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SPECIAL FEATURE

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Leaf elemental composition of species growing on contrasting soils in two adjacent rainforests: Serpentinized ultramafic versus volcano-sedimentary rock

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Abstract

The flora of New Caledonia is renowned as one of the world's most significant biodiversity hotpots. The contrasting soil conditions that characterize this small archipelago profoundly influence species local diversity and distribution. Because the difference between soil chemistry is likely to cause variation in leaf elemental composition, we wanted to test how different soil properties affect plant community and leaf elemental concentration. We focused on two adjacent forests, of similar physiognomy, growing on serpentinite (ultramafic rock), and on volcano-sedimentary rock. Both soils strongly differed in their pH, cation exchange capacity, and element concentration (Al, Mn, and Ni). The two adjacent forests have a diverse endemic flora and share a relatively high proportion of species (35%–42%). The tree composition differs more than the total vascular flora. Leaf element concentrations of 30 tree species that grow on both soil types, as well as the corresponding soil–plant-available nutrients, were analyzed. Leaf element concentrations indicated N, P, K, and Ca deficiency. Despite higher plant-available Mn concentration in ultramafic soil than volcano-sedimentary soil, leaf Mn concentrations were significantly higher for plants growing on volcano-sedimentary soil. Leaf Ni concentrations were higher on ultramafic soil and Al concentration was higher on volcano-sedimentary soil. Major differences in leaf elemental concentration were for micronutrients (metals) while macronutrients varied in much lower proportion between the two soil types, suggesting a tight regulation of macronutrients compared to micronutrients.

KEYWORDS

leaf elemental composition, metal, New Caledonia, rain forest, ultramafic

1 | INTRODUCTION

New Caledonia is a small archipelago (~19,000 km^2) located in the southwest Pacific (20°–23° S, 164°–167° E) that is renowned for its diverse, endemic flora (Isnard & Jaffré, 2024; Morat et al., 2012; Pillon et al., 2017). The climate, topography, and diversity of ultramafic (UM) soils of New Caledonia have greatly influenced the evolution and diversity of the endemic flora (Isnard et al., 2016; Pillon et al., 2021). Rainforests cover around 20%–30% of the archipelago's surface area and are home to more than 60% of the vascular plant species on the archipelago. About 90% of the plant species within the rainforest are endemic (Ibanez et al., 2017; Morat, 1993).

Most rainforests occur on two rock formations on the Grande Terre including (1) UM (1200 km^2) and (2) volcano-sedimentary (VS, 1800 km^2) (Isnard et al., 2016). The floristic richness is equivalent on both substrates (ca. 1200 species of vascular plants) (Isnard et al., 2016), whereas the floristic composition differs markedly between the two substrates (Ibanez et al., 2014; Jaffré et al., 1997). Forest degradation on the two different rock types results in different vegetation trajectories. Disturbed forests on VS substrates transition to savannahs and secondary thickets (Ibanez et al., 2012). In comparison, disturbed forests on UM substrates transition to maquis vegetation (Isnard et al., 2016; Jaffré, 2023b).

Although grouped under the heading of "UM soils," soils derived from UM rocks are diverse and host a wide array of vegetation types (Fritsch, 2012; Jaffré, 2023a, 2023b). UM rocks include unaltered peridotite and serpentinite. Serpentinite is formed from the hydrothermal alteration of peridotite. Soils derived from these rock types are collectively referred to as UM soils. The vast majority of UM rock area in New Caledonia is peridotite. Areas of serpentinite rock are limited in extent, occurring primarily along the periphery of the peridotite mass, at the geologic boundary. These serpentinite areas around the mass of peridotite are located at lower altitudes. Two primary soil types have developed on UM rocks in New Caledonia (Trescases, 1969; Trescases, 1973). Ferralsols are the most extensive and derived from peridotites. Magnesic Cambisols ("brown hypermagnesian soils," Jaffré, 2023c) the second type, are derived from serpentinite (Latham et al., 1978; Proctor, 2003).

In New Caledonia, serpentinite areas represent a small fraction of UM areas, and are principally found as small patches or outcrop veins at the base of mountains. Rainforests located on serpentinite, at lower altitudes, have been more affected by fire than rainforests on Ferralsols on peridotite. In both cases, the disturbed forest areas are replaced by maquis (Jaffré, 2023a). The rainforests at lower altitudes on serpentinite have experienced extensive disturbance by fire and now persist merely as isolated relics, rarely exceeding a hectare in extend, and have been poorly studied (but see Jaffré, 2023a).

Since the Ferralsols and Magnesic Cambisols are derived from different parent material (peridotite vs. serpentinite), and they are subject to somewhat different abiotic and biotic conditions, they differ in their chemical characteristics (Echevarria, 2021; Jaffré, 2023c). Previous studies of the New Caledonian UM flora have primarily focused on maquis growing on peridotite and serpentinite and forest growing on peridotite only (Birnbaum et al., 2023; Jaffré, 2023a). The vegetation composition, and plant tissue elemental concentration of forests on serpentinite have never been studied.

