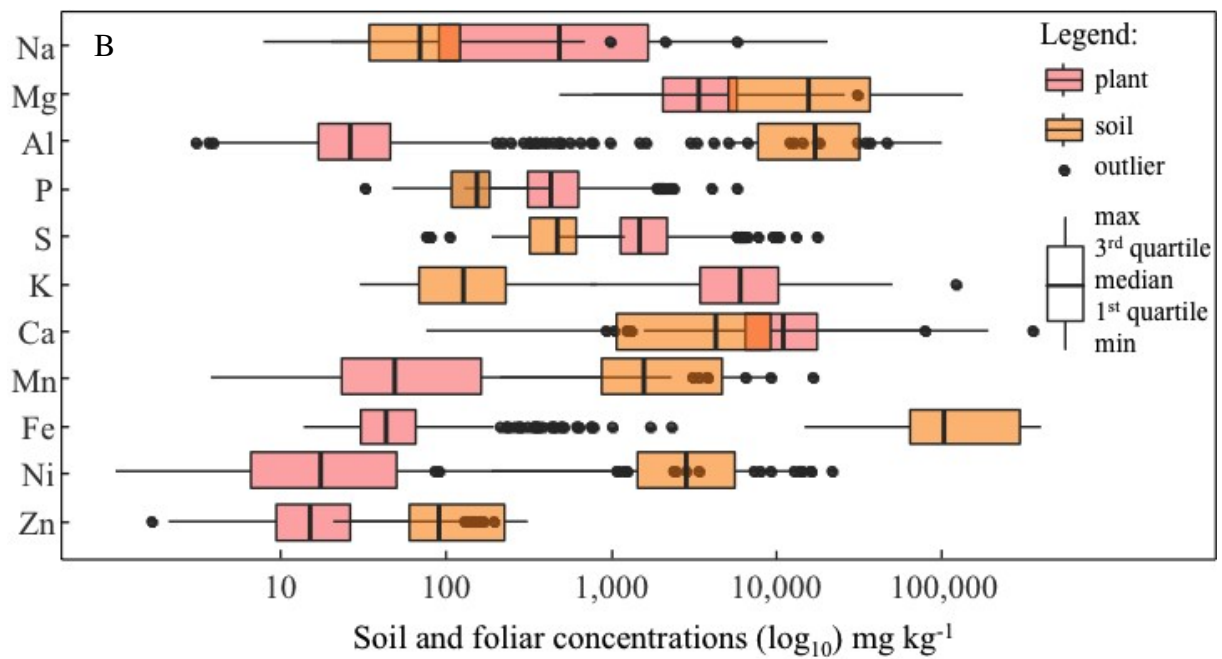
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Figure 5. X-Ray Diffractograms of the fine earth fraction (< 50 μm) of the B horizons of 5 representative profiles on ultramafic bedrock and of the A-organo-mineral horizon of the Rendzic Leptosol on Limestone. CALC=Calcite; DIOP=Diopside; ENST=Enstatite; GIBBS=Gibbsite; GOET=Goethite; HEM=Hematite; MAGN=Magnetite; QUARTZ=Quartz; TREM=Tremolite; SERP=Serpentine.



