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RESEARCH ARTICLE

Community ionomics reveals a diversity of mineral nutrition in a species-rich shrubland on infertile soil

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Abstract

Questions: High species richness is observed in certain shrublands on infertile substrates. Mineral nutrients are likely to be the primary limiting resources in these ecosystems, and below-ground plant interactions may be crucial to understanding their diversity. Using ionomics, we investigated whether there were nutritional variations between plant species that coexist in a shrubland located in an edaphically extreme environment.

Location: New Caledonia.

Methods: We set up a 20 m × 20 m plot in a diverse shrubland ("maquis") on ultramafic (infertile) substrate, in which we sampled all 475 plants taller than 1 m and characterized their ionome (22 elements).

Results: In our study, 37 species were identified in the plot, representing all major forms of mycorrhizal symbioses, as well as nitrogen-fixing plants, cluster rooted and parasitic plants. Notably, both nickel hyperaccumulating and manganese hyperaccumulating species were present. Hypervolume approaches were used to assess ionome overlap among the nine most abundant species, with the results revealing limited overlap. Moreover, it was observed that the rarest species in the plot also had the most functionally distinct features.

Conclusions: Different nutritional strategies were present in the plot, as demonstrated by the variety of root symbioses and leaf ionomes. Our findings indicate coexistence of multiple species within this infertile shrubland may be achieved by species partitioning into different highly specialized biogeochemical niches.

KEYWORDS
biogeochemical niche, ionomics, mycorrhiza, OCBIL, open ecosystems, serpentine, symbiosis

1 | INTRODUCTION

Shrublands suffer from a biased perception as secondary, degraded, early-successional vegetation in comparison to forests, which are traditionally considered the climax state of terrestrial ecosystems (Pausas & Bond, 2019). However the most diverse temperate flora, the Cape Province of South Africa, is dominated by a shrubby vegetation, the fynbos, where plant diversity rivals with that of some

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rainforests (Latimer et al., 2005). Understudied, neglected, inappropriately managed, open ecosystems tend to fall within the climate envelope "ecosystems uncertain" in the temperature/precipitation plane of Whittaker (1975), which is typically warm and neither arid nor humid (Bond, 2019).

New Caledonia, an archipelago in the southwest Pacific, is a biodiversity hotspot known for the extent of its ultramafic rocks (Myers et al., 2000; Lowry et al., 2004). Soils derived from peridotites and serpentinites are characterized by their low concentrations of essential nutrients and high concentrations of metals (e.g., Ni, Cr, Mn, Co) at phytotoxic levels (Proctor, 2003; Kazakou et al., 2008). The first European botanists to visit the island noted the originality and richness of shrubby vegetation on these ultramafic substrates (Balansa, 1872). These ecosystems were later described in more detail by resident ecologists under the name "maquis" or "maquis minier" (Virot, 1956; Jaffré, 1980, 2023b), by analogy with the Mediterranean vegetation. These ecosystems are characterized by sclerophyllous and microphyllous shrubs and a herbaceous layer (sometimes poorly developed) composed mainly of Cyperaceae, or occasionally ferns, but with an almost complete absence of Poaceae (Morat, 1978). New Caledonian maquis can be species-rich (Jaffré, 2023a) and a total of 840 species, mostly endemic to New Caledonia, have been recorded in the shrubby vegetation across the archipelago (Isnard et al., 2016). At least 17 associations can be distinguished within the New Caledonian maquis (Jaffré, 2023a). The occurrence of these open ecosystems could be explained by disturbances such as fire, and possibly cyclones, but probably not by herbivory, given the absence of native ground mammals (Pillon et al., 2021). In contrast, non-forest vegetation on non-ultramafic substrates of New Caledonia are mostly savannas (Jaffré, 1993; Jaffré et al., 2012), a much less diverse ecosystem with a herbaceous layer dominated by Poaceae and a tree layer dominated by *Melaleuca quinquenervia*. The prevalence of maquis on ultramafic substrates indicates a likely role of infertile soils in their occurrence, persistence and diversity.

Edaphic conditions likely affect the functional traits occurring in plant communities. However, due to their under-ground nature plant–soil interactions are difficult to study, whereas an ideal functional trait should be easy and quick to measure in a standardized manner (Garnier et al., 2016). A representation of plant strategies for mineral nutrition is the leaf ionome (Lahner et al., 2003; Salt et al., 2008), alternatively called the elementome (Peñuelas et al., 2019; Fernández-Martínez, 2022), which consists of all essential nutrients (N, P, K, Ca, etc.) beneficial elements (Al, Na, Si, etc.) and other trace elements present in the organism, which are not a priori necessary for its growth (Cd, Co, Cr, etc.), but which can nevertheless provide information on the nutritional status of essential elements. For example, Al can be associated with P nutrition because both can be solubilized by plants that release organic acids (Watanabe & Osaki, 2002). Cd and Co can enter the plant via the same transporters as Fe, but their concentrations are less tightly regulated (Baxter et al., 2008). The ionome includes the organic and inorganic ions and molecules of cellular and extracellular compartments (Lahner et al., 2003; Salt et al., 2008; Baxter, 2009). Ionomics, the study of the ionome, has largely been applied to functional studies in model organisms such as *Arabidopsis thaliana* (e.g., Lahner et al., 2003; Morrissey et al., 2009). To date, few studies have examined wild species, but some studies have shown differences in the ionome of sympatric *Erica* species in heathlands (Pillon, Petit, et al., 2019) and of coexisting mosses in springs (Fernández-Martínez et al., 2021).