In New Caledonia, the ecological discontinuity from UM to adjacent non-UM (normal) substrate is well known (Jaffré, 2023a). UM soils are known to be stressful for plant establishment and growth due to their extreme nutrient imbalance and low pH (Bini & Maleci, 2014). Plant species that have a high affinity or are strict endemics to UM soil typically have distinctive morphological and physiological adaptations for growing on this chemically extreme soil type (Brooks, 1987; Palm & Van Volkenburgh, 2016). Plant species growing on UM soil are able to tolerate, exclude, or actively uptake particular nutrients and heavy metals. This is manifested within the leaf chemistry and can be analyzed as tissue elemental concentration. Specific physiological tolerance mechanisms of the plant species occurring on UM soil can then be interpreted from tissue elemental concentrations, as compared to tissue elemental concentrations of species growing on more normal soils (Brady et al., 2005; Oze et al., 2008; Pope et al., 2010). Some plant species accumulate elements including Mn, Ni, and Cr to extreme level and are known as hyperaccumulators (Reeves et al., 2017; Reeves et al., 2021). New Caledonia UM soils support a high diversity of hyperaccumulator species (Gei et al., 2020; Jaffré et al., 2013). Few species, however, cross the edaphic boundary and grow on both UM and non-UM soils.

In this study, we analyzed how different UM and non-UM soils affect vegetation composition and plant tissue elemental concentration. We compared the vegetation composition and leaf elemental concentrations of plant species in two adjacent forests occurring on serpentinized peridotite (UM) versus VS substrates (non-UM). We hypothesized that (1) UM and non-UM soil types are chemically distinct, (2) chemical conditions influence vegetation composition and structure and (3) leaf tissue element concentration of plant growing on the two different soil types will be distinct.

2 | MATERIALS AND METHODS

2.1 | Floristic data and sample collection

This study was conducted atthe Mont Koghi forest (22° 11′ S, 166° 30′ E), located 20 km north of Nouméa (Figure 1). The study area is at a geological boundary between UM and VS rocks at 450–550 m elevation. Soils on UM are derived from slightly serpentinized peridotite. Soils on VS were derived from acidic VS tuff. The studied forests belong to the dense humid forest of low and medium altitude as defined in the Atlas of New Caledonia (Jaffré et al., 2012). Mean annual precipitation is 1500–2000 mm and mean annual temperatures are about 20°C (Météo-France, 2008). These forests were selectively logged 60–80 years ago for large trees of *Agathis lanceolata* (Kaori) on UM and *Montrouziera cauliflora* (Houp) on VS (Service des Forêts de la Nouvelle-Calédonie. Pers. Com.).

Ten 0.1-ha forest plots (50 m × 20 m) are established (Figure 1**)** on each substrate type (UM and VS). Within each plot, all vascular plant species are identified and all individuals with diameter at breast height (DBH) ≥10 cm were measured. All scientific names were thoroughly cross-checked in the New Caledonia floristic list "Florical" (Munzinger et al., 2023). Soil samples were arbitrarily sampled within the study area, taking into account pedological variability (topography, gradient, and texture). A total of 35 samples were collected for UM and VS. Plant litter was removed from the soil surface and soil samples were collected from 0 to 15 cm depth. Leaf tissue samples were collected from four to nine individuals per species of the 30 most abundant species growing on both soil types.

2.2 | Soil chemical analysis

Soil analysis was conducted at the Analysis Laboratory of Centre IRD de Nouméa. Soil samples were air dried and sieved to <2 mm. Soil pH was measured from a soil suspension in water in a ratio soil/solution of 1/2.5. Exchangeable cations were extracted using Tucker's method by a 1 M solution of ammonium chloride at pH 7.0 in ethanol at 60% (Pétard, 1993). Diethylenetriamine pentaacetate (DTPA) extraction method was used to analyze soil bioavailability of Al, Mn, and Ni. DTPA extraction solution consisted of 5 mM DTPA +0.01 M $CaCl_2$ solution adjusted to pH 5.3 by acetic acid. A volume of 25 mL of solution per 1 g of soil was used for extraction, according to the method of Lindsay and Norvell (1978) adapted to Ferralsols soils of New Caledonia (Becquer et al., 1995; L'Huillier & Edighoffer, 1996; Pétard, 1993). Ammonium-exchangeable and DTPA-