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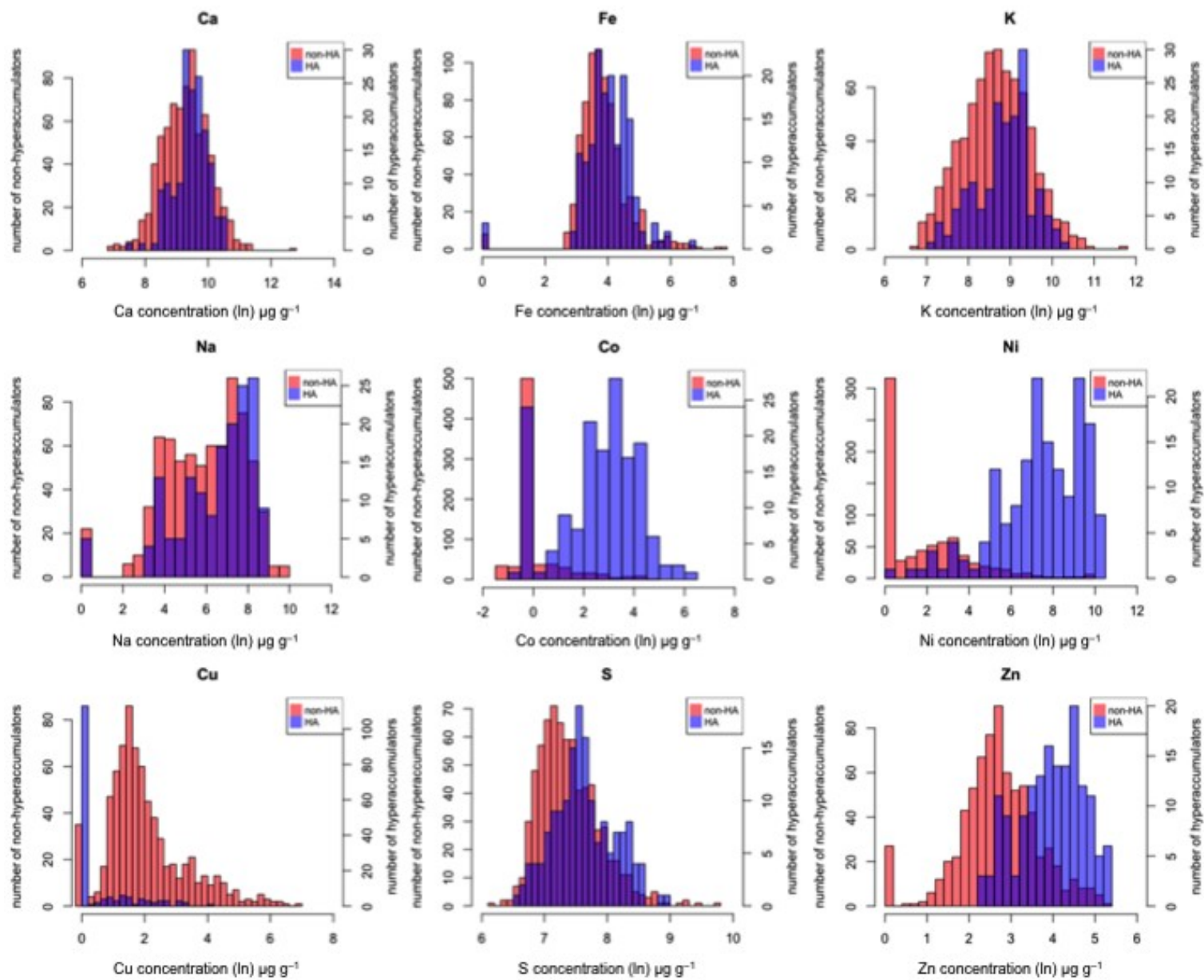


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43 **Figure 6.** Plant part and soil total concentrations of different elements for non-
 44 hyperaccumulator plants (A) and hyperaccumulator plants (B). All concentrations are
 45 expressed as mg kg^{-1} dry mass.