Plant–soil interactions are likely an important parameter to explain the occurrence and diversity of shrublands. Under-ground biomass is larger than above-ground biomass on infertile substrates (Chapin, 1980) and in shrublands (Ottaviani et al., 2020), where maximum rooting depth is higher than average (Canadell et al., 1996). Under-ground interactions may therefore be the key to understanding these rich ecosystems where light is generally not a limiting factor. Here we wanted to test whether plant species coexisting in a New Caledonian shrubland differ in the ways they exploit soil resources, that is, mineral nutrition. A shrubland plot on an infertile substrate was designated for the purpose of sampling all plants in a systematic manner and analyzing their mineral nutrition strategies based on their root symbioses and leaf ionome. It was hypothesized that these traits could define the biogeochemical niche of a species. The objective was to test whether community-level coexistence of numerous species could be explained by niche partitioning.

2 | MATERIALS AND METHODS

Sampling—We chose a flat area with a diverse maquis (Figure S1) in the Plaine des Lacs, in the south of Grande Terre of New Caledonia at an altitude of about 200 m. The vegetation is developed on ultramafic iron crust soil (Petroplinthic Plintosol, Ferritic) (Fritsch, 2012), developed by the degradation of ferruginous crust on peridotite. We established a 20 m × 20 m plot, which was further subdivided into 2 m × 2 m subplots to facilitate sampling for each plant (shrub, herb, liana) that reached 1 m in height. This height was set with the intention of encompassing the majority of the permanent ligneous strata, while excluding the majority of herbs, which may be short-lived and where the notion of individuality may be difficult to ascertain (vegetative reproduction). Additionally, seedlings that may be abundant at the feet of adult shrubs but also short-lived were excluded. The lower herbaceous layer, which was less than 1 m in height, was very sparse and composed of occasional Cyperaceae. Consequently, few plants were excluded by our sampling strategy. From each individual, we collected a short branch or a few leaves to obtain several grams of photosynthetic organs for ionome characterization. Due to the difficulty of accessing fine roots, in particularly on hard substrates, mycorrhizal status and other root strategies were inferred from the literature (Pillon et al., 2021).

Ionomics—Leaf samples were washed in a detergent bath (Alconox 1% w/v), rinsed, and dried in an oven (approximately 40°C) for a few days. Between 500 mg and 1 g of leaf material was placed in a 15 mL Falcon tube with a mixture of ceramic beads (4–6 beads of 5.2 mm diameter and 2 of 6.35 mm) (MP Biomedicals LLC,

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Solon, USA) and ground to powder in a high-speed benchtop homogenizer (FastPrep®-24, MP Biomedicals, Solon, OH, USA) twice at 4 m/s for 40 s. Between 15 and 20 mg of leaf powder was then digested with 750 µL of 65% HNO_3 and 250 µL of 30% H_2O_2. The mixture was homogenized and left at room temperature for 12 h to allow the gas to evaporate. The samples were then heated to 85°C for 48 h. Subsequently, samples were diluted five times with water (10–40 times for major elements like Ca and Na) before analysis by Microwave Plasma-Atomic Emission Spectroscopy (MP-AES 4210, Agilent Technologies, Santa Clara, CA, USA) (Chay & Mari, 2017). Concentrations of the following 21 elements were quantified: aluminum (Al), barium (Ba), calcium (Ca), cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), molybdenum (Mo), sodium (Na), nickel (Ni), phosphorus (P), scandium (Sc), strontium (Sr), titanium (Ti), thallium (Tl), vanadium (V), zinc (Zn). The concentration of total nitrogen (N) was measured by the dry combustion method using a CHN SERCON INTEGRA 2® analyzer (Crew, United Kingdom).

