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1 Title: **Stocks and biogeochemical cycling of soil-derived nutrients in an**
2 **ultramafic rain forest in New Caledonia**

3

4 Running Title: **Nutrient Cycling in an ultramafic forest**

5

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26

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37

38 **CONFLICTS OF INTEREST/COMPETING INTERESTS**

39 The authors declare no conflict of interest.

40

41 **ABSTRACT**

42 Ultramafic rain forests in New Caledonia evolved on some of the most nutrient impoverished
43 soils globally and are some of the slowest-growing tropical forests known. This study aimed to
44 determine nutrient stocks and elucidate the biogeochemical cycling of nutrients in a remnant
45 lowland rain forest in southern New Caledonia. Based on an inventory of a 1-ha permanent
46 plot, exhaustive plant tissue sampling was undertaken of all large trees (diameter at breast
47 height ≥ 15 cm) in a 0.25-ha subset of the plot in concert with 100 soil samples. All samples
48 were analyzed for major nutrient concentrations and the results show that most of the
49 magnesium was contained in the soil (96.9%), whereas a large fraction of calcium (46.5%) and
50 phosphorus (16.0%), and the majority the potassium (81.5%) were contained in the standing
51 biomass. This study has shown how tightly these soil-derived nutrients are cycling in this
52 system. Ultimately, this information will be essential for efforts to restore rain forest in New
53 Caledonia, where the biomass (and contained nutrients) has been removed.

54

55 **KEYWORDS**

56 Environmental restoration, New Caledonia, Nutrient Cycling, Potassium, Radiocarbon dating,
57 Rain Forest, Ultramafic.

58 **INTRODUCTION**

59 The biogeochemical cycling of nutrients comprises a broad array of direct and indirect
60 interactions and processes (*e.g.* nutrient uptake and storage, litter production and
61 decomposition) involving microbiome, plant, and abiotic factors such as topography and
62 climate (Hobbie 1992, Foster and Bhatti 2006, Bahram et al. 2018). The complexity of
63 deciphering rain forest nutrient cycling lies in estimating the quantities of nutrients in the
64 various pools and the prevalence of the interconnecting flows (Proctor 1987). These processes
65 occur at different time scales, and ecosystem stability relies on their synchrony, as disturbance
66 of one process, if not compensated, may start a chain reaction causing asynchrony (Myers et al.
67 1994). Simplified nutrient cycling conceptual models use two arbitrary categories, ‘short’ and
68 ‘long’, to describe the processes responsible for mineral turnover in ecosystems (Proctor 1987).
69 Short cycling includes small litterfall and immediate processes occurring during and after
70 rainfall (*e.g.*, stemflow, throughflow). In contrast, long cycling includes tree biomass growth,
71 weathering, leaching, and other soil processes that concomitantly and continuously occur over
72 extended periods (Proctor 1987).

73

74 Nutrients in forests need to be supplied *via* ecosystem enrichment processes and internally
75 recycled to satisfy growth requirements (Wanek et al. 2008). Generally, nutrients escape from
76 ecosystems *via* soil leaching and erosion after incorporation through weathering or atmospheric
77 deposition onto ecosystems that have developed on weathered soils (Chadwick et al. 1999). The
78 nutrient limitations observed in many terrestrial ecosystems (especially nitrogen – N – and
79 phosphorus – P) result from the concomitant occurrence of numerous constraining mechanisms.
80 In the case of P, the primary mechanism leading to the widespread occurrence of nutrient-
81 limited ecosystems is the low concentration found in parent materials (Vitousek 1984, Vitousek
82 and Sanford 1986). Furthermore, a high content of iron (Fe)-oxides naturally occludes P and

83 significantly limits its availability (Vitousek et al. 2010). In New Caledonia, this is especially
84 true for substrates derived from ultramafic rocks that are naturally rich in Fe-oxides
85 (Schwertmann and Latham 1986, Quantin et al. 1997). The storage and partitioning of nutrients
86 in rain forest ecosystems are diverse and complex as they occur over a broad range of substrates
87 (Proctor 1987). For example, a study in New South Wales, Australia, comparing ‘rich’ and
88 ‘poor’ soils showed that specific nutrient utilization varied significantly between localities with
89 lower nutrient availability synonymous with higher nutrient use efficiency (Lambert et al.
90 2016). Nonetheless, little is known about rain forest nutrient flows and nutrient budgets in
91 ultramafic areas because of the complexity and the wide range of mechanisms involved (*e.g.*
92 bedrock weathering, microbial activity) despite the reporting of more and more sophisticated
93 studies (*e.g.* Johnson et al. 2001, Fujii et al. 2011, Nasto et al. 2017).

94
95 The ‘biogeochemical niche’ hypothesis suggests that multiple plant species thrive in the same
96 ecosystem as a result of a balance in nutrient uses obtained through time to limit competition
97 (*e.g.* growth, uptake, soil space – Garten 1978, Peñuelas et al. 2010, 2019, Urbina et al. 2017).
98 According to Ågren and Weih (2012), plant nutrient concentration differences within
99 ecosystems mainly result from the soil elemental availability diversities. The co-occurrence of
100 these factors, especially in slow-growing plant communities, ultimately leads to extremely
101 complex and diverse plant assemblages. It also possibly explains the high elemental
102 concentrations found in certain species compared to the substrate on which they are growing
103 (van Breemen 1995, Fyllas and Troumbis 2009). Slow-growing species are *de facto* adapted by
104 their low nutrient needs, efficient recycling, and uptake mechanisms to nutrient-limited
105 ecosystems (Chapin 1980).

106

107 Ultramafic soils which develop from the weathering of ultramafic rocks cover ~3% of the
108 Earth's surface. Most ultramafic substrates are highly infertile, but ultramafic substrates and
109 especially Ferralsols are among the most constraining soils for plant growth due to the lack of
110 clay minerals, acidic pH, low CEC, major nutrient deficiencies, and high cobalt (Co), chromium
111 (Cr), manganese (Mn) and nickel (Ni) concentrations (van der Ent et al. 2015, Pillon et al. 2020,
112 Echevarria 2021). One of the largest ultramafic terranes (~5500 km²) occurs in New
113 Caledonia – an archipelago ~1500 km east of Australia in the southern tropical zone north of
114 the Tropic of Capricorn (Maurizot et al. 2020). It is renowned for its exceptional biodiversity
115 with ~3300 vascular plant species, of which ~2100 grow on ultramafic substrates including
116 over 180 metal hyperaccumulator species (Isnard et al. 2016; Gei et al. 2020).

117

118 These plants that may accumulate more than 100 times more of a metal than most other
119 metallophytes and represent one of the best examples of plant adaptation to harsh environments
120 (van der Ent et al. 2013). Two highly discernible vegetation types occur on New Caledonian
121 ultramafic soils: various types of rain forests and the maquis (Jaffré 1980). The presence of
122 some families (*e.g.* Myrtaceae, Rubiaceae) or conifers (Gymnosperms) on ultramafic soils
123 results from the occurrence of specific physiological attributes, which include low foliar P and
124 potassium (K) or the ability to cope with an imbalanced calcium (Ca)/magnesium (Mg) quotient
125 or high concentrations of Ni and Mn in the soil (Jaffré 1980).