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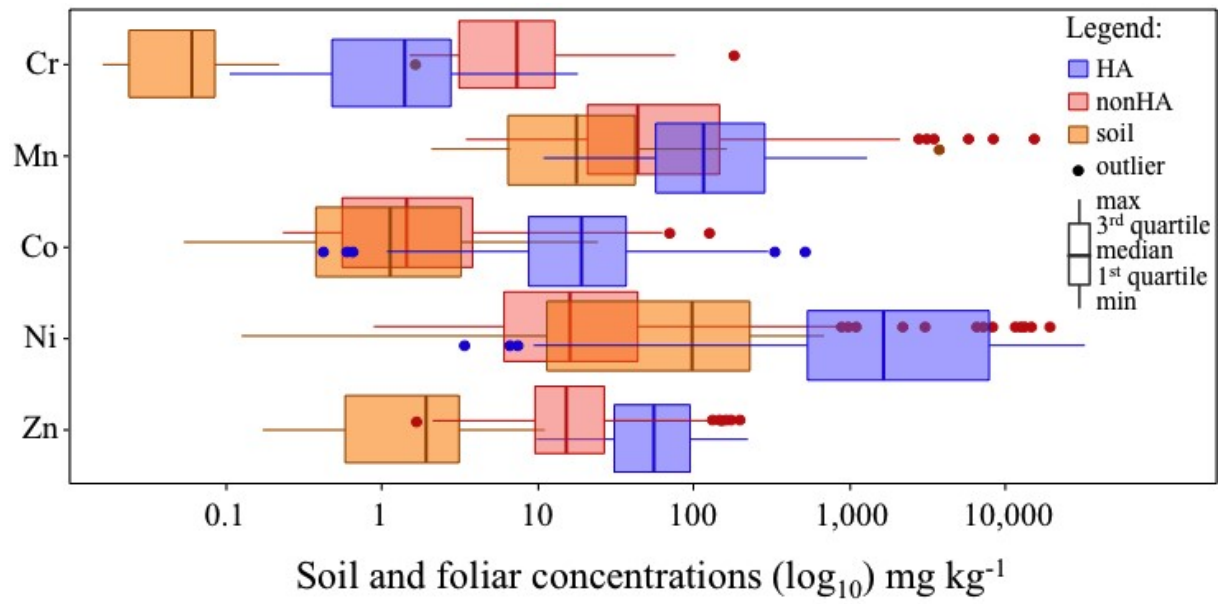


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Figure 7. Correlations between element concentrations in plant parts (natural logarithm scale) and number of hyperaccumulator (93 samples) and non-hyperaccumulator (724 samples) plants.



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Figure 8. Plant foliar and soil bioavailable concentrations with DTPA extractions of different elements for non-hyperaccumulator plants and hyperaccumulator plants. All concentrations are expressed as mg kg^{-1} dry mass.



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Figure 9. The mistletoe *Amyema cuernosensis* parasitizing the Ni hyperaccumulator *Ficus trachypison* near the Casuarina site. Panel **A** shows the white mistletoe plant attached to the host; panel **B** shows the inflorescences of *Amyema cuernosensis*; and Panel **C** shows a section of woody stem of *Ficus trachypison* with the mistletoe stems attached with haustoria.

Sites	Plot	Elevation (m asl)	GPS coordinates	Soil class	Vegetation type
Bukit Limber	Plot 1	909	0°32'49"N, 127°58'35"E	Rhodic Plinthic Ferralsol (Hypereutric, Hypermagnesian)	Lower montane forest
	Plot 2	1020	0°32'58"N, 127°59'31"E	Geric Rhodic Plinthic Ferralsol (Magnesian)	Lower montane forest
Casuarina	plot 1	189	0°31'41"N, 127°54'37"E	Leptic Hypereutric Rhodic Cambisol (Magnesian)	Medium tall lowland forest
	plot 2	190	0°31'41"N, 127°54'40"E	Leptic Hypereutric Rhodic Cambisol (Magnesian)	Medium tall lowland forest
	plot 3	204	0°31'57"N, 127°54'22"E	Rhodic Plinthic Mollic Ferralsol (Dystric, Magnesian)	Medium tall lowland forest
Doromesmesan Limestone	plot 1	73	0°29'20"N, 127°54'36"E	Rendzic Leptosol	Medium tall lowland forest
Jira	–	92	0°36'19"N, 127°55'08"E	-	Medium tall lowland forest
Location 2A	–	83	0°28'42"N, 127°56'9"E	Chromic Hypereutric Cambisol (Hypermagnesian)	Short graminoid scrub
Location 2B	–	82	0°28'40"N, 127°56'10"E	Leptic Hypereutric Cambisol (Hypermagnesian)	Short graminoid scrub
Location 2C	–	62	0°28'55"N, 127°55'57"E	Hypereutric Vertic Leptic Cambisol (Hypermagnesian)	Short graminoid scrub
Sake River	–	109	0°29'18"N, 127°58'57"E	Ferralic Rhodic Hypereutric Cambisol	Medium tall lowland forest
Sake South	–	28	0°28'51"N, 127°59'22"E	Ferralic Rhodic Eutric Cambisol (Magnesian)	Medium tall lowland forest