Soil characterization—Local soil conditions were characterized to assess the degree of fertility of the substrate. Soil samples were taken with a hand shovel in the first five centimeters in 8–10 sites within the plot and pooled into one single sample. The fine-earth fraction of sampled soil was examined, i.e., up to 2 mm. Soil pH was determined on the 2-mm fraction, both in water and in 1 M KCl solution using a 1/5 (solid/liquid) ratio according to NF ISO 10390. Briefly, the soil volume was mixed under agitation for 1 h with water or KCl. The suspension was left to settle for 1 h, and then the pH measurement was taken under agitation with a glass pH combination electrode (WTW SenTix™ 81, Xylem Analytics, Germany). The organic matter content was assessed by the loss of ignition (LOI) method by measuring the loss of mass after heating oven-dried soil at 550°C for four hours (Heiri et al., 2001).

For the other soil analyses, a subsample of the 2-mm fraction was crushed to 0.1 mm. CEC and concentrations of exchangeable cations, i.e., Ca, Mg, Na, and K, were measured using Metson's ammonium acetate method at pH 7 (NF X31-130, 1999). Total concentrations of 19 elements, i.e., Al, Ba, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Mo, Na, Ni, P, Si, Sc, Ti, V, Zn were measured by inductively coupled plasma optical emission (ICP-OES) or mass spectroscopy (ICP-MS) after total dissolution of the sample by the alkali fusion method (EN ISO 14869-2:2002) and according to internal protocols (LAMA U.S. IMAGO, Noumea, New Caledonia).

Ionomic data analyses—Leaf element concentrations below the detection threshold were replaced by zero values. The few samples (four) with missing values were excluded from the statistical analyses so that 471 samples are considered in further analyses. No soil contamination, that is, no Fe leaf concentration above 1000 $\mu g\,g^{-1}$ and no high Cr leaf concentration (>50 $\mu g\,g^{-1}$), was found in the leaf samples. Univariate distributions of all leaf element concentrations highlighted the presence of extreme values that could strongly influence structures identified by multivariate analysis. Hence, we applied the Mahalanobis distance procedure (Aggarwal, 2017) to detect and remove outliers from the data set and most subsequent analyses (unless indicated). We applied principal component analysis (PCA) to this new sample-by-element table, excluding 68 samples considered as outliers, to identify the main variations in ionomic composition. This approach excluded seven species represented by few individuals (1–3). We projected outlier species individuals, a posteriori, so that all species could be displayed in the PCA space without affecting the computation of axes. A test of dimensionality (Dray, 2008) was used to identify the number of dimensions that give the best fit to represent the data in the PCA. We then performed a between-class analysis (BCA, Dolédec & Chessel, 1989) to focus on interspecific differences and control for intraspecific differences. This method is equivalent to a weighted PCA applied to averages of concentrations per species.

Because ionomic variations could be explained by spatial differences in soil conditions, we assessed the spatial structure of elemental concentrations in the study area for the most abundant species (*Dracophyllum ramosum*) by calculating and testing the statistical significance of spatial autocorrelation using Moran's index (Moran, 1948). As the positions of individuals were not precisely recorded during sampling (only the subplot was known), we assigned spatial coordinates to each individual (randomly in the subplot where the individual was sampled) and defined the spatial neighborhood as a Gabriel's graph (see Gabriel & Sokal, 1969 for more details). We then computed Moran's index and tested statistical significance by randomization using the *adespatial* package for R (Dray et al., 2023).

To consider the phylogenetic non-independence of species, we reconstructed a dated phylogenetic tree of the species represented in the plot from published data (see supplement for sources and Figure S2 for the tree). We then fitted a phylogenetic PCA to identify variation in ionomic composition that could be explained by the evolutionary history. We used the R packages *ade4* (Dray & Dufour, 2007) and *adephylo* (Jombart et al., 2010) to perform these multivariate analyses.

We conducted two analyses to quantify differences between species ionomes. First, we examined the overlap of ionomic niches between the nine species represented by more than 10 individuals. We computed convex hulls and the associated volume for each species in the space formed by the first eight dimensions of the original PCA. We also computed the volume of intersections between species to quantify their overlap and reported the volume of the intersection divided by the volume of the union of two hulls. To account for differences in individual number effectives, we performed 20 rounds of subsampling, and averaged the result across replicates. We used the R package *hypervolume* (Blonder et al., 2023) for these analyses. We also calculated Jaccard's index to measure the spatial overlap between each pair of dominant species. We used a Mantel test to measure the correlation between hypervolume overlap and Jaccard's index.

A second approach was applied to measure niche for species with small sample size for which it is not possible to reconstruct hypervolumes. We calculated the functional distinctiveness of each species (Violle et al., 2017) using the *funrar* R package (Grenié et al., 2017). In this analysis, we include all samples as we expect that extreme values correspond also to species with higher distinctiveness. We

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tested the correlation between functional distinctiveness and abundance using Spearman's rank correlation coefficient.