126

127 The current study aimed to determine the biogeochemical cycling of nutrients and to establish
128 to what degree these nutrients are 'locked up' in living biomass in a New Caledonian ultramafic
129 forest. To that end, exhaustive sampling was undertaken to calculate the amounts of N, P, K,
130 Ca, and Mg in both standing biomass and soil, as well as the topsoil enrichment and the returns

131 from litterfall. Ultimately, this information will help restore rain forests in New Caledonia
132 where clear-felling has taken place.

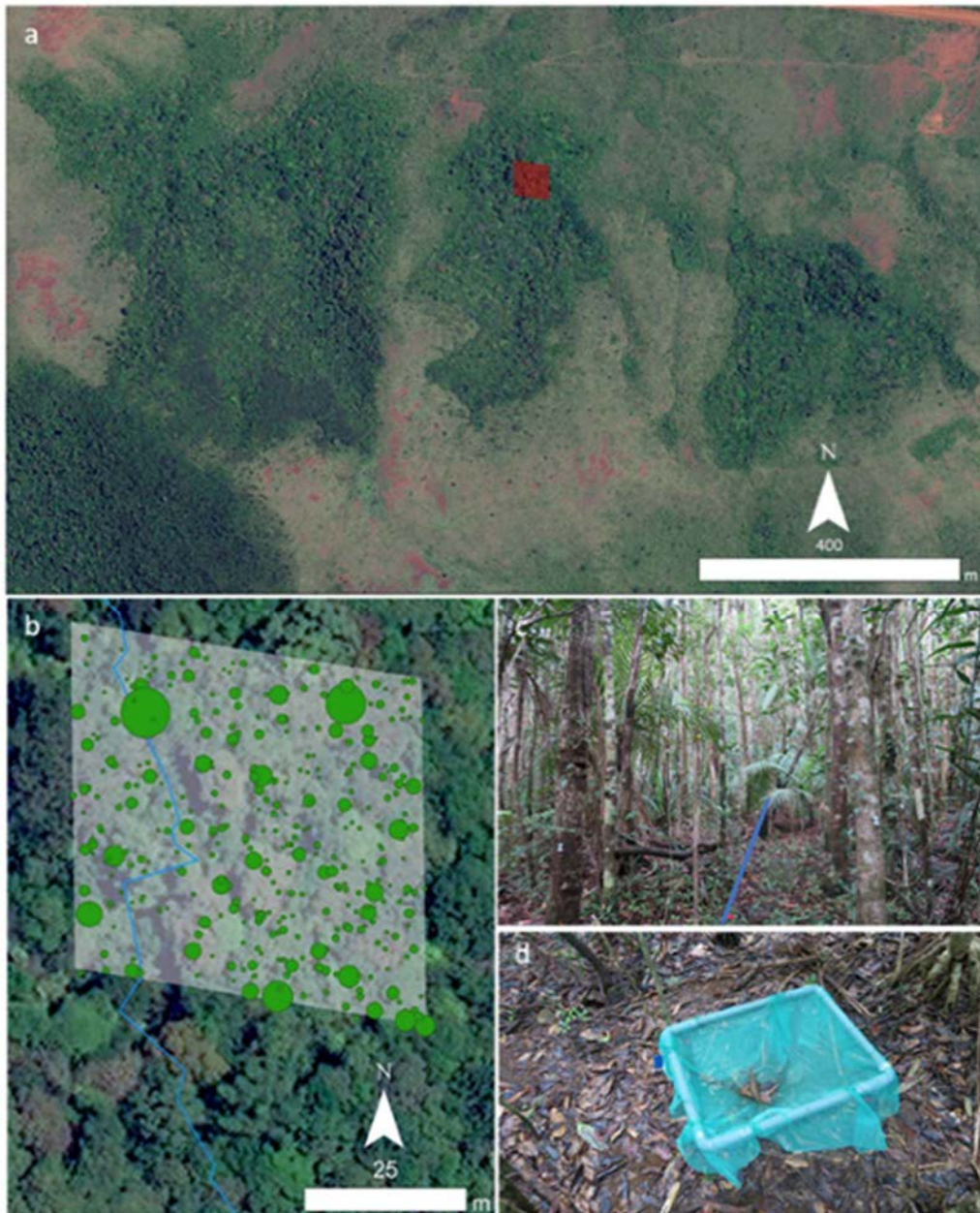
133

134 **MATERIALS AND METHODS**

135

136 *Location and condition of the plot and census of tree flora*

137 The study plot (22° 16'29" S, 166° 54'14" E; ~270 to ~300 a.s.l) was in the Grand Massif
138 du Sud, one of the world's largest ultramafic massifs which dominates the southern part of
139 Grande Terre in New Caledonia (Figure S1). The local rain forest established over harzburgite
140 bedrock (Table S1) that weathered into a Geric Ferralsol (Becquer et al., 2001). The area is in
141 a tropical oceanic zone with an annual rainfall of ~3300 mm. The climate of New Caledonia is
142 divided into 'hot' and 'cool' seasons (Météo France 2020). The hot season
143 (>300 mm precipitation month⁻¹ and mean temperature >28 °C) lasts from January to April and
144 the cool season (<250 mm precipitation month⁻¹ and mean temperature <25 °C) continues from
145 June to September while transition periods occur in May and later from October to December
146 (Météo France 2020). Plot data were obtained from the rain forest plot network NC-PIPPN
147 established across New Caledonia (Ibanez et al. 2013, Birnbaum et al. 2015). The current study
148 was undertaken in a 0.25-ha subplot located in the center of a 1-ha plot (Figure 1). The 0.25-ha
149 plot was subdivided into 100 subplots (5 m × 5 m).



150

151

152 **Figure 1.** Location of the plot and trees in the Plaine de Lac (New Caledonia) and collection

153 protocol. a: Remnant primary lowland rain forest surrounding the plot. b: Close-up image of

154 the plot with all the trees overlaying. Worldview-3 imagery. The size of the filled circles

155 indicates the individual tree diameters, and the blue line indicates the position of the creek. c:

156 Picture of the plot on the first day of collection as the plot was delineated with cords

157 (highlighted in blue). d: Picture of one of the twelve 0.25 m² litterfall traps.

158 *Collection of plant and soil samples*

159 One or two branches (~2 cm diameter) accessible with a long-reach tree pruner (20 m long)
160 were cut off from all trees with a dbh (diameter at breast height) >15 cm and Ni
161 hyperaccumulators with a dbh >10 cm for chemical analysis. Old leaves (first four leaves),
162 young leaves (last four leaves), twigs (last few centimeters), wood/branch (first few
163 centimeters), and the xylem sap (using a vacuum pump – Alexou and Peuke 2013) were
164 collected from each branch (Paul et al. 2021). Twelve litterfall traps (0.25 m²) were set up
165 randomly to collect the litterfall monthly over 12 months (Figure 1d). Soil samples were
166 collected at four different depths in each subplot (0–5 cm, 5–10 cm, 10–15 cm, and 15–20 cm)
167 using a soil core sampler (5 cm diameter).