Sake West	–	105	0°29'9"N, 127°57'50"E	Rhodic Plinthic Ferralsol (Eutric, Magnesian)	Medium tall lowland forest
Serpentine River	–	122	0°36'19"N, 127°56'50"E	-	Riparian vegetation
Uni-Uni	plot 1	233	0°29'31"N, 127°56'11"E	Geric Plinthic Rhodic Ferralsol	Short graminoid scrub
	plot 2	160	0°29'3"N, 127°56'25"E	Rhodic Hypereutric Cambisol (Magnesian)	Short graminoid scrub
Woi Mioseng	–	45	0°30'41"N, 127°54'27"E	Rhodic Hypereutric Cambisol (Magnesian)	Medium tall lowland forest

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3 **Table 1.** Sites properties showing plot enumeration, location, soil class and dominant vegetation type.
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Location	Primary minerals						Quartz	Clay minerals				Iron oxides, Spinels and Al hydroxides			
	Tremolite	Diopside	Enstatite	Fayalite	Palygorskite	Calcite		Smectite group clays	Chlorite (clinochlore)	Talc	Serpentine	Goethite	Hematite	Magnetite	Gibbsite
Blue Hill		+	(+)				+	+++	(+)		+++	+	(+)	+	
Bukit Limber Plot 1							+			+	++ (clinochrys.)	+++	+	+	
Bukit Limber Plot 2										++		+++	(+)	+	+
Casuarina Plot 1		+	+				++	++			++	+	++	++	
Casuarina Plot 2	+++						+	++	+	(+)	+	+	+		
Casuarina Plot 3							++					+++	+	++	
Doromesmesan Limestone Plot 1						+++	(+)								
Location 2A							+	+++	(+)		+	+	+	(+)	
Location 2B		++	+		+			+++	+	+					
Location 2C					(+)			+++							
Sake River								(+)			(+)	+++	+	+	
Sake South								(+)			+	+++	++	+	
Sake West							+			(+)		+++		+	
Uni-Uni plot 1											(+)	+++		+	
Uni-Uni plot 2								++			+++	+	++		
Woi Mioseng	+	+					+	+	(+)		+++	+	+	+	

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6 **Table 2.** Mineralogy of the soils (Mineral horizons – 10–25 cm layer) sampled at each site. For the soil in Doromesmesan, the mineralogy was based on the
7 organo-mineral Horizon (0-5 cm layer). +++ (most abundant mineral); ++ (abundant mineral); + (frequent mineral); (+) (detectable traces).

Location	Al (g kg ⁻¹)	Ca (g kg ⁻¹)	Fe (g kg ⁻¹)	K (mg kg ⁻¹)	Mg (g kg ⁻¹)	Mn (g kg ⁻¹)	Na (mg kg ⁻¹)	Ni (g kg ⁻¹)	P (mg kg ⁻¹)	S (mg kg ⁻¹)	Zn (mg kg ⁻¹)
Blue Hill	6.2	2.5	83	< LOD	133	0.8	26	3.5	32	76	69
Bukit Limber plot 1	45	0.1	317	< LOD	29	1.8	< LOD	4.4	71	299	190
Bukit Limber plot 2	33	< LOD	227	51	0.9	0.2	29	1.5	104	582	93
Casuarina plot 1	7.1	5.6	67	217	29	0.9	155	2.1	157	504	70
Casuarina plot 2	21	14	44	183	26	1.0	209	0.6	117	368	36
Casuarina plot 3	22	0.6	398	51	2.1	6.1	24	6.4	129	462	285
Doromesmesan Limestone Plot 1	26	188	27	145	5.2	0.5	69	0.3	328	635	27
Location 2A	6.4	4.2	96	83	20	2.4	61	2.3	133	474	71
Location 2C	13	10.6	82	483	86	1.3	690	1.5	92	105	85
Sake River	20	1.6	309	61	5.3	9.5	43	9.8	132	467	314
Sake South	10	0.2	301	66	14	7.1	30	14	295	419	268
Sake West	32	0.3	318	30	7.0	8.1	< LOD	8.2	111	800	255
Uni-Uni plot 1	39	0.1	358	30	0.8	2.8	< LOD	5.5	90	748	206
Uni-Uni plot 2	7.0	4.1	156	100	60	4.1	36	4.6	48	212	119
Woi Mioseng	7.8	4.3	67	114	112	1.0	110	2.0	135	285	59

8 < LOD: under the limit of detection

9

10 **Table 3.** Total elements for mineral soil (10–25 cm layer) samples from each site.