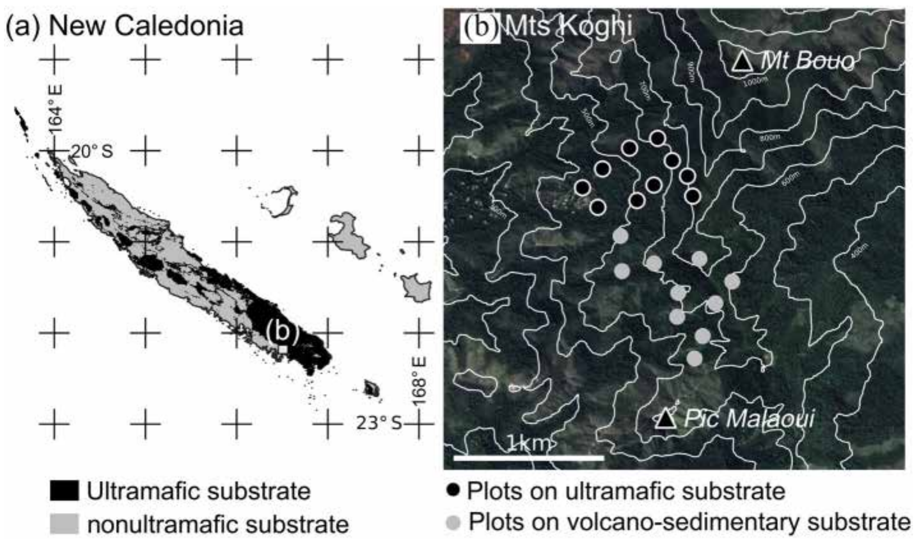

FIGURE 1 Map of New Caledonia showing (a) the distribution of ultramafic substrate and the study site on the main island (Grande Terre) and (b) the location of the study plots.

TABLE 1 Number of vascular species and trees only (diameter at breast height [DBH] ≥10 cm) for the ten 0.1-ha forest plots on ultramafic (UM) and volcano-sedimentary (VS) soils at Mont Koghi.

	Total sp.	Nb. Sp. UM	Nb. Sp. VS	Nb. Sp. UM only	Nb. Sp. VS only	Nb. of shared species
Total vascular sp.	303	217	216	87	86	130 (42%)
Tree (DBH ≥10 cm)	162	109	111	51	53	58 (35.8%)

Note: Percent of total flora in bracket.

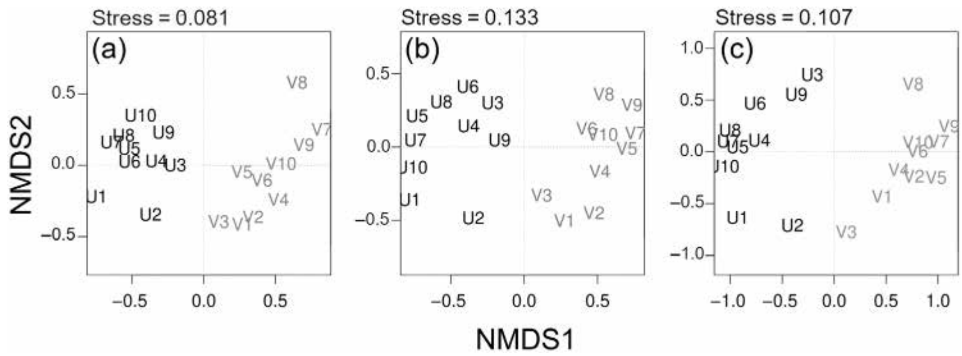

FIGURE 2 Nonmetric multidimensional scaling (NMDS) ordination computed for the ten field plots on the two soil types. U, ultramafic. V, volcano-sedimentary. (a) Presence–absence data for the total vascular flora; (b) Presence–absence data for trees (diameter at breast height [DBH] ≥10 cm); (c) Relative abundance data for trees (DBH ≥10 cm). The stress value indicates the goodness-of-fit, that is, the quality of the representation (stress ranges from 0 to 1: The smaller the stress, the better the representation). DBH: diameter at breast height.

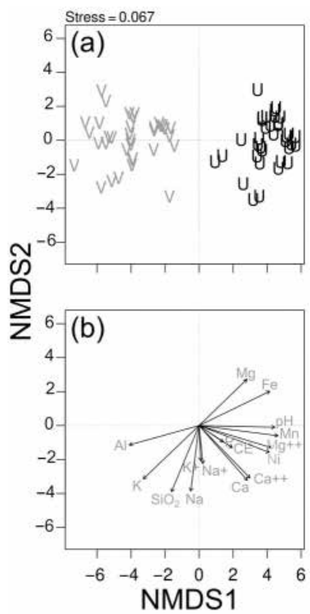

FIGURE 3 Nonmetric multidimensional scaling (NMDS) ordination computed for soil chemistry from the ten field plots on the two soil types. U, ultramafic. V, volcano-sedimentary. (a) Ordination according to soil chemical composition of plot; (b) The NMDS vectors displaying the direction and strength of influence of soil properties. The stress value indicates the goodness-of-fit, that is, the quality of the representation (stress ranges from 0 to 1: The smaller the stress, the better the representation). Al, Mn, and Ni are DTPA extract concentrations (μg g^{-1}).

extractable methods provide a measure of the cations (nutrients) available to plants in soil.