168

169 *Processing of collected samples*

170 Solid plant samples were oven-dried at 60 °C for 72 h, wood and bark were separated using a
171 sharp box cutter and the bulk litterfall was weighted. All plant materials were subsequently
172 ground to a fine powder using an impact mill, thoroughly homogenized, and weighed to create
173 ~300 mg samples. Xylem sap and latex samples were freeze-dried (-85 °C at <0.003 mbar) for
174 two days. All plant samples were then pre-digested with 7 mL HNO₃ (70%) for 48 h before
175 being digested in a microwave oven (Milestone Start D) at 125 °C for 45 min. Soil samples
176 were air-dried for five days and subsequently sieved through 2 mm screens. Soil pH was
177 measured in a 1:2.5 soil:water slurry after 1-hour equilibration time. Sub-samples (~300 mg)
178 were digested with 2 mL HCl (37%) and 5 mL HNO₃ (70%) in a ColdBlock system at 50%
179 power (CB15S 15 channel system, ColdBlock Technologies Inc) to determine pseudo-total
180 trace element concentrations (Wang et al. 2013). The cation exchange capacity (CEC) and
181 exchangeable cations of the soil (Ca_{ex}, K_{ex}, and Mg_{ex}) were determined by weighing 800 mg of
182 each of the samples into 50 mL tubes to which 40 mL of unbuffered silver thiourea

183 (0.01 M Ag⁺) was added. Tubes were then shaken overnight (16–20 h) in the dark and
184 subsequently centrifuged to collect the clear supernatant liquid (Dohrmann 2006). All samples
185 were diluted if needed using ultrapure water (Millipore 18.2 MΩ cm at 25 °C) before analysis
186 via Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES; Thermo Scientific
187 iCAP 7400 instrument) in radial mode for Ca, K, Mg and P (Material S1). Soils (top 5 cm only),
188 young leaves and litterfall nitrogen was analyzed using a Vario ELcube (Elementar
189 Analysensysteme GmbH).

190

191 *¹⁴C analysis of a large Pycnandra acuminata tree*

192 The age of a large individual of *Pycnandra acuminata* (Sapotaceae) was determined to obtain
193 insight into the age of the forest stand. The sampled core for ¹⁴C dating was collected in March
194 2019 using a Haglöl increment borer from one large *P. acuminata* (dbh ~35 cm). The sample
195 was sent to the NEIF Radiocarbon Laboratory for pre-treatment (Material S2) and subsequently
196 on to the Scottish Universities Environmental Research Centre AMS Laboratory for ¹⁴C dating
197 using an NEC accelerator mass spectrometer.

198

199 *Statistical analyses*

200 Statistical analyses were done using version 1.2.5042 of the Rstudio software (PBC). The
201 Waller-Duncan K-ratio t-test was used when data were both normal and homoscedastic. If one
202 of the assumptions was violated, data were transformed to meet both assumptions. A α level of
203 0.05 was used to define statistical significance for each test. Near neighbor interpolations were
204 carried out with ArcMap software (ESRI), version 10.7.1 (2019-06-27) to create the elemental
205 maps. For all families, the family importance value (FIV) was calculated based on the formula
206 developed by Mori et al. (1983). Additionally, the importance value index (IVI) was used to
207 demonstrate the importance of a species in the plot and was defined as the sum of relative

208 frequency, relative dominance, and relative density (Misra 1968). Total plant biomass was
209 calculated *via* the 7th model proposed by Chave et al. (2014), while plant part masses (*i.e.* leaves,
210 branches, stems) were estimated using ratios determined from the tropical rain forest allometric
211 formula proposed by Yamakura et al. (1986). Wood densities were obtained from external
212 organization databases from the literature (*e.g.* ICRAF Database 2019) or in the NC-PIPPN
213 database (Birnbaum et al. 2015). In the absence of value for a species, wood density was
214 extrapolated from the values known for the genus (Chave et al. 2006). Nutrient stocks in
215 biomass were obtained by multiplying tree plant part biomass by the corresponding plant part
216 concentration. Nitrogen concentrations in wood were calculated using the equation: wood N =
217 $(0.33 \times \text{leaf N}) - 0.15$ developed from Malaysian tropical forest trees (F. Q. Brearley,
218 unpublished). Nutrient stocks in the soil were obtained by multiplying the concentration in each
219 layer (top 20 cm) by the soil's estimated mass in that layer.

220

221 **RESULTS**

222

223 *Forest floristic diversity and physiognomy of the plot*

224 The 0.25-ha plot had 349 trees in total (189 trees over 15 cm dbh) belonging to 35 families, 52
225 genera, and 64 species, corresponding to a Fisher's alpha of 23.0. Only two families (Myrtaceae
226 and Sapotaceae) had more than three species in the plot with 10 and 6 species, respectively.
227 The Myrtaceae and Sapotaceae also had the highest FIV (42.7 and 36.3), making them the most
228 important families in the plot (Table S2). Seven other families had a FIV >10, with the
229 Sapindaceae (25.8) and Bignoniaceae (15.6) having the largest values while the first nine
230 families accounted for >60% of the overall FIV (Result S1). *Storthocalyx chryseus*
231 (Sapindaceae), *Deplanchea speciosa* (Bignoniaceae), and *P. acuminata* were the three most
232 important species according to the IVI and the most abundant in the plot along with

233 *Sparattosyce dioica* (Moraceae), and *Cunonia balansae* (Cunoniaceae) (Table S3 and
234 Result S1).

| | Ca | K | Mg | P | P |
|--------------|---------------------------|-------------------------|------------------------|-----------------------|----------------------|
| Young leaves | 5690 d (513–26 400) | 8390 a (1250–36 900) | 2690 a (792–9380) | 9.50 (4.60–26.4) | 347 a (127–1800) |
| Old leaves | 7510 c (557–36 200) | 4570 b (1140–16 600) | 2660 a (609–9280) | – | 245 b (111–825) |
| Twigs | 13 300 a (1420–65 600) | 7470 a (206–32 300) | 2640 a (457–12 300) | – | 329 a (74.0–1740) |
| Bark | 9860 b (796–57 400) | 4050 c (501–13 100) | 1140 b (378–6250) | – | 133 c (34.6–772) |
| Wood | 2540 e (346–21 000) | 2560 d (355–12 200) | 455 c (95.8–4820) | – | 84.5 d (19.3–713) |
| Xylem sap | 42.7 f (4.86–464) | 108 f (1.19–506) | 20.8 f (1.03–121) | 1.82 f (<LoD–36.1) | |