3 | RESULTS

Soil properties—The soil of the study plot exhibited low concentrations of macronutrients and high concentrations of transition metals. The main physico-chemical characteristics of the soil studied are described in Table S2. The soil pH, measured in water and KCl, was slightly acidic (6.6 and 5.4 respectively), suggesting no acidity effect on plant growth. Cation exchange capacity (CEC) was low, at 8.6 cmol^{+} kg^{-1}, the sum of Ca–Mg–K–Na (S) was very low, at 1.71 cmol^{+} kg^{-1}; and subsequently, the cation saturation was only 19.9% (S/CEC). Exchangeable calcium, equal to 0.83 cmol^{+} kg^{-1}, was particularly low, indicating the possibility that Ca was limiting plant productivity. The ratios of exchangeable Ca/Mg and exchangeable K/Mg were 1.27 and 0.11, respectively, indicating low to very low availability of Ca and K relative to Mg. Total Mg concentration was 3580 mg kg^{-1}, while Ca and P concentrations were below 300 mg kg^{-1}, and Na and K below 150 mg kg^{-1}. Thus, the conventional major elements were lower than in average soils, while total metal concentrations, especially Ni, Mn, Cr and Fe, were very high, with iron concentrations as high as 435,950 mg kg^{-1}.

Taxonomic and physiological diversity—A diversity of species and root symbioses were present in the 20 m × 20 m plot. A total of 475 individuals taller than 1 m were reported, representing 37 species and 22 families (Figure 1). The most common species, *D. ramosum*, was represented by 77 individuals, while seven species were represented by a single individual. Although most of the 37 species presumably have arbuscular mycorrhiza, other root strategies were represented: ectomycorrhiza (*Melaleuca gnidioides*, *Sannantha leratii*, *Tristaniopsis glauca*, all Myrtaceae), ericoid mycorrhiza (*D. ramosum*, *D. verticillatum*, *Styphelia cymbulae*, all Ericaceae of subfamily Epacridoideae), orchidaceous mycorrhiza (*Eriaxis rigida*, Orchidaceae), rhizothamnia (nodules containing nitrogen-fixing *Frankia*) and mycorrhizal nodules (*Gymnostoma deplancheanum*, Casuarinaceae), cluster roots (*Grevillea gillivrayi*, Proteaceae), aerial parasitism (*Amyema scandens*, Loranthaceae), and root parasitism (*Exocarpos neocaledonicus*, Santalaceae).

Metal accumulation—We observed in the plot both nickel and manganese hyperaccumulators. *Homalium kanaliense*, represented by three individuals, had leaf concentrations of Ni (875, 1208 and 1905 µg g^{-1}) above 1000 µg g^{-1} (Figure 2), the currently accepted threshold for Ni hyperaccumulation (van der Ent et al., 2013). The maximum value observed in other species was 265 µg g^{-1}. For Mn (Figure 2), a single individual among 64 *Polyscias pancheri* (average 4540 µg g^{-1}), the third most abundant species, had a leaf concentration exceeding 10,000 µg g^{-1} (13,111 µg g^{-1}), the currently accepted threshold for Mn hyperaccumulation (van der Ent et al., 2013). Several other species had high Mn concentrations, sometimes with a higher average than *Po. pancheri* and there was a continuum of values between the highest and the lowest value (13 µg g^{-1}). *Gr. gillivrayi*, the only Proteaceae species present in the plot, ranked only ninth in average Mn concentration (average 3450 µg g^{-1}).

Spatial trends—We observed some variation of the ionome through space. For the most abundant species, *D. ramosum*, a gradient was observed from one side to the other (from line A–J) of the plot for several elemental concentrations (Figure S3). Spatial autocorrelation was significant for 17 out of 22 elements (all but Al, Cr, Na, Ca and Mg) according to Moran's index (Table S2). However, there was no obvious