Soil samples were ground to fine powder and treated with hot acid perchloride acid (2%) to dissolve minerals. Si was determined gravimetrically after precipitating the residue in NaOH. Total P was determined by acid digestion (nitric solution) (Pétard, 1993). The measure of the phosphovanadomolybdate complex developed in nitric solution was made by automatic colorimetry by Technicon. Total elements (K, P, Ca, Mg, Na, Al, Mn, Fe, and Ni), exchangeable cations (K^+, Ca^{2+}, Mg^{2+}, and Na^+), and DTPA-extractable cations (Al^{2+}, Mn^{2+}, and Ni^{2+}) were measured by atomic spectrometry of absorption or emission (Varian AA 300). Cation exchange capacity (CEC) was calculated as the sum of exchangeable cations.

2.3 | Leaf elemental analysis

Fresh leaf samples were rinsed with distilled water, dried at 60°C in a drying oven and ground to a fine powder in a ball mill. The samples were then further dried at 105°C in a drying oven. Aliquot 2 g samples of powdered leaf tissue sample were weighed on a laboratory balance and dry ashed for 2 h in a muffle furnace at 450°C. The ash was then dissolved in concentrated HCl. Elemental analysis for K, Ca, Mg, Na, Mn, Fe, and Ni was conducted with an atomic absorption spectrometer (VARIAN AA 300). Foliar N content was determined by sulfuric acid etching and nitrate reduction with salicylic acid. N fixed in the ammonium sulfate state was measured volumetrically.

2.4 | Statistical analysis

We first analyzed variation in the floristic composition and soil chemical characteristics using nonmetric multidimensional scaling (NMDS) and the *metaMDS* function from the *vegan* R package (Oksanen et al., 2013). This statistical method of analysis finds the most stable NMDS solution (i.e., which minimizes stress) using random reiteration, set here to a maximum of 1000 reiterations. We used Bray–Curtis distances computed on species presence/absence and tree species (DBH ≥10 cm) relative abundances as two different floristic dissimilarity indices.

For soil chemical characteristics, we used Euclidean distances performed on log-transformed values as dissimilarity index. Sixteen soil chemical characteristics were included in the analysis: pH, CEC, exchangeable cation concentration (K^+, Ca^{2+}, Mg^{2+}, and Na^+), and total elemental concentration (SiO^2, K, P, Ca, Mg, Na, Al, Mn, Fe, and Ni). Comparisons of mean values between the two soil types were carried out using T-tests.

We then compared the leaf elemental composition (N, P, K, Ca, Mg, Ca/Mg, Na, Al, Mn, Fe, and Ni) of plants collected on UM and VS. Comparisons were computed at the species and the community levels using Wilcoxon rank sum tests. At the species level, we tested for each species and chemical characteristic whether leaves collected from individuals growing on UM differed from those collected from individuals growing on VS. Only species with at least five samples on each substrate were tested. At the community level, we compared species mean foliar composition on the different substrates ($N = 30$ species).

3 | RESULTS

3.1 | Floristic composition

About the same number of vascular plant species (217 and 216) and tree species (109 and 111) were found on the 1-ha of UM and VS forests (Table 1). Numbers of species growing only on UM or VS were also very similar. Species composition differed between soil types, with only 42.0% of the vascular plant species and 35.8% for the tree species occurring on UM and VS. This pattern is confirmed by NMDS ordination (Figure 2). The plots showed distinct and soil-specific occupancy of the NMDS space defined by floristic data (Figure 2). Stress value (0.08) indicates distinctive flora on each soil type. Ordination is lower, although still important, for trees based on presence–absence data (stress 0.133) or relative abundance data (0.107).

TABLE 2 Soil chemical analysis of ultramafic (UM) and volcano-sedimentary (VS) soils collected from Mont Koghi.

	UM soils Mean (SD)	VS soils Mean (SD)	T	p value
pH	6.0 (0.6)	4.1 (0.3)	16.69	***
Exchange cations (cmolc/kg)				
K^+	0.2 (0.1)	0.2 (0.1)	−0.03	ns (0.97)
Ca^{2+}	3.6 (3.3)	0.4 (0.5)	5.87	***
Mg^{2+}	12.0 (8.6)	1.0 (0.6)	7.59	***
Ca/Mg molar	0.7 (1.1)	0.3 (0.2)	1.89	ns (0.06)
Na^+	0.2 (0.1)	0.2 (0.1)	0.74	ns (0.46)
Cation exchange capacity (cmolc/kg)	19.4 (5.8)	15 (4.5)	3.52	***
Saturation rate %	79.3 (24.2)	11.9 (6.4)	15.90	***
DTPA (μg g^{-1})				
Al	13.3 (25.9)	521.7 (102.8)	−28.31	***
Mn	919.4 (203.7)	19.1 (20.6)	26.00	***
Ni	348.1 (164.5)	3.3 (3.2)	12.40	***
Total (mg g^{-1})				
P	0.5 (0.2)	0.4 (0.2)	1.76	ns (0.08)
SiO_2	143 (126)	382 (248)	−5.08	***
Ca	1.6 (1.4)	0.2 (0.2)	5.65	***
Mg	22.1 (15.6)	4.0 (3.9)	6.65	***
K	0.9 (1.3)	8.7 (2.1)	−18.73	***
Na	0.4 (0.5)	0.5 (0.4)	−0.42	ns (0.67)
Fe	299 (106)	44.7 (13.2)	14.13	***
Al	21.2 (10)	74.3 (18.6)	−14.86	***
Mn	7.1 (2.1)	0.3 (0.3)	18.71	***
Ni	7.2 (2.7)	0.3 (0.2)	15.07	***