235

236 **Table 1.** Concentration of Ca, K, Mg and P in plant tissue parts in the Plaine de Lac (New Caledonia). Concentrations (mg kg⁻¹) are summarized
237 as median (minimum-maximum). *Footnote: Medians followed by the same letter are not significantly different at the 5% level according to the*
238 *Waller-Duncan means separation test.*

239 *Concentrations of major nutrients in trees of the plot*

240 Median Ca concentrations varied from 2540 mg Ca kg⁻¹ to 13 300 mg Ca kg⁻¹ across all tissues,
241 being greatest in twigs and was ~42.7 mg kg⁻¹ in xylem sap (Table 1). Of the FIV top 10, the
242 Clusiaceae and Cunoniaceae had the highest Ca concentrations (twigs over 18 000 mg kg⁻¹)
243 while Sapindaceae (*S. chryseus*) had the lowest concentrations (<2000 mg kg⁻¹ in twigs) in the
244 plot (Table S4). Young leaves and twigs were significantly enriched in K (>7000 mg kg⁻¹)
245 compared to other plant parts (Table 1), while Moraceae, Bignoniaceae and Sapindaceae
246 presented, on average, the highest median K concentrations within the prominent families
247 (Table S5). The median Mg concentrations ranged from 455 mg to 2690 mg kg⁻¹ with
248 significantly higher concentrations in the twigs, young leaves, and old leaves (Table 1). Among
249 the main families in the plot, Moraceae had the highest Mg concentrations up to 12 300 mg
250 Mg kg⁻¹ in twigs (Table S6). No significant differences in foliar N concentrations were
251 observed across families nor species (Table S7) with concentrations ranging from 4.8 mg to
252 26.4 mg N g⁻¹. Median P concentrations varied from 84.5 mg to 347 mg P kg⁻¹ in tissues with
253 higher concentrations in young leaves and twigs (> 320 mg P kg⁻¹) while xylem sap
254 concentrations were below the limits of detection (ICP reading below 0.10 mg L⁻¹) for most
255 species (Table 1). Among the main families, Sapindaceae had significantly higher P
256 concentrations than others (Table S7). Calcium was the only element that was found to be
257 strongly and negatively correlated with both IVI and FIV ($p < 0.001$), while no trends could be
258 observed for the other elements.

259

260 *Soil chemistry of the plot*

261 The soil in the plot was slightly acidic (mean pH ~5.7 with a range of 3.85–6.63) and had an
262 identifiable pattern as lower pH values (down to pH 3.85) were found in the southwestern part
263 of the plot (Figure S2 and Table S9). The CEC decreased significantly with depth as higher

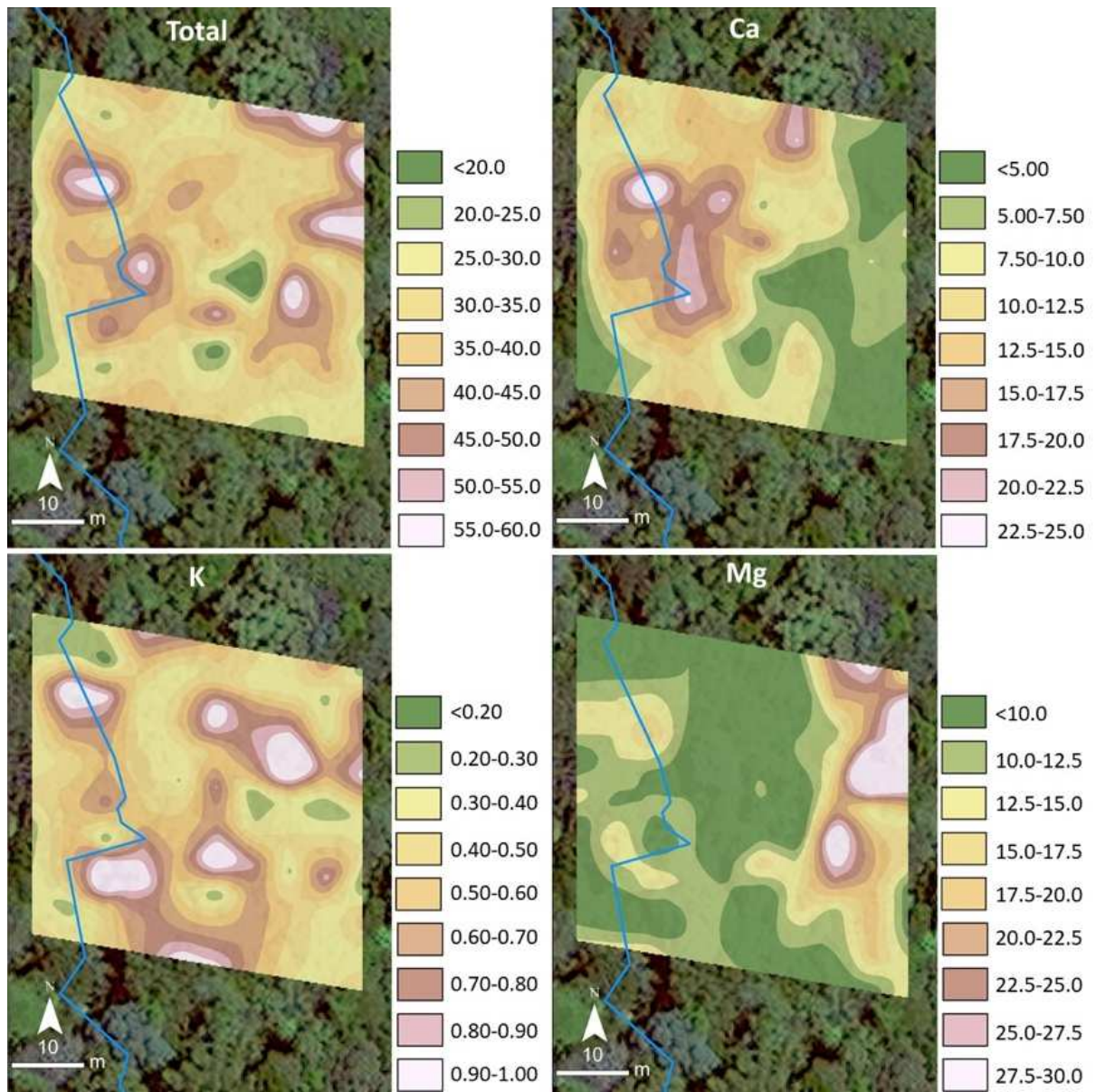
264 values were found in the surface horizon ($\sim 34.5 \text{ cmol}^{(+)} \text{ kg}^{-1}$ vs. $\sim 14.7 \text{ cmol}^{(+)} \text{ kg}^{-1}$ at 20 cm
265 depth) while higher CEC values were observed in the north-eastern part of the plot (Table 2,
266 Figure 2 and S3).