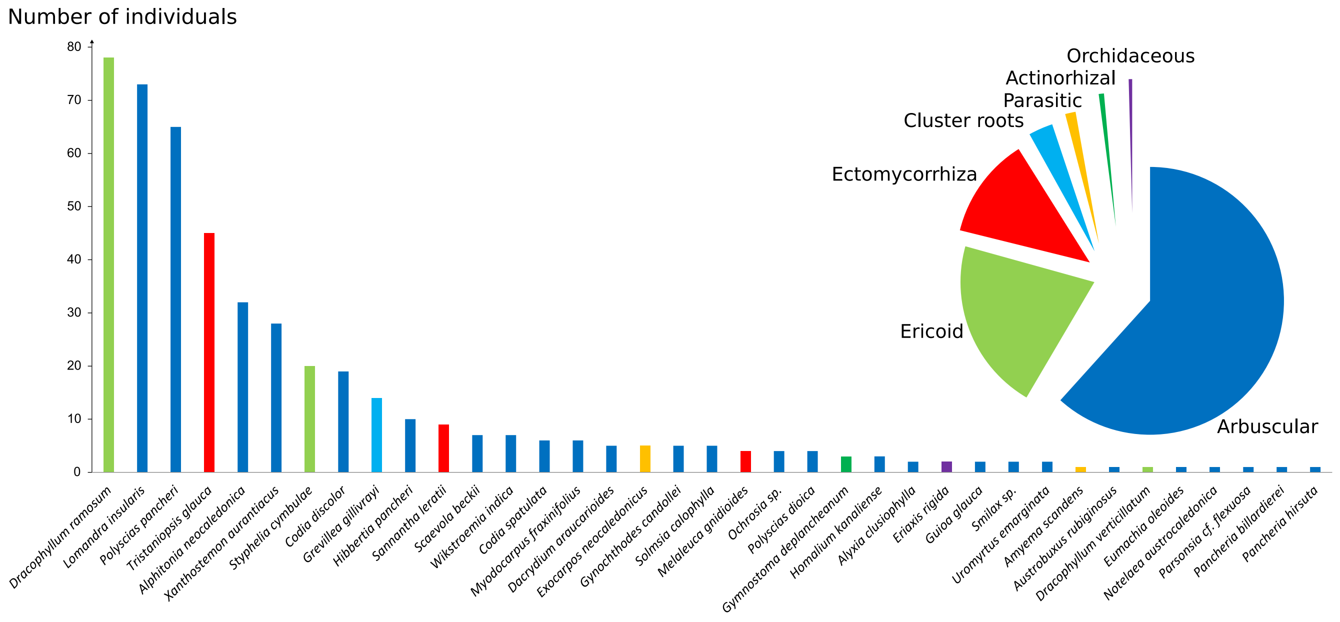

FIGURE 1 Species abundances in the 20 m × 20 m plot. A total of 475 individual plants exceeding 1 m in height were sampled, representing 37 species and several different root strategies/symbioses. The pie chart represents the proportions (in term of individual numbers) of each main root strategy.

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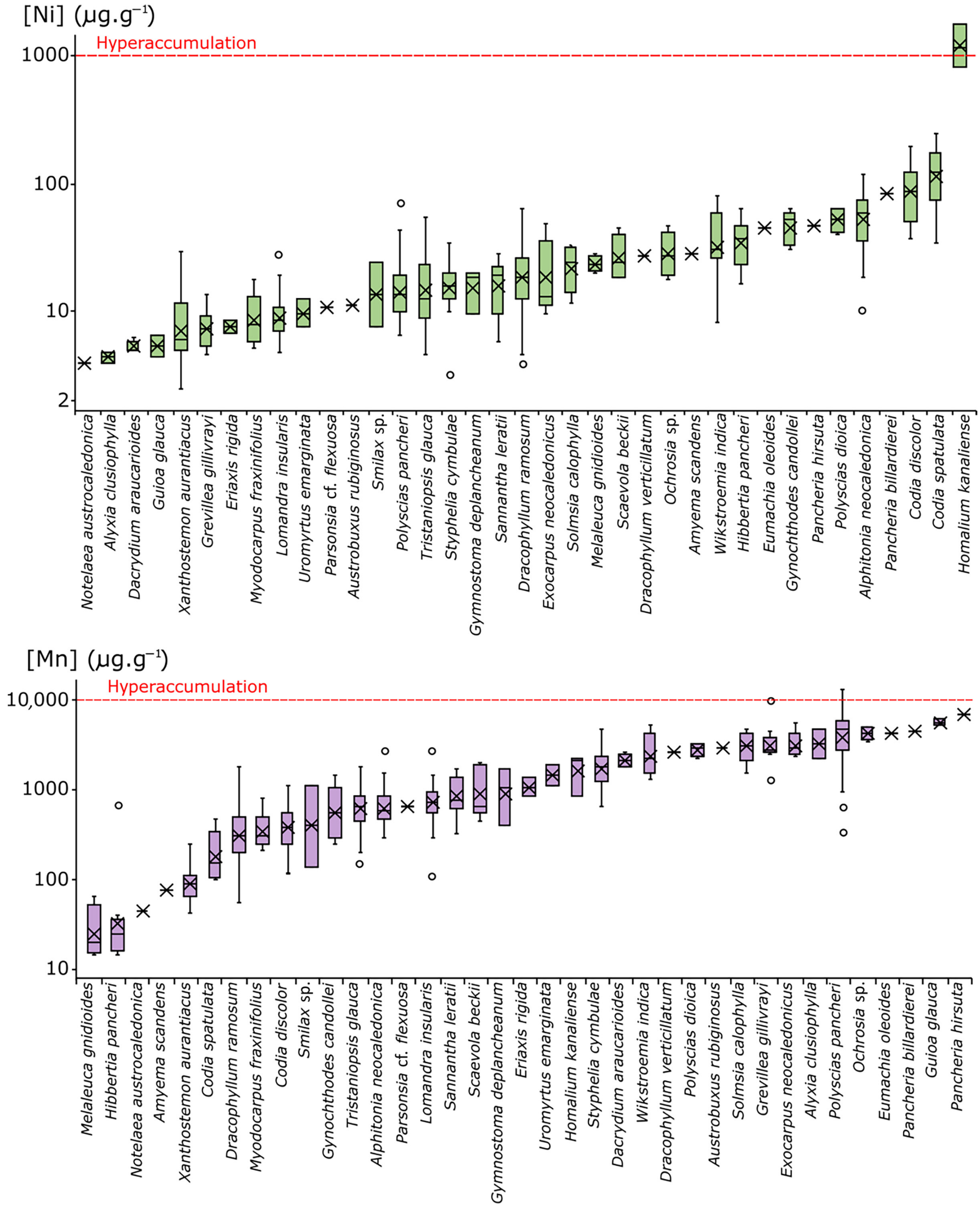