11

Location	Al (g kg ⁻¹)	Ca (g kg ⁻¹)	Fe (g kg ⁻¹)	K (mg kg ⁻¹)	Mg (g kg ⁻¹)	Mn (g kg ⁻¹)	Na (mg kg ⁻¹)	Ni (g kg ⁻¹)	P (mg kg ⁻¹)	S (mg kg ⁻¹)	Zn (mg kg ⁻¹)
Blue Hill	6.6	7.9	67	254	113	1.0	83	3.4	170	400	89
Bukit Limber plot 1	39	0.2	296	56	35	1.8	< LOD	4.5	169	470	186
Bukit Limber plot 2	18	0.6	111	324	1.9	0.2	113	0.8	316	1 198	57
Casuarina plot 1	5.2	8.2	49	311	26	0.6	111	1.7	262	927	62
Casuarina plot 2	18	14	40	235	23	0.9	180	0.6	159	523	36
Casuarina plot 3	14	5.5	272	234	2.6	5.2	64	5.1	194	894	230
Doromesmesan Limestone Plot 1	12	190	15	209	4.2	0.3	85	0.2	414	1 008	21
Location 2A	5.6	5.7	89	117	17	2.3	67	2.1	164	587	71
Location 2B	100	24	29	70	15	0.5	5 797	0.1	< LOD	< LOD	26
Location 2C	21	21	84	809	65	1.4	992	1.2	128	80	94
Sake River	17	3.4	266	132	4.9	8.5	69	8.4	159	625	277
Sake South	8.3	0.7	265	114	12	6.3	30	12	340	527	237
Sake West	32	1.9	313	76	6.9	9.7	21	7.8	178	352	262
Uni-Uni plot 1	40	2.8	341	66	1.1	4.6	21	5.7	155	615	222
Uni-Uni plot 2	8.1	5.2	180	141	39	4.1	46	4.9	74	200	132
Woi Mioseng	7.8	5.2	57	251	87	0.9	115	1.8	223	547	62

< LOD: under the limit of detection

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14 **Table 4.** Total elements for organo-mineral soil (0–5 cm layer) samples from each site.

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Location	Co (mg kg ⁻¹)	Fe (mg kg ⁻¹)	Mg (mg kg ⁻¹)	Mn (mg kg ⁻¹)	Ni (mg kg ⁻¹)	Zn (mg kg ⁻¹)
Blue Hill	0.2	46	1 409	4.0	75	0.7
Bukit Limber plot 1	0.3	19	216	3.0	14	0.3
Bukit Limber plot 2	0.1	369	4.9	2.3	4.5	0.5
Casuarina plot 1	1.5	182	1 068	20	335	3.8
Casuarina plot 2	1.4	141	1 032	47	110	2.0
Casuarina plot 3	27	59	95	180	119	2.8
Doromesmesan Limestone Plot 1	0.1	13	69	6.0	2.4	0.5
Location 2A	0.6	82	911	15	158	1.6
Location 2C	0.2	28	688	7.4	25	0.5
Sake River	12	37	176	146	208	3.4
Sake South	4.0	11	552	4.5	704	4.1
Sake West	16	30	63	50	17	0.4
Uni-Uni plot 1	3.2	71	2.2	122	4.0	0.4
Uni-Uni plot 2	1.3	70	1 353	20	267	1.9
Woi Mioseng	0.7	61	965	13	107	1.0

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17 **Table 5.** DTPA-extractable elements for mineral soil (10–25 cm layer) samples from each site.