| | Depth (cm) | CEC | Ca | K | Mg | N | P | Ca/Mg |
|---------------------|------------|-----------------------|------------------------|-----------------------|-------------------------|---------------------|---------------------|-----------------------|
| Total | 0–5 | - | 2490 a (558–10 500) | 224 a (60.7–791) | 5780 d (1290–25 400) | 7.60 (2.40–24.2) | 175 b (99.1–253) | - |
| | 5–10 | - | 1190 b (157–5910) | 148 b (43.5–340) | 6860 c (1210–26 600) | - | 175 b (106–247) | - |
| | 10–15 | - | 1100 b (61.8–4810) | 148 c (3.72–459) | 7570 b (1250–35 500) | - | 180 a (86.9–230) | - |
| | 15–20 | - | 686 c (89.3–5670) | 145 b (34.3–551) | 9400 a (1360–37 100) | - | 174 ab (113–302) | - |
| Exchangeable | 0–5 | 34.5 a (12.8–66.8) | 9.11 a (1.00–28.9) | 0.52 a (0.17–1.41) | 10.4 a (5.35–42.9) | - | - | 0.91 a (0.06–3.56) |
| | 5–10 | 19.4 b (5.39–54.9) | 4.08 c (0.17–19.4) | 0.30 b (0.10–1.02) | 7.51 c (2.2–31.4) | - | - | 0.54 b (0.03–3.29) |
| | 10–15 | 20.9 b (4.12–51.5) | 4.31 b (0.48–22.2) | 0.29 b (0.10–0.74) | 7.89 b (2.41–26.1) | - | - | 0.56 b (0.06–3.45) |
| | 15–20 | 14.7 d (0.68–55.0) | 2.00 d (0.06–12.9) | 0.19 c (0.06–1.24) | 6.15 d (2.48–34.5) | - | - | 0.29 c (0.01–2.57) |

267

268 **Table 2.** Soil chemistry from the profiles in the plot in the Plaine de Lac (New Caledonia). Concentrations are summarized as median (minimum-
269 maximum). *Footnote: According to the Waller-Duncan means separation test, medians followed by the same letter are not significantly different*
270 *at the 5% level. All total concentrations are in mg kg⁻¹ while exchangeable concentrations are in cmol⁽⁺⁾ kg⁻¹.*

271 Significant differences in Ca_{ex} and Ca_{tot} were found according to depth and location, but despite
272 an observable pattern with higher values around the creek, no statistical significance was found
273 (Table 2, Figure 2, 3, S4 and S5). The Ca^{2+} component was responsible for 28.3%, 22.9%,
274 21.7%, and 13.2% of the total CEC at 5, 10, 15, and 20 cm depths, respectively (Table S10).
275 Almost half of the plot (44.4%) had a $\text{Ca}_{\text{ex}} > 10.0 \text{ cmol}^{(+)} \text{ kg}^{-1}$ in the topsoil (0-5 cm), while
276 8.7% in the intermediary horizons (10 cm and 15 cm depths) and only a negligible part (0.7%)
277 of the deepest horizon exceeded $10 \text{ cmol}^{(+)} \text{ kg}^{-1}$ (Figure 2 and S4).
278



279

280

281 **Figure 2.** Spatial distribution of CEC and exchangeable cations ($\text{cmol}^{(+)} \text{kg}^{-1}$) in topsoil (0-5

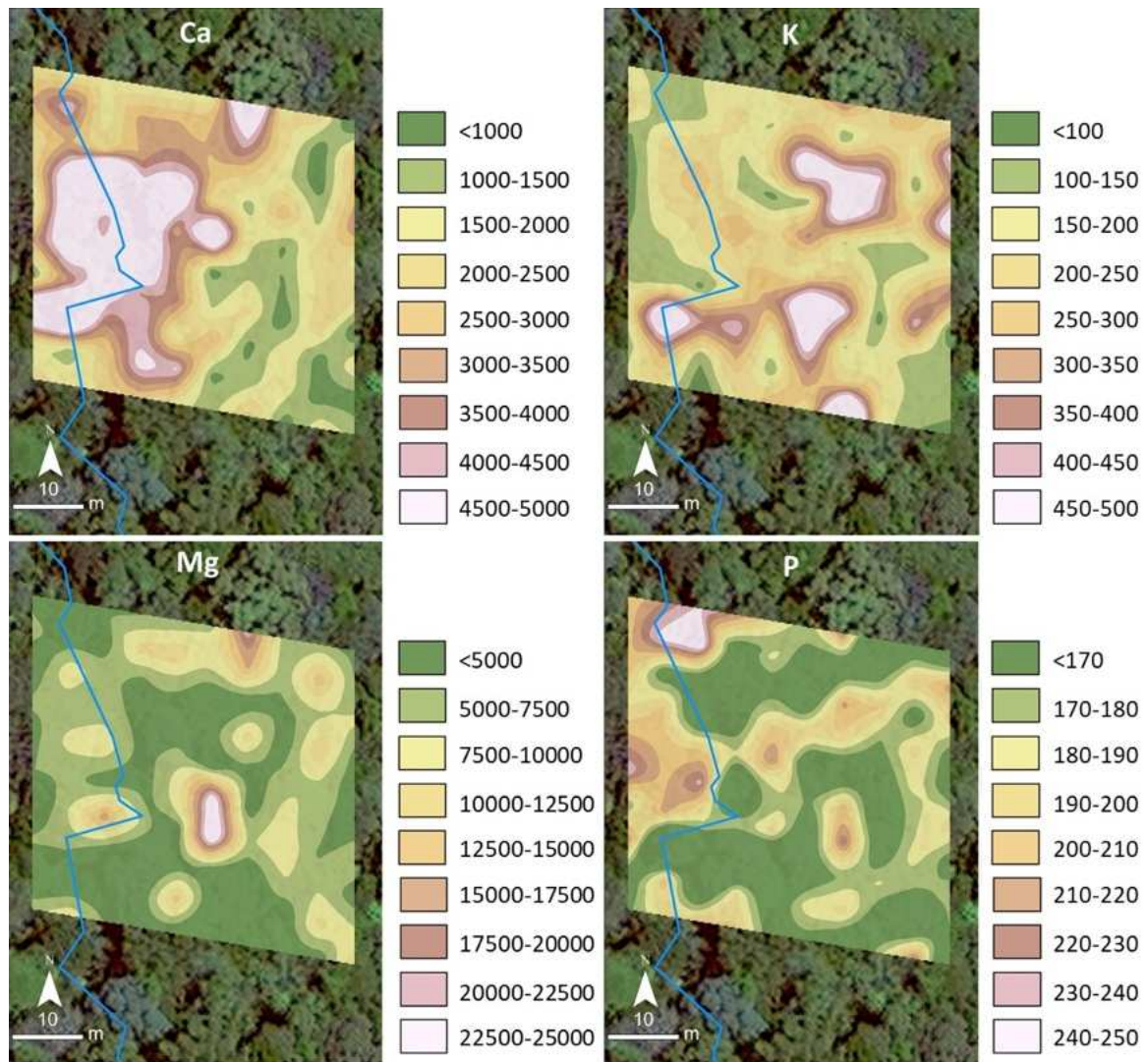
282 cm) across the tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based

283 on one hundred (one per subplot) samples.