FIGURE 2 Distribution of leaf Ni (top) and Mn (bottom) concentration (µg g^{-1}, logscale) in the 37 species of the plot. For each species, values are summarised by a boxplot, mean (×) and outliers (◦). Hyperaccumulation threshold follows van der Ent et al. (2013).

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spatial heterogeneity in the plant community as indicated by the distributions of the most abundant species within the plot (Figure S4).

Multivariate analyses—The combined analyses of all elements measured revealed differences between species within the plot. The test of dimensionality indicated that eight dimensions give the best fit to represent the data in the PCA. The first axis (Figure 3) explains 17.18% of the total variation and appears to distinguish individuals with high concentrations of most macronutrients (N, P, K, Mg, …) from those with low concentrations. The second axis (12.74%) separates metals: Al, Cr, Co, V, Ni on one side and Zn, Mn on the other. The BCA indicated that 47.74% of the total variation was explained by the between-species differences, which was statistically significant ($p < 0.001$, randomization test). On the BCA (Figure S5), the cloud of points for each species was relatively tight despite intraspecific variation. When grouping individuals by symbiosis type, BCA indicated that 10.89% of the total variation was explained by root strategy differences, which was a significant effect ($p < 0.001$).

When measuring the overlap of the eight-dimension hypervolumes (Figure S6) based on the ionome profiles of the nine most abundant species ($n > 10$), three species had no or very limited overlap with others: *D. ramosum*, *Po. pancheri*, and *Xanthostemon aurantiacum*. We found larger overlap (but always below 10%) between *Alphitonia neocaledonica*, *Gr. gillivrayi*, *St. cymbulae*, and *T. glauca*. We found not significant correlation between the extent of overlap of their ionomic hypervolume and their distribution overlap (measured by the Jaccard's index) with a Mantel's test ($p = 0.346$).

The most functionally distinct species was *Ho. kanaliense* (Figure S7). It has the highest mean concentration for Ba, Co, N, Ni, Sr, and Tl. The least functionally distinct were *St. cymbulae*, *T. glauca*, *Sa. leratii*, *Gr. gillivrayi* and *Lomandra insularis*. Four of them were among the nine most abundant species and with the most overlapping hypervolumes (see above). We found a negative and statistically significant correlation between functional rarity and abundance ($\rho = -0.59$, $p = 0.000122.9 \times 10^{-6}$): the species with the smallest number of individuals tended to be the most distinct, and the most abundant species the least distinct.

Phylogenetic variations—The phylogenetic signal in variation of individual elemental concentrations was limited (Table S3, Figure S8). The phylogenetic PCA (Figure 4), which takes into account the non-independence of the species, revealed two main axes; the first correlated mainly with certain metals: Al, Co, Cr, Ni, V, with high values observed in the two *Codia* species (Cunoniaceae). The second axis was mostly correlated with macronutrients (N, P, K), and some other metals (Mn, Zn, …). *Wikstroemia* (Thymelaeaceae) and *Polyscias* species (Araliaceae) displayed high values, while Ericaceae and Myrtaceae, lower values.

4 | DISCUSSION

Despite its challenging edaphic conditions, the plot investigated here harbors a species-rich plant community. The soil of the plot