Note: Values are mean (standard deviation [SD]) from 35 random locations within the study area for each soil type. T-test value and significance *** ($p < 0.001$) are reported in the last columns.
Abbreviations: DTPA, diethylenetriamine pentaacetate; ns, non significant.

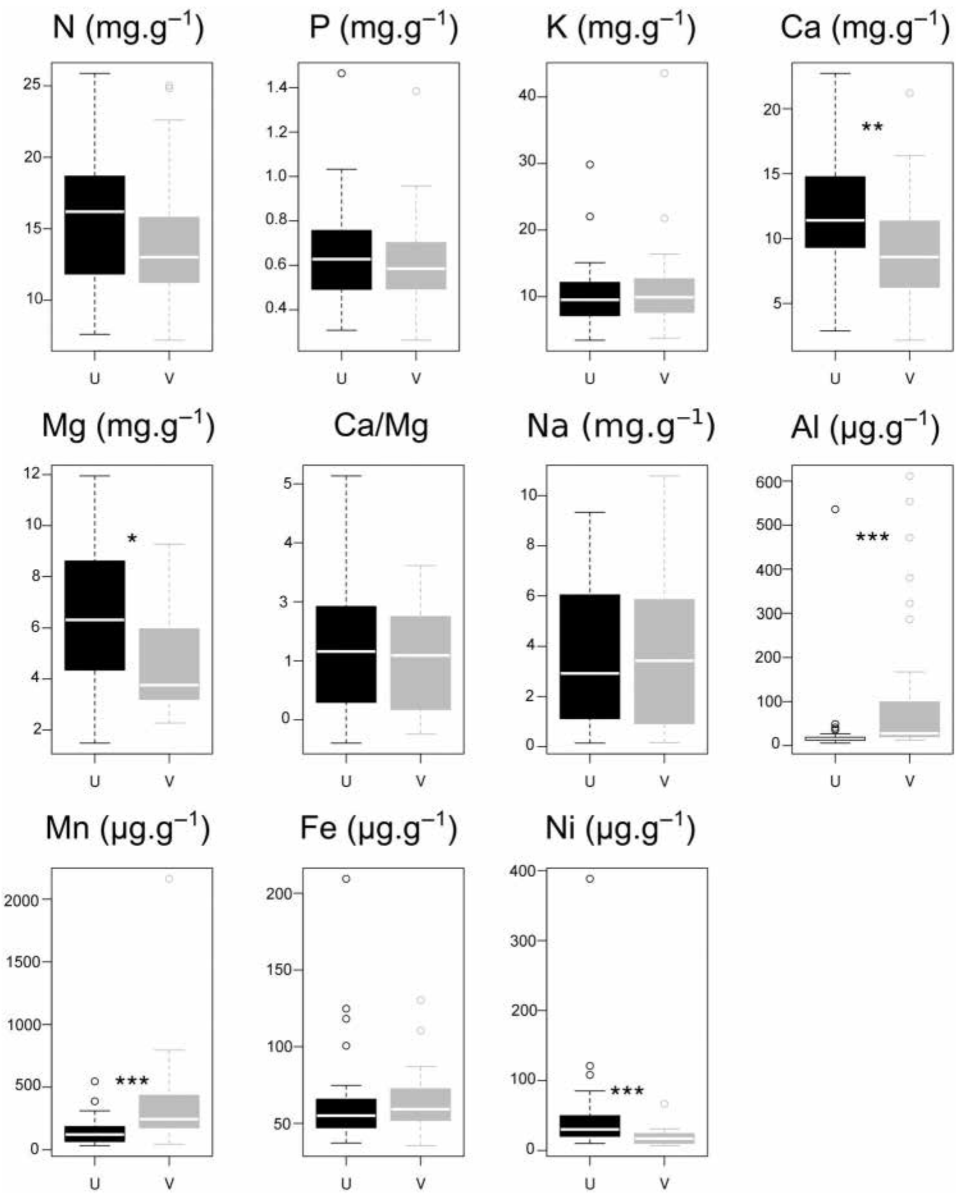

FIGURE 4 Community level comparison of leaf elemental concentration (μg g^{-1}) for N, P, K, Ca, Mg, Ca/Mg, Na, Al, Mn, and Ni on ultramafic (U) and volcano-sedimentary (V) substrates. Wilcoxon rank sum test. $n = 30$ species.