284

285 Calcium pseudo-total concentrations mimicked Ca_{ex} trends with higher concentrations in the
286 surface horizon and around the creek (~ 3500 compared to ~ 1000 $mg\ kg^{-1}$ – Table 2, Figure 3
287 and S5). Higher K_{ex} values were found in the surface horizons (~ 0.52 compared to 0.19 $cmol$
288 $^{(+)}\ kg^{-1}$), but the relative importance of K_{ex} to CEC remained stable ($\sim 1.5\%$) through the soil
289 profile while no spatial pattern was observable (Table 2, S10, Figure 2). Pseudo-total
290 concentrations of K mirrored that of K_{ex} with higher concentrations (~ 220 compared to
291 ~ 145 $mg\ kg^{-1}$) in the top layers of the soil (Table 2, Figure 3). The contribution of Mg_{ex} to the
292 CEC increased significantly with depth (median increased from 31.2 to 49.3%) despite
293 significantly lower Mg_{ex} values in the deeper horizons (Table 2 and S6). Higher values were
294 observed in the northeastern part of the plot in the deeper horizons and around the creek for
295 Mg_{ex} while no defined pattern existed for pseudo-total Mg concentrations which significantly
296 increased with depth (Figure 2, 3, S6 and S7).

297



298

299 **Figure 3.** Spatial distribution of pseudo-total concentrations (mg kg⁻¹) in topsoil across the

300 tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based on one hundred

301 (one per subplot) samples.

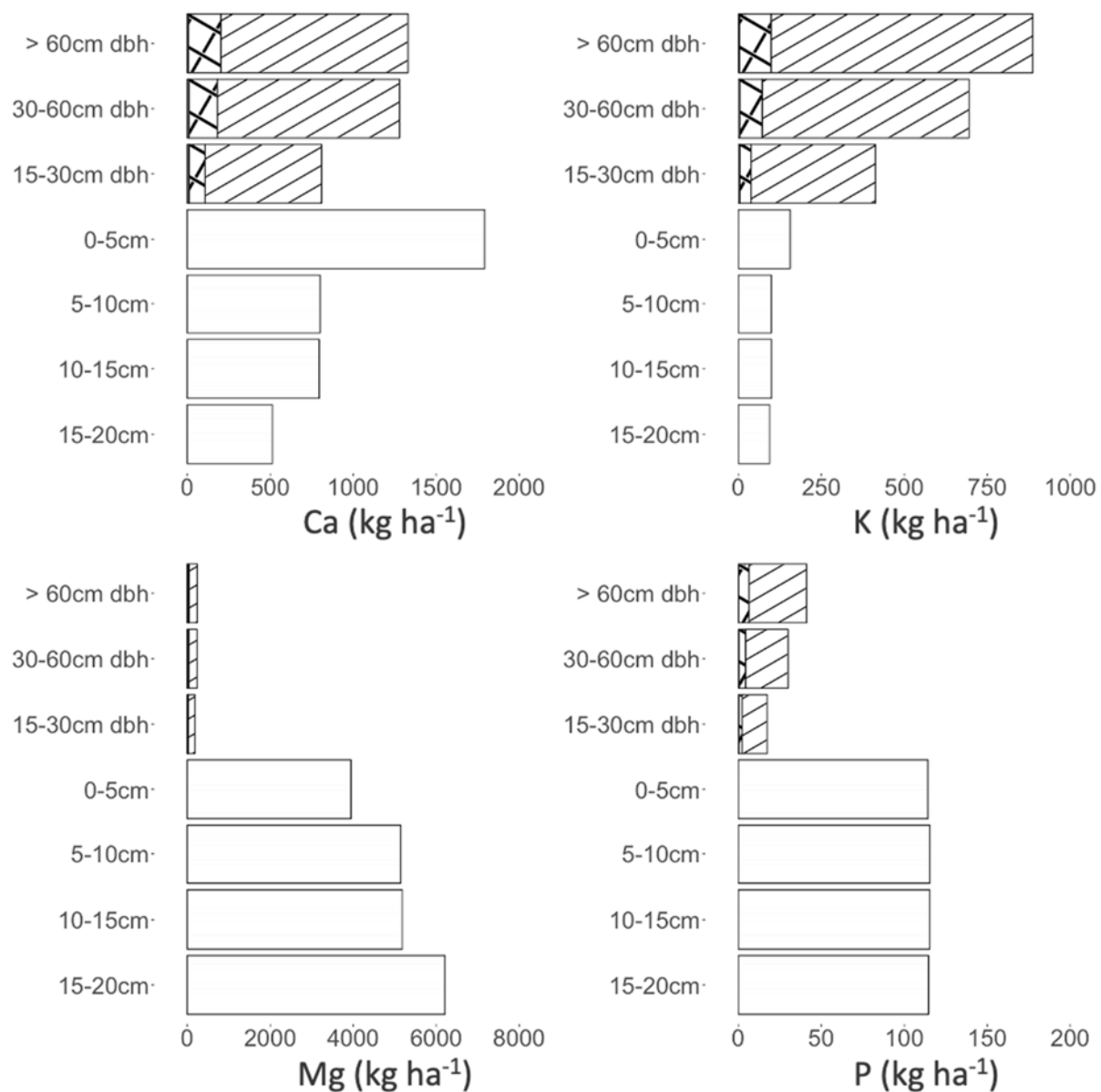
302

303 Across the plot, the Ca/Mg ratio decreased with depth (from ~0.91 to ~0.29) while lower values
304 were found in the eastern half of the plot (Table 2 and Figure S8). Unlike the other major
305 nutrients, P distribution was relatively homogeneous with a slight increase through the soil
306 profile and no identifiable spatial pattern (Table 2, Figure 3). Nitrogen concentrations (top 5
307 cm only) did not show any spatial pattern in the plot with concentrations varying from 2.40 g
308 to 24.2 g N kg⁻¹ (Table 2; spatial data not shown).

309

310 *Quantities of major nutrients in living standing tree biomass and soil*

311 All estimates were calculated based on a biomass of 225 tonnes ha⁻¹, that being ~80% of the
312 total plot biomass (~281 tonnes ha⁻¹ when trees >10 cm were included). The total mass was
313 divided as follows: stems ~83.7%, branches ~14.6%, and leaves (old and young leaves) ~1.6%.
314 Trees from the Myrtaceae and Sapotaceae comprised the greatest quantities of total nutrients in
315 the plot due to their high combined biomass (Table S11). In total, the standing biomass was
316 made up of ~470 kg N ha⁻¹, ~3390 kg Ca ha⁻¹, ~1970 kg K ha⁻¹, ~660 kg Mg ha⁻¹ and ~87.5 kg
317 P ha⁻¹ while the first 20 cm of soil contained ~3900 kg Ca ha⁻¹, 448 kg K ha⁻¹, ~20 500 kg
318 Mg ha⁻¹, and 460 kg P ha⁻¹(Figure 4).