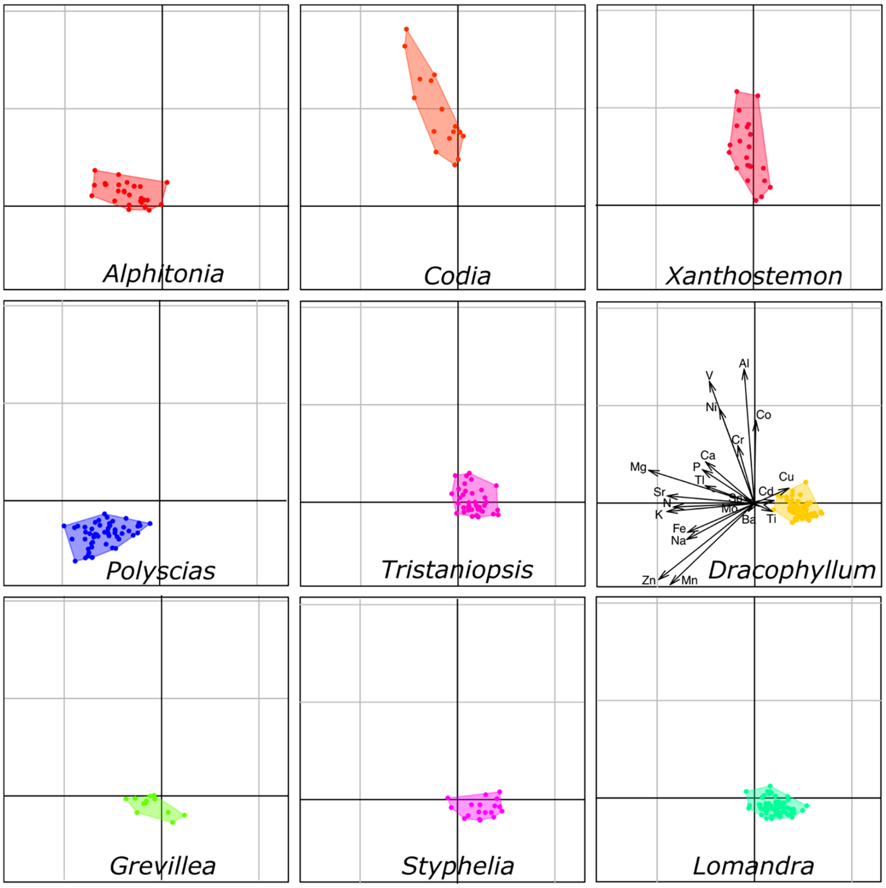

FIGURE 3 Results of between-class analysis (axes 1 and 2) of the 9 most abundant species ($n > 10$): *Alphitonia neocaledonica*, *Codia discolor*, *Dracophyllum ramosum*, *Grevillea gillivrayi*, *Lomandra insularis*, *Polyscias pancheri*, *Styphelia cymbulae*, *Tristaniopsis glauca*, and *Xanthostemon aurantiacus*. On the factorial map, each species is represented by a convex hull that surrounds the individuals.

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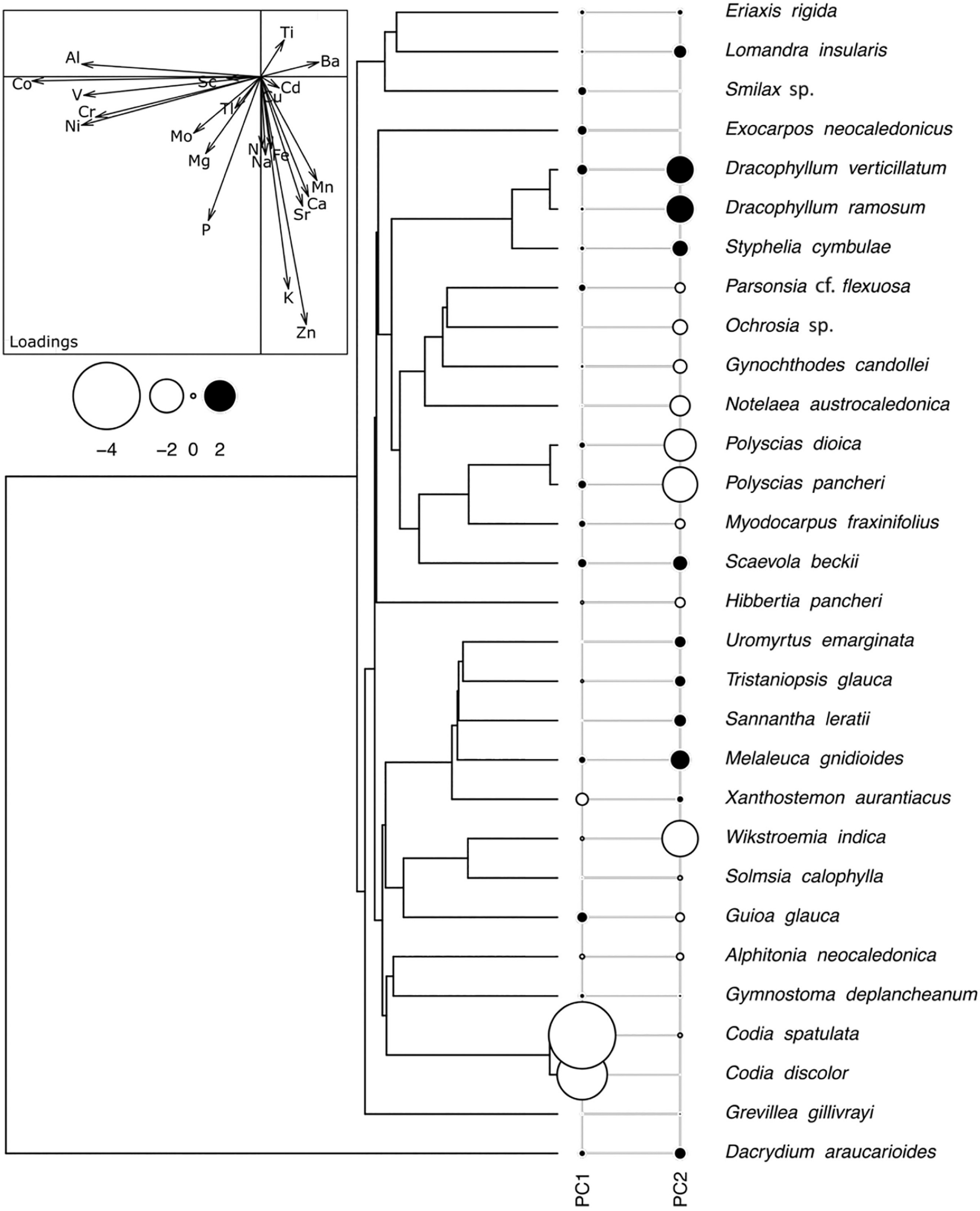