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Location	Co (mg kg ⁻¹)	Fe (mg kg ⁻¹)	Mg (mg kg ⁻¹)	Mn (mg kg ⁻¹)	Ni (mg kg ⁻¹)	Zn (mg kg ⁻¹)
Blue Hill	0.5	31	1 032	10	140	2.4
Bukit Limber plot 1	0.7	18	352	7.2	24	0.6
Bukit Limber plot 2	0.1	1 065	145	6.9	11	1.3
Casuarina plot 1	2.7	147	1 176	33	375	9.4
Casuarina plot 2	0.6	80	949	19	156	3.2
Casuarina plot 3	15	42	209	55	518	11
Doromesmesan Limestone Plot 1	0.6	20	196	35	6.0	2.2
Location 2A	0.9	120	784	21	243	3.1
Location 2B	0.1	5.7	593	7.4	0.1	0.2
Location 2C	0.3	20	701	9.3	15	0.7
Sake River	11	38	164	146	276	5.1
Sake South	4.7	15	529	5.4	773	5.1
Sake West	5.5	26	53	94	8.7	0.8
Uni-Uni plot 1	2.2	38	13	145	12	1.1
Uni-Uni plot 2	1.4	59	1 275	23	326	2.3
Woi Mioseng	1.4	127	1 016	24	167	2.6

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20 **Table 6.** DTPA-extractable elements for organo-mineral soil (0–5 cm layer) samples from each

21 site.

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Location	pH	CEC (cmol+ kg ⁻¹)	K (cmol+ kg ⁻¹)	Ca (cmol+ kg ⁻¹)	Mg (cmol+ kg ⁻¹)	Mn (cmol+ kg ⁻¹)	Na (cmol+ kg ⁻¹)	Ni (cmol+ kg ⁻¹)	%N	%C	%Corg
Blue Hill	7.30	33	0.09	12	50	0.01	0.07	0.12	0.09	1.5	1.6
Bukit Limber plot 1	7.17	4.4	0.01	0.12	3.5	0.00	0.01	0.00	0.08	1.7	1.5
Bukit Limber plot 2	5.31	2.1	0.08	0.03	0.13	0.01	0.04	0.01	0.36	6.0	5.3
Casuarina plot 1	6.49	41	0.40	6.1	31	0.03	0.08	0.12	0.56	8.2	8.1
Casuarina plot 2	6.23	23	0.21	5.7	25	0.14	0.09	0.06	0.37	5.9	6.7
Casuarina plot 3	5.61	29	0.09	1.4	2.0	0.17	0.04	0.23	0.38	4.9	5.8
Doromesmesan Limestone Plot 1	8.16	54	0.19	53	1.9	< LOD	0.12	< LOD	0.56	13	7.6
Location 2A	6.86	38	0.17	13	21	0.02	0.08	0.10	0.55	7.3	6.9
Location 2C	7.00	32	0.09	18	12	0.00	0.06	0.00	0.11	2.0	1.9
Sake River	6.11	13	0.11	5.8	4.2	0.14	0.11	0.29	0.46	5.6	5.2
Sake South	5.92	17	0.15	0.28	13	0.29	0.08	1.4	0.48	5.3	4.8
Sake West	4.76	5.1	0.03	1.1	1.2	0.30	0.02	0.15	0.18	1.9	1.8
Uni-Uni plot 1	4.07	2.0	0.05	0.17	0.07	0.24	0.01	0.01	0.36	4.5	4.2
Uni-Uni plot 2	6.91	39	0.16	3.5	33	0.06	0.06	0.27	0.29	3.8	3.8
Woi Mioseng	6.06	21	0.08	0.28	19	0.00	0.04	0.03	0.36	4.6	5.0

23 < LOD: under the limit of detection

24

25 **Table 7.** pH, exchangeable cations (cmol⁺ kg⁻¹) and nitrogen and carbon content for mineral soil (10–25 cm layer) samples from each site.

26 Abbreviations: Cation Exchange Capacity (CEC), % of soil total nitrogen (%N), % of soil total carbon (%C), % of soil organic carbon (%Corg).