319

320 **Figure 4.** The amounts of calcium, potassium, magnesium, and phosphorus in the above-
 321 ground vegetation by components and soils in the tropical forest plot in the Plaine des Lacs,
 322 New Caledonia. Stem: thin oblique lines, Branches: grid, Leaves: circles, Soil: blank.

323

324 Therefore, K was the only nutrient that was predominantly contained in the standing biomass
325 (~81.5% of total K in the system). About half of the Ca was contained in the standing biomass
326 (~46.5%), while Mg and P were primarily found in the soil (with just ~3.1% and ~16.0% in the
327 standing biomass).

328

329 *Leaf litterfall and nutrients chemistry*

330 During the one-year study period, around 6.1 tonnes ha⁻¹ of litterfall was recorded, depositing
331 approximately ~47 kg ha⁻¹ of N, ~80 kg ha⁻¹ of Ca, ~11 kg ha⁻¹ of K, ~17 kg ha⁻¹ of Mg, and
332 ~700 g ha⁻¹ of P (Table 3).

333

| Month | Mass | N | Ca | K | Mg | P |
|-------------------------------|-----------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| <i>Feb 18</i> | 1720 (714–4880) a | 13.1 (5.29–38.6) | 12.7 (2.87–27.5) | 1.32 (0.45–3.35) | 2.88 (1.28–6.84) | 0.18 (0.09–0.37) |
| <i>Mar 18</i> | 435 (0–806) abc | 3.02 (0–6.26) | 5.61 (1.95–11.3) | 0.66 (0.20–1.82) | 1.09 (0.55–2.04) | 0.05 (0.03–0.12) |
| <i>April 18</i> | 238 (130–419) c | 1.47 (0–3.05) | 2.77 (0.65–7.25) | 0.53 (0–1.37) | 0.62 (0.25–1.2) | 0.03 (0.01–0.05) |
| <i>May 18</i> | 395 (0–1080) c | 2.47 (0–8.44) | 5.26 (0–14.5) | 0.88 (0–3.98) | 0.98 (0–2.59) | 0.04 (0–0.10) |
| <i>Jun 18</i> | 93.0 (0–241) d | 0.71 (0–2.09) | 1.34 (0–5.32) | 0.29 (0–1.63) | 0.29 (0–0.87) | 0.01 (0–0.06) |
| <i>Jul/Aug 18[†]</i> | 398 (0–1300) c | 3.13 (0–8.44) | 4.65 (0–11.7) | 0.53 (0–1.59) | 1.05 (0–2.81) | 0.06 (0–0.20) |
| <i>Sept 18</i> | 533 (0–1230) bc | 3.54 (0–8.15) | 7.27 (0–17.1) | 1.21 (0–2.49) | 1.76 (0–5.20) | 0.07 (0–0.18) |
| <i>Oct 18</i> | 916 (0–1480) abc | 6.84 (0–13.1) | 10.3 (0–16.9) | 2.48 (0–5.12) | 2.73 (0–4.52) | 0.11 (0–0.17) |
| <i>Nov/Dec 18[†]</i> | 2250 (924–8060) ab | 18.3 (6.84–79.8) | 29.9 (10.3–118) | 3.36 (1.04–10.1) | 6.63 (2.99–27.3) | 0.25 (0.06–0.90) |
| <i>Jan/Feb 19[†]</i> | 830 (0–2720) bc | 7.60 (0–46.5) | 11.4 (0–44.2) | 0.75 (0–1.89) | 2.02 (0–4.89) | 0.11 (0–0.37) |
| <i>Total</i> | 6090 | 47.1 | 78.5 | 10.7 | 17.2 | 0.73 |

334

335 **Table 3.** Total quantities (kg ha⁻¹) of nutrients returning to the soil via litterfall per month over a one-year period in the Plaine de Lac (New

336 Caledonia). *Footnote: Means followed by the same letter are not significantly different at the 5% level according to the Waller-Duncan means*

337 *separation test. [†] values are for two months.*

338 The quantity of litterfall significantly differed depending on the season (Table 3). The greatest
339 quantities were collected in the two months during the ‘hot’ season, whereas the lowest
340 quantities of litterfall were collected during the April to August period, corresponding to the
341 ‘cooler’ season (Table 3).

342

343 *¹⁴C dating of a Pycnandra acuminata tree*

344 The ¹⁴C analysis (SUERC-95134) analyses presented uncertainties because of ¹⁴C cosmogenic
345 variations (AD 1700–1950 plateau) but it was determined that the sample was at least ~224
346 years old (or up to ~360 years), suggesting a growth rate between 0.9 mm and 1.5 mm year⁻¹.

347

348

349 **DISCUSSION**

350 Ultramafic soils exert selective edaphic pressures as these soils are naturally deficient in two
351 (K and P) of the main nutrients that limit primary production (Brooks 1987, Proctor 2003).
352 Furthermore, these soils have highly imbalanced Ca/Mg quotients, which are toxic to plant
353 species that have not developed adaptations (Echevarria 2021). Calcium was the only element
354 correlated with both family and species importance index, suggesting that a low physiological
355 requirement for Ca gives these species a competitive advantage in this ultramafic system. Other
356 evolutionary adaptations may have conferred certain species competitive advantages, such as
357 in the Ni hyperaccumulator *P. acuminata* (Sapotaceae), a plant species with 23 individuals in
358 the plot, which, by virtue of containing a latex with up to 250 000 mg Ni kg⁻¹, is ostensibly
359 protected from herbivory and developed allopathic functions (Jaffré et al. 1976, 2018). A
360 companion study focused on the biogeochemical cycling of trace elements and the influence of
361 this tree species in the system and revealed, *via* Ni stable isotope analysis, the biotic origins of
362 the Ni present in the soil upper layers highlighting extensive biogenic Ni cycling (Paul et al.
363 2021).

364
365 Although calculation of the nutrients in the biomass may be underestimated (branch nutrient
366 content may not sufficiently reflect the stem nutrient concentrations while stem radial
367 differences may also occur), more than 80% of K was contained in the standing biomass of the
368 forest system feeding the debate around the nature of nutrient limitations in tropical rain forest
369 soils (Meerts 2002, Brearley 2005). Most tropical soils are typically deficient in P
370 (Vitousek 1984; Vitousek and Sanford 1986; Rao et al. 1999), but K is one of the most deficient
371 elements for plants growing on ultramafic soils as shown in the plot (Brooks 1987;
372 Meerts 2002). The total (~200 mg K kg⁻¹) and exchangeable (~0.2 to ~0.5 cmol⁽⁺⁾ kg⁻¹) K
373 concentrations in the plot are in the typical range for many tropical ultramafic soils (Table 2).