3.2 | Soil chemistry

The UM and VS soil types were markedly different in chemical properties, as supported by the NMDS ordination (Figure 3a). The two soil types markedly differed in chemical properties (Table 2), but some of them particularly influenced their ordination, as shown by the NMDS vectors (Figure 3b). Soil pH, DTPA-extractable Al, Mn and Ni, and exchangeable Mg most strongly explained the difference between both soils. The Ca/Mg molar ratio was, however, not significantly different between the two soil types and was <1.

The VS soil was strongly acidic with a lower CEC, whereas the UM soil had a more neutral pH and a higher CEC (Table 2). DTPA-extractable Al, Mn, and Ni showed high variation between both soils. Al was 40 times higher on VS than UM. Mn was 50 times higher on UM than VS. DTPA-extractable Ni was 100 times higher on UM than VS. Among exchangeable cations, Na and K had similarly low concentration for the two soil types, whereas Mg was more than 10 times higher in the UM soil. Exchangeable Ca value was 10 times higher in UM soil. P concentrations were very low in the two soil types.

3.3 | Leaf tissue elemental concentrations

Comparison of leaf tissue elemental concentration was based on 30 species occurring on both soil types (UM and VS; Figure 4). We found no significant difference in leaf elemental concentration of N, P and K for plant species occurring on both UM and VS. Leaf tissue elemental concentrations were lower than 2% for N, lower than 0.06% for P, and just above 1% for K. UM and VS plants differed in their Ca and Mg leaf concentrations, with low significance level however, but the Ca/Mg ratio was low and not significantly different between both soils.

Leaf Fe concentrations did not significantly differ between UM and VS plant communities, but significant differences were found for leaf Al, Mn, and Ni. Al and Mn were significantly higher on VS, while Ni was significantly higher on UM. Some species had exceptional values (outliers on box plot) in both UM and VS.

Figures 5 and 6 show the detailed leaf elemental concentrations for the 30 species occurring on both soils. For most species, leaf P and K concentrations are not significantly different for plants on UM or VS. For about a third of the species leaf N, Ca and Mg concentration were significantly different, but concentrations were in the low range for all species. The Ca/Mg ratio often exceeded 1 and reached high values (between 4 and 8) for several species (e.g., *Cryptocarya odorata*, *Meryta balansae*). For all species, leaf Mn concentration was higher or not significantly different on VS. Ni concentration was consistently higher or not significantly different on UM, and varied in low range mean values from 50 μg g^{-1} on UM to 20 μg g^{-1} on VS. Leaf Al concentration was also consistently higher or not significantly different on VS, except for one individual of *Ptisana attenuata*. Except for a few outliers, leaf Al concentration was low with values, around 35 μg g^{-1} on UM and 115 μg g^{-1} on VS.

High leaf Mn concentrations were found for *Alyxia tisserantii* on both soils and reached particularly high concentration on VS soil (3000–5000 μg g^{-1}). On UM soil, a few species exhibited higher Ni concentration (e.g., *Ptisana attenuata*, *Dysoxylum rufescens*), but did not exceed 500 μg g^{-1}.

On VS soils, few species exhibited high leaf Al concentration, and the highest Al concentration was found