27

Location	pH	CEC (cmol+ kg ⁻¹)	K (cmol+ kg ⁻¹)	Ca (cmol+ kg ⁻¹)	Mg (cmol+ kg ⁻¹)	Mn (cmol+ kg ⁻¹)	Na (cmol+ kg ⁻¹)	Ni (cmol+ kg ⁻¹)	%N	%C	%Corg
Blue Hill	7.10	39	0.18	18	22	0.01	0.06	0.01	0.43	7.9	5.2
Bukit Limber plot 1	6.96	7.5	0.05	0.37	6.5	< LOD	0.01	< LOD	0.23	3.0	2.6
Bukit Limber plot 2	4.65	5.2	1.2	1.8	4.1	0.21	0.57	0.06	1.7	35	33
Casuarina plot 1	6.34	61	0.76	15	40	0.05	0.14	0.08	1.0	23	16
Casuarina plot 2	6.78	45	0.42	12	27	0.06	0.09	0.05	0.53	9.4	9.3
Casuarina plot 3	5.98	28	0.52	20	5.9	0.42	0.20	0.39	0.98	17	17
Doromesmesan Limestone Plot 1	7.41	64	0.35	62	4.6	0.01	0.21	< LOD	0.98	22	16
Location 2A	6.74	24	0.20	20	13	0.01	0.09	0.03	0.60	9.9	8.8
Location 2B	6.90	28	0.01	18	9.8	0.01	0.35	< LOD	0.01	0.42	0.41
Location 2C	8.07	45	0.20	35	14	0.01	0.06	< LOD	0.08	2.0	1.5
Sake River	6.49	17	0.26	9.9	4.4	0.17	0.21	0.26	0.68	11	9.5
Sake South	6.01	20	0.26	2.0	14	0.18	0.08	1.2	0.60	7.6	6.9
Sake West	6.59	8.7	0.07	6.0	1.4	< LOD	0.02	< LOD	0.21	2.7	2.5
Uni-Uni plot 1	5.77	4.3	0.03	2.9	0.38	0.21	0.01	0.01	0.38	6.5	5.8
Uni-Uni plot 2	6.66	21	0.17	5.0	31	0.06	0.04	0.24	0.31	4.2	4.0
Woi Mioseng	6.86	37	0.24	3.7	31	0.03	0.09	0.04	0.63	11	10

28 < LOD: under the limit of detection

29

30 **Table 8.** pH, exchangeable cations (cmol⁺ kg⁻¹) and nitrogen and carbon content for organo-mineral soil (0–5 cm layer) samples from each site.

31 Abbreviations: Cation Exchange Capacity (CEC), % of soil total nitrogen (%N), % of soil total carbon (%C), % of soil organic carbon (%Corg).

32

Sites	Leaves		Mineral soils			Organic soils		
	Hyperaccumulators	Non-hyperaccumulators	Ni-DTPA (mg kg ⁻¹)	Ni-CEC (cmol ⁺ kg ⁻¹)	Ni-T (g kg ⁻¹)	Ni-DTPA (mg kg ⁻¹)	Ni-CEC (cmol ⁺ kg ⁻¹)	Ni-T (g kg ⁻¹)
Blue Hill	n.d	375 (< LOD–2824)	75	0.012	3.5	140	0.001	3.4
Bukit Limber plot 1	851	255 (< LOD–21439)	14	< LOD	4.4	24	< LOD	4.5
Bukit Limber plot 2	n.d	8.7 (< LOD–95)	4.5	0.001	1.5	11	0.006	0.8
Casuarina plot 1	11819 (1808–18636)	454 (< LOD–15904)	335	0.012	2.1	375	0.008	1.7
Casuarina plot 2	10946 (10728–11163)	357 (< LOD–13762)	110	0.006	0.6	156	0.005	0.6
Casuarina plot 3	6395 (1473–11317)	293 (< LOD–2473)	119	0.023	6.4	518	0.039	5.1
Doromesmesan Limestone Plot 1	8.1	n.d	2.4	< LOD	0.3	6.0	< LOD	0.2
Location 2A	15817	14 (< LOD–45)	158	0.010	2.3	243	0.003	2.1
Location 2C	152	4.1 (< LOD–32)	25	< LOD	1.5	15	< LOD	1.2
Sake River	1821 (215–5179)	351 (< LOD–3344)	208	0.029	9.8	276	0.026	8.4
Sake South	3721 (25–22178)	955 (< LOD–15934)	704	0.144	14	773	0.119	12
Sake West	815 (147–1203)	36 (< LOD–182)	17	0.015	8.2	8.7	< LOD	7.8
Uni-Uni plot 1	6871 (986–11141)	587 (< LOD–7191)	4.0	0.001	5.5	12	0.001	5.7
Uni-Uni plot 2	3917 (2825–5014)	409 (< LOD–12814)	267	0.027	4.6	326	0.024	4.9
Woi Mioseng	6030 (1117–10943)	2.8 (< LOD–17)	107	0.003	2.0	167	0.004	1.8