374 However, the soil concentration gradient indicated that K predominantly originated from
375 atmospheric deposition, throughfall and litterfall, as might be expected for an extremely
376 weathered soil where most K has been leached (Bruijnzeel 1989; Galey et al. 2017). Although
377 K is highly mobile, it is assumed that a rapid reuptake of K returned to the soil by plant roots
378 and a high resorption efficiency of K contribute to the ‘tight’ cycling of this element (Chadwick
379 et al. 1999; Maillard et al. 2015, Galey et al. 2017). Atmospheric K inputs in the plot are
380 assumed to be of the same order (~ 2 and ~ 20 kg ha⁻¹ year⁻¹) as litterfall inputs
381 (Bruijnzeel 1989). In humid tropical systems, Ca, K and Mg atmospheric inputs are typically
382 similar, while atmospheric P inputs tend to be relatively low (Bruijnzeel 1989). Due to logistical
383 difficulties, the nutrient soil inputs *via* stemflow and throughflow were not assessed in this
384 study despite their potential significance as highlighted in a Bornean ultramafic rain forest
385 ecosystem in which both processes were responsible for 53%, 96%, 81% and 70% of Ca, K,
386 Mg and P soil inputs respectively (Tisserand et al. 2021).

387

388 The absence of a P soil gradient in the plot indicates fast recycling of available P provided by
389 the litterfall decomposition which supplies ~ 730 g P ha⁻¹ year⁻¹ to this system (Table 2).
390 However, the availability of soil P was not determined in this study but the nature of the local
391 soil (*i.e.* strongly weathered and comprised mainly of Aluminum (Al) and Fe-oxides) suggests
392 that a large part of the total P is occluded and therefore unavailable for uptake by plants (Dieter
393 et al. 2010). The solubilization or desorption of poorly available PO₄³⁻ by the soil microbiome
394 may also be important (Oberson and Joner 2005).

395

396 Nitrogen did not show any pattern in the plot as no species differences nor soil spatial trends
397 could be observed (Table S8) while the quantity of N returned to the soil via litterfall was well
398 within the range generally observed for tropical forests (Vitousek 1984). Although ultramafic

399 soils have low concentrations of N, both observations suggest that N is not limiting (similarly
400 to most non-ultramafic tropical environments) unlike K and most likely P (Vitousek 1984;
401 Brearley 2005).

402

403 Calcium and Mg are not limiting in the plot, but the low Ca/Mg quotient in the plot, especially
404 in the deeper soil layers (0.29) poses edaphic stresses to plants (Table 2). The difference in
405 origins and biogeochemical cycling of these elements become clear when Ca_{ex} and Mg_{ex} values
406 are normalized to the CEC. The relative Mg_{ex} values increase with depth (31.2% to 49.3%),
407 while, in contrast, relative Ca_{ex} values decrease (28.3% to 13.2%). This fact alone suggests a
408 difference in the origin of both elements as Ca is retained in the topsoil horizon and Mg leaches
409 down the soil profile because of different degrees of uptake. The greater Ca_{ex} and Mg_{ex} in the
410 surface horizon of the creek area may indicate that both elements are removed from the system
411 due to runoff (Figure 2, S4 and S6), despite organic matter retention (van der Heijden et al.
412 2014). The litterfall was enriched in Ca, which can be explained by the mobility of Mg in plants
413 (e.g. active redistribution from old leaves to young leaves) and Ca precipitation to form deposits
414 providing structural support for cell walls (Demarty et al. 1984).

415

416 Abiotic and biotic processes continuously (and simultaneously) occur and are responsible for
417 nutrient mobility across ecosystems (e.g. uptake and storage in the vegetation, litter production,
418 and decomposition or weathering; Proctor 1987). Although roots play an essential role in many
419 of the fundamental functions of a plant from acquiring nutrients to providing anchorage, most
420 studies to date, including ours, focused on above-ground processes due to the challenging nature
421 of root sampling (Cusack et al. 2021). Hence, despite the undeniable connections between
422 above and below-ground processes, nutrient cycling research including the latter compartment
423 are extremely scarce especially in tropical ecosystems (Vitousek and Sanford 1986, Johnson

424 and Turner 2019). Furthermore, the processes occurring belowground are not only extremely
425 complex and specific but also poorly predictable because of – but not only – the numerous
426 methodological problems still existing nowadays (Vogt et al., 1996; Freschet et al. 2021).
427 Nevertheless, few trends have been observed across the world in nutrient-limited ecosystems
428 including shallow and dense rooting systems adapted to capture nutrients rapidly from litterfall
429 (observed in the plot through indirect observations) or lower shoot:root nutrient ratios (Vitousek
430 and Sanford 1986, Foster and Bhatti 2006, Lambers et al. 2008, Ge et al. 2013, Wurzbürger and
431 Wright 2015). Both suggest a great contribution of the belowground compartment in tropical
432 forests nutrient cycling especially in low-fertility soils but processes occurring in ultramafic are
433 both chemically and physically diverse (Brearley, 2005; Echevarria, 2021).

434

435 Based on the values of nutrients contained in the biomass (Table S11), the total removal of
436 biomass through logging would empty most stocks of nutrients essential for the existence forest
437 systems. In the plot, it would remove around two tonnes ha⁻¹ of the most limiting element (K –
438 Figure 4, Table S11). Future studies should focus on measuring the yearly biomass increments
439 to determine the quantities of each element taken up by plants annually. Nonetheless, it would
440 probably correspond to several centuries of atmospheric deposition. Moreover, clear-felling
441 results in major soil runoff and erosion, which further drastically increases nutrient losses in
442 this ecosystem (Bormann et al. 1968), which would hamper efforts to re-establish forest once
443 cleared. Furthermore, these forests are typically slow growing, as the radiocarbon dating of a
444 large *P. acuminata* in this study demonstrates. *Agathis ovata* (Araucariaceae) occurring on
445 ultramafic soils in the plot area has demonstrated an even slower mean growth rate of 0.5-mm
446 year⁻¹, meaning that trees with a diameter of 30 cm are at least 700 years old (Enright et al.
447 2003).

448

449 This study focused on a rain forest developed over millennia on exceptionally nutrient-poor
450 ultramafic soils, with the results showing how major soil-derived nutrients are cycled in this
451 system. New Caledonia is a biodiversity hotspot of global significance, but its forests are highly
452 threatened, with only 17.5% of the natural vegetation remaining (Sloan et al. 2014). Of 1160
453 plant species evaluated, 117 species are now critically endangered and ten likely extinct
454 (Bouchet et al. 1995, RLA-NC 2019). Land clearance, bush fires, and mining activities are the
455 leading causes of the New Caledonian vegetation cover disappearance (RLA-NC 2019) and
456 significantly impact rain forest on ultramafic soils (Ibanez et al. 2018).

457

458 Although the sampling in this study was extensive, the high complexity of the ecosystem
459 necessitates more detailed measurements collected over a longer period focusing on roots but
460 also tree growth rates and nutrient inputs and outputs to advance a fuller mechanistic
461 understanding of nutrient fluxes in the New Caledonian ultramafic rain forest ecosystems.

462

463

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