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Title: Stocks and biogeochemical cycling of soil-derived nutrients in an 1 ultramafic rain forest in New Caledonia 2 3 4 Running Title: Nutrient Cycling in an ultramafic forest 5 Adrian L. D. Paul¹, Sandrine Isnard^{2,3}, Francis Q. Brearley⁴, Guillaume Echevarria⁵, Alan J. 6 7 M. Baker^{1,5,6}, Peter D. Erskine¹, Antony van der Ent *^{1,5} 8 9 ¹Centre for Mined Land Rehabilitation, Sustainable Minerals Institute, The University of 10 Queensland, Brisbane, QLD 4072, Australia. 11 12 ²AMAP, Université Montpellier, IRD, CIRAD, CNRS, INRAE, Montpellier, France. 13 14 ³AMAP, IRD, Herbier de Nouvelle-Calédonie, Nouméa, Nouvelle Calédonie. 15 ⁴Department of Natural Sciences, Manchester Metropolitan University, Chester Street, 16 17 Manchester, M1 5GD, UK. 18 19 ⁵Laboratoire Sols et Environnement, Université de Lorraine-INRAE, Vandœuvre-lès-Nancy, 20 UMR 1120, France. 21 ⁶School of BioSciences, The University of Melbourne, Parkville, VIC 3010, Australia 22 23 *Corresponding author: a.vanderent@uq.edu.au 24 25 26

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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 soils globally and are some of the slowest-growing tropical forests known. This study aimed to 43 44 determine nutrient stocks and elucidate the biogeochemical cycling of nutrients in a remnant lowland rain forest in southern New Caledonia. Based on an inventory of a 1-ha permanent 45 46 plot, exhaustive plant tissue sampling was undertaken of all large trees (diameter at breast 47 height \geq 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 interactions and processes (e.g. nutrient uptake and storage, litter production and 60 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 'long', to describe the processes responsible for mineral turnover in ecosystems (Proctor 1987). 68 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 (Schwertmann and Latham 1986, Quantin et al. 1997). The storage and partitioning of nutrients 85 86 in rain forest ecosystems are diverse and complex as they occur over a broad range of substrates (Proctor 1987). For example, a study in New South Wales, Australia, comparing 'rich' and 87 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 $\sim 3\%$ 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, Echevarria 2021). One of the largest ultramafic terranes (~5500 km²) occurs in New 112 113 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

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

133

134 MATERIALS AND METHODS

135

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

The study plot (22° 16'29" S, 166° 54'14" E; ~270 to ~300 a.s.l) was in the Grand Massif 137 138 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 'hot' and 'cool' seasons (Météo France 2020). The hot season divided into (>300 mm precipitation month⁻¹ and mean temperature >28 °C) lasts from January to April and 143 the cool season (<250 mm precipitation month⁻¹ and mean temperature <25 °C) continues from 144 145 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 was undertaken in a 0.25-ha subplot located in the center of a 1-ha plot (Figure 1). The 0.25-ha 148 149 plot was subdivided into 100 subplots ($5 \text{ m} \times 5 \text{ m}$).



Figure 1. Location of the plot and trees in the Plaine de Lac (New Caledonia) and collection
protocol. a: Remnant primary lowland rain forest surrounding the plot. b: Close-up image of
the plot with all the trees overlaying. Worldview-3 imagery. The size of the filled circles
indicates the individual tree diameters, and the blue line indicates the position of the creek. c:
Picture of the plot on the first day of collection as the plot was delineated with cords
(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 collected from each branch (Paul et al. 2021). Twelve litterfall traps (0.25 m²) were set up 164 165 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 (Caex, Kex, and Mgex) were determined by weighing 800 mg of each of the samples into 50 mL tubes to which 40 mL of unbuffered silver thiourea 182

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 M Ω 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 Haglöf 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 demonstrate the importance of a species in the plot and was defined as the sum of relative 207

frequency, relative dominance, and relative density (Misra 1968). Total plant biomass was 208 calculated via the 7th model proposed by Chave et al. (2014), while plant part masses (*i.e.* leaves, 209 210 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 x 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 important species according to the IVI and the most abundant in the plot along with 232

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

	Ca	K	Mg	Р	Р
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)< td=""><td></td></lod-36.1)<>	

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
as median (minimum-maximum). *Footnote: Medians followed by the same letter are not significantly different at the 5% level according to the Waller-Duncan means separation test.*

239 Concentrations of major nutrients in trees of the plot

Median Ca concentrations varied from 2540 mg Ca kg⁻¹ to 13 300 mg Ca kg⁻¹ across all tissues, 240 being greatest in twigs and was ~42.7 mg kg⁻¹ in xylem sap (Table 1). Of the FIV top 10, the 241 Clusiaceae and Cunoniaceae had the highest Ca concentrations (twigs over 18 000 mg kg⁻¹) 242 while Sapindaceae (S. chryseus) had the lowest concentrations (<2000 mg kg⁻¹ in twigs) in the 243 plot (Table S4). Young leaves and twigs were significantly enriched in K (>7000 mg kg⁻¹) 244 245 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 (Table S5). The median Mg concentrations ranged from 455 mg to 2690 mg kg⁻¹ with 247 248 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 Mg kg⁻¹ in twigs (Table S6). No significant differences in foliar N concentrations were 250 251 observed across families nor species (Table S7) with concentrations ranging from 4.8 mg to 26.4 mg N g⁻¹. Median P concentrations varied from 84.5 mg to 347 mg P kg⁻¹ in tissues with 252 higher concentrations in young leaves and twigs (> 320 mg P kg⁻¹) while xylem sap 253 concentrations were below the limits of detection (ICP reading below 0.10 mg L⁻¹) for most 254 255 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

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

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

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

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

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
- 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 $Ca_{ex} > 10.0 \text{ cmol}^{(+)} \text{ kg}^{-1}$ in the topsoil (0-5 cm), while
- 8.7% in the intermediary horizons (10 cm and 15 cm depths) and only a negligible part (0.7%)
- of the deepest horizon exceeded 10 cmol $^{(+)}$ kg⁻¹ (Figure 2 and S4).