33 < LOD: under the limit of detection

34 n.d.: no data

35

36 **Table 9.** Ni distribution in leaf samples (mg kg^{-1}) and soil samples for each site. Abbreviations: Extractable Ni (Ni-DTPA, mg kg^{-1}), Exchangeable
37 Ni (Ni-CEC, cmol+ kg^{-1}) and Ni total (Ni-T, g kg^{-1}), no data (n.d).
38

Site	Family	Species	Al mg kg ⁻¹
Uni-Uni Plot 2	–	–	14 500
Bukit Limber Plot 1	–	–	1 630
Bukit Limber Plot 1	–	–	3 260
Bukit Limber Plot 2	Cunoniaceae	<i>Schizomeria serrata</i>	4 160
Bukit Limber Plot 2	Rubiaceae	<i>Psychotria</i> sp.	1 510
Bukit Limber Plot 2	Theaceae	<i>Gordonia</i> sp.	5 120
Bukit Limber Plot 2	Lauraceae	<i>Cryptocarya</i> sp.	36 300
Bukit Limber Plot 2	Symplocaceae	<i>Symplocos lucida</i>	12 100
Bukit Limber Plot 2	Melastomataceae	<i>Melastoma</i> sp.	6 740
Bukit Limber Plot 2	Myrtaceae	<i>Syzygium</i> sp.	12 800
Bukit Limber Plot 2	Rubiaceae	<i>Psychotria</i> sp.	18 300
Bukit Limber Plot 2	Symplocaceae	<i>Symplocos maliliensis</i>	46 300
Bukit Limber Plot 2	Symplocaceae	<i>Symplocos henschelii</i>	31 200
Jira Plot 1	–	–	35 000
Jira Plot 1	–	–	17 800

39

40

41 **Table 10.** Aluminium (mg kg⁻¹) hyperaccumulator plant records (identified and unidentified specimens) from the Weda Bay area.

42

Species	Plant part	Ca mg kg ⁻¹	K mg kg ⁻¹	Mg mg kg ⁻¹	Mn mg kg ⁻¹	P mg kg ⁻¹	S mg kg ⁻¹	Zn mg kg ⁻¹	Co mg kg ⁻¹	Ni mg kg ⁻¹
<i>Amyema cuernosensis</i>	leaves	9495	3648	10 559	56	361	761	18	4.0	262
		8211	4619	9525	53	382	706	16	3.9	242
		10 978	2732	11 654	68	341	899	24	6.1	314
		7202	7102	8737	48	536	823	13	3.4	231
	flowers	1205	18 897	3419	28	1801	870	< LOD	< LOD	42
	haustoria	4803	2866	1324	7	186	738	22	< LOD	8.6
	twigs	5966	2740	3843	15	486	518	16	0.04	0.6
	wood	4653	2089	1130	129	217	253	19	16	170
<i>Ficus trachypison</i>	roots	11 459	2365	4742	264	173	380	24	60	621
	leaves	12 356	1576	14 593	74	418	1200	21	< LOD	194
		15 838	1272	18 176	100	330	1114	29	3.8	228
		12 716	2046	15 873	82	477	1126	17	4.0	228
	twigs	7524	2136	4016	16	385	813	18	0.1	2.8
	wood	6698	669	1454	10	105	255	5.1	0.02	0.5

43 < LOD: under the limit of detection

44

45 **Table 11.** Elemental concentrations (mg kg⁻¹) in the mistletoe *Amyema cuernosensis* (Loranthaceae) and the host *Ficus trachypison* (Moraceae).

46