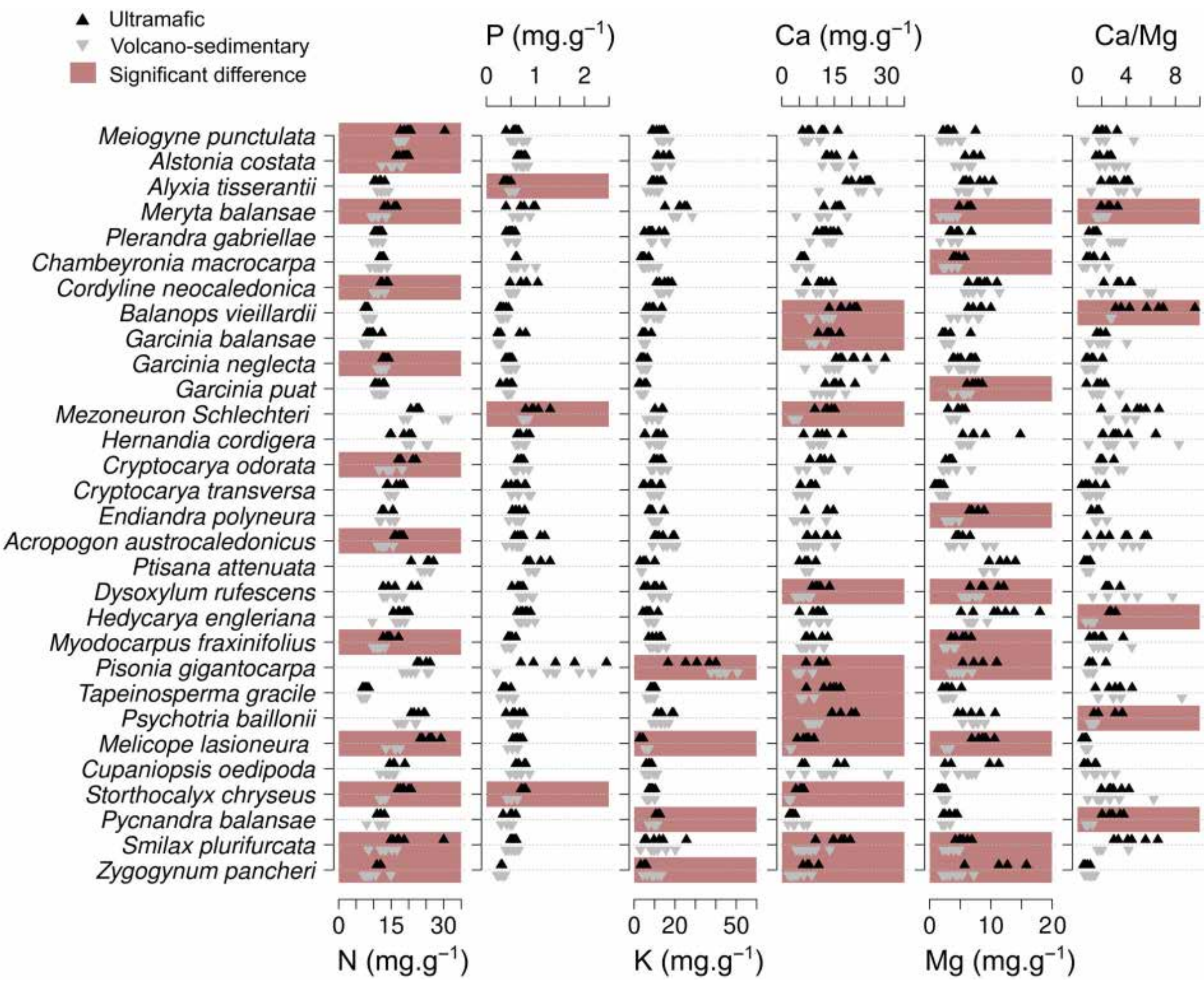

FIGURE 5 Species level comparison of leaf elemental concentration of N, P, K, Ca, Mg, Ca/Mg on ultramafic (black triangle), and volcano-sedimentary (white triangle) substrates. Wilcoxon rank sum test. Only species with at least five samples on each substrate were included.

for *C. odorata* (1250 μg g^{-1}). *Ptisana attenuata* had high Al concentration on both soil types.

4 | DISCUSSION

The juxtaposition of UM and VS rock, at Mont Koghi offered the opportunity to study the influence of strongly contrasting soil on rainforest vegetation.

The UM and VS soils were chemically distinct and significantly differed in their pH, CEC, and plant-available concentrations of Al, Mn, and Ni. The UM soil had a high CEC but was saturated by exchangeable Mg^{2+}. The VS soil is a Ferric Cambisol. It is more acidic and had a lower CEC. Both the UM and VS soils were deficient in plant-available P, K, and Ca. UM soil had higher plant-available Mn and Ni than VS soil. VS soil had higher plant-available Al than UM soil. In New Caledonia, chemically stressful soil conditions are not only restricted to UM soils and most non-UM soils could also be regarded as infertile and chemically stressful (Pillon et al., 2021).

4.1 | Forest structure and composition

Contrary to the prediction that the UM forest would have distinctive vegetative structure as compared to the VS forest, we found that both had similar species richness and similar proportion of soil specialist species. Species richness was also not affected by soil conditions. This result is similar to previous studies of forests on UM and VS soils in central New Caledonia (Jaffré & Veillon, 1995). The deeper soil and higher organic matter content of UM soil in the forests appears to reduce the effects of adverse chemistry on plant productivity.

Floristic richness of the two forests were within the range of tropical rainforests, which typically support more than 200 plant species per hectare, including about