Figure 2. Spatial distribution of CEC and exchangeable cations (cmol⁽⁺⁾kg⁻¹) in topsoil (0-5
cm) across the tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based
on one hundred (one per subplot) samples.

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



Figure 3. Spatial distribution of pseudo-total concentrations (mg kg⁻¹) in topsoil across the
 tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based on one hundred
 (one per subplot) samples.

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

All estimates were calculated based on a biomass of 225 tonnes ha⁻¹, that being ~80% of the 311 total plot biomass (~281 tonnes ha⁻¹ when trees >10 cm were included). The total mass was 312 313 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 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 316 317 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).



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

- Therefore, K was the only nutrient that was predominantly contained in the standing biomass (~81.5% of total K in the system). About half of the Ca was contained in the standing biomass (~46.5%), while Mg and P were primarily found in the soil (with just ~3.1% and ~16.0% in the 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
- 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 \sim 700 g ha⁻¹ of P (Table 3).

Month	Mass	Ν	Ca	K	Mg	Р
Ech 19	1720	13.1	12.7	1.32	2.88	0.18
<i>F eb 1</i> 8	(714–4880) a	(5.29–38.6)	(2.87–27.5)	(0.45 - 3.35)	(1.28-6.84)	(0.09–0.37)
Man 19	435	3.02	5.61	0.66	1.09	0.05
Mar 10	(0-806) abc	(0-6.26)	(1.95–11.3)	(0.20 - 1.82)	(0.55 - 2.04)	(0.03–0.12)
April 18	238	1.47	2.77	0.53	0.62	0.03
April 18	(130–419) c	(0-3.05)	(0.65 - 7.25)	(0–1.37)	(0.25 - 1.2)	(0.01–0.05)
M 19	395	2.47	5.26	0.88	0.98	0.04
May 18	(0–1080) c	(0-8.44)	(0–14.5)	(0-3.98)	(0-2.59)	(0-0.10)
Ium 19	93.0	0.71	1.34	0.29	0.29	0.01
Jun 10	(0–241) d	(0-2.09)	(0-5.32)	(0–1.63)	(0-0.87)	(0-0.06)
Int/Ana 19t	398	3.13	4.65	0.53	1.05	0.06
Jul/Aug 10	(0–1300) c	(0-8.44)	(0–11.7)	(0–1.59)	(0-2.81)	(0-0.20)
C	533	3.54	7.27	1.21	1.76	0.07
Sept 18	(0–1230) bc	(0-8.15)	(0–17.1)	(0-2.49)	(0-5.20)	(0-0.18)
Oct 18	916	6.84	10.3	2.48	2.73	0.11
	(0–1480) abc	(0–13.1)	(0–16.9)	(0-5.12)	(0-4.52)	(0-0.17)
Nov/Dec 18^{\dagger}	2250	18.3	29.9	3.36	6.63	0.25
	(924–8060) ab	(6.84–79.8)	(10.3–118)	(1.04-10.1)	(2.99-27.3)	(0.06 - 0.90)
Jan/Feb 19 [†]	830	7.60	11.4	0.75	2.02	0.11
	(0–2720) bc	(0-46.5)	(0-44.2)	(0–1.89)	(0-4.89)	(0-0.37)
Total	6090	471	78.5	10.7	17.2	0.73

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.

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

- years old (or up to \sim 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 the plot, which, by virtue of containing a latex with up to 250 000 mg Ni kg⁻¹, is ostensibly 358 359 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; Meerts 2002). The total (~200 mg K kg⁻¹) and exchangeable (~0.2 to ~0.5 cmol $^{(+)}$ kg⁻¹) K 372 concentrations in the plot are in the typical range for many tropical ultramafic soils (Table 2). 373

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 assumed to be of the same order (~ 2 and $\sim 20 \text{ kg ha}^{-1}$ year⁻¹) as litterfall inputs 380 381 (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

The absence of a P soil gradient in the plot indicates fast recycling of available P provided by the litterfall decomposition which supplies ~730 g P ha⁻¹ year⁻¹ to this system (Table 2). However, the availability of soil P was not determined in this study but the nature of the local soil (*i.e.* strongly weathered and comprised mainly of Aluminum (Al) and Fe-oxides) suggests that a large part of the total P is occluded and therefore unavailable for uptake by plants (Dieter et al. 2010). The solubilization or desorption of poorly available PO_4^{3-} by the soil microbiome may also be important (Oberson and Joner 2005).

395

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

soils have low concentrations of N, both observations suggest that N is not limiting (similarly
to most non-ultramafic tropical environments) unlike K and most likely P (Vitousek 1984;
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 Caex and Mgex values 406 are normalized to the CEC. The relative Mgex values increase with depth (31.2% to 49.3%), 407 while, in contrast, relative Caex 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 Caex and Mgex 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 methodological problems still existing nowadays (Vogt et al., 1996; Freschet et al. 2021). 426 427 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, Wurzburger 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 systems. In the plot, it would remove around two tonnes ha⁻¹ of the most limiting element (K - K)437 438 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).

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.

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