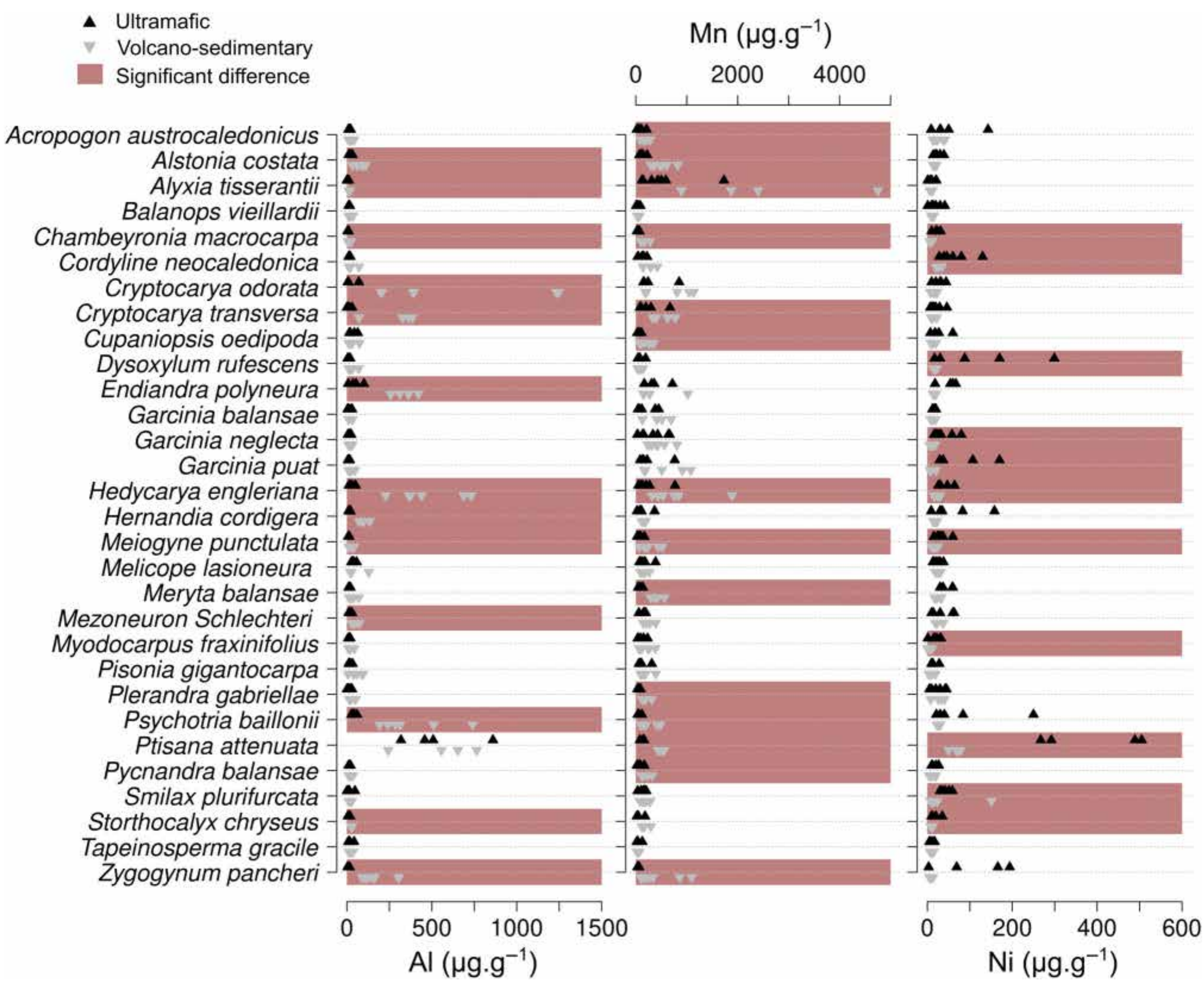

FIGURE 6 Species level comparison of leaf elemental concentration of Al, Mn, Ni on ultramafic (black triangle), and volcano-sedimentary (white triangle) substrates. Wilcoxon rank sum test. Only species with at least five samples on each substrate were included.

a hundred trees (Gentry, 1988; Whitmore, 1984). This pattern reflects the distribution of species richness found in the archipelago, where the total floristic richness is equivalent on UM and VS substrates (ca. 1200 species of vascular plants) (Isnard et al., 2016).

Although vegetation composition markedly differs between the two substrates (Ibanez et al., 2014; Jaffré et al., 1997), 42% (for the vascular flora) and 35% (for the trees, DBH >10 cm) of species are found in both forests. The tree flora had a lower proportion of shared species than the total flora and trees would therefore be more specialized than other growth forms.

4.2 | Leaf elemental concentration and physiological tolerance

Leaf elemental concentrations largely reflect the chemical composition of the soil, except for Mn. Leaf Mn concentration averaged 10 times higher for plant species growing on VS, compared to UM, although plant-available Mn was substantially higher on UM. This highlights the importance of soil pH (more acidic on VS) for the uptake of this element. Leaf Ni concentration is higher on UM soil and leaf Al concentration is higher on VS soil; however, no species accumulated Ni to extreme concentrations. The majority of plant species physiologically respond to phytotoxic metals (e.g. Al, Mn, Ni) either by exclusion at the root level or sequestration in root tissue (Rascio & Navari-Izzo, 2011). Only a few plant species that accumulate metal were found to grow on both soil types, but no hyperaccumulators (Ni >10,000 $\mu g\ g^{-1}$ or Mg >10,000 $\mu g\ g^{-1}$) were found growing on both soils. Major differences in leaf elemental concentration were for micronutrients (metals) while macronutrients varied in much lower proportion between the two soil types, suggesting a tight regulation of macronutrients compared to micronutrients.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

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