FIGURE 4 Phylogenetic PCA on the ionomic data averaged at the species level. Results are given for the first two axes that best summarize the multivariate phylogenetic structures. Loadings are shown in the top left corner. Species scores are shown on the right: Black (vs. white) circles indicate positive (vs. negative) scores.

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exhibited typical features of ultramafic substrates (low concentrations of macronutrients, high concentration of metals) and therefore likely low natural fertility (Becquer et al., 2001, 2006, 2010; Dubus & Becquer, 2001; Garnier et al., 2021). However, the number of species (37) reaching a height of 1 m in our 20 m × 20 m maquis plot was high, matching the average number of tree species with a diameter at breast height of 5 cm or more observed in 201 plots of the same surface in New Caledonian forests (37 ± 12 species per plot, Ibanez et al., 2014). Species diversity in shrublands can indeed be compared with that of tropical rainforests (Latimer et al., 2005). The abundance of species in the plot follows a typical log series distribution (Fisher et al., 1943). A few species were very abundant while many were rare. In terms of species composition, the shrubland community was intermediate between the *Codia discolor*–*Eugenia stricta* association and the *Ho. kanaliense*–*Tetraria comosa* association (Jaffré, 2023a).

The diversity of nutritional strategies observed in the study plot is reflected in the diversity of root symbioses present. All major mycorrhizal types are represented in this 20 m × 20 m square, as well as rhizothamnia, cluster roots and parasitism. A similar overrepresentation of ectomycorrhizal plants, parasitic plants, Ericaceae (ericoid mycorrhiza) and plants with cluster roots, has also been observed in the flora of Australia (Brundrett, 2017). This similarity could be explained by the biogeographical connection of the two floras and/or convergence on substrate with low fertility. The plot lacked two other functional groups namely carnivorous plants and Fabaceae. Despite the diverse range of Fabaceae observed in New Caledonia, these plants are not well-represented on ultramafic substrates (Pillon et al., 2010; Pillon, González, et al., 2019), and might be ecologically displaced by another nitrogen-fixing family, Casuarinaceae. The only common legume in New Caledonian maquis is the ectomycorrhizal *Acacia spirorbis*, which is relatively rare in the south of New Caledonia, but common and locally dominant in the northwest (Jaffré, 2023a). The root strategies accounted for a significant proportion (11.85%) of the observed differences in the plant ionomic profiles. However, because symbioses are also strongly clumped phylogenetically (e.g., ericoid mycorrhiza restricted to Ericaceae, and ectomycorrhiza here to Myrtaceae), it is difficult to separate phylogenetic and symbiotic effects on the ionome. The variety of root strategies observed aligns with the theory of old, climatically buffered, infertile landscapes (OCBILs, Hopper, 2009). The OCBIL theory was developed to explain the high diversity and endemism of shrubby vegetation in regions that combine great antiquity, low large-scale disturbance (past climate oscillations and orogenesis), and low fertility, such as the Cape Province or Southwest Australia. Hopper (2009) predicted that plants would evolve greater nutritional specialization to cope with infertile substrates. These adaptations include including root symbioses, specific root systems for phosphorus mining, carnivory, and parasitism, as observed here.

Another rare and original nutritional physiology occurring in the plot is Ni hyperaccumulation. According to van der Ent et al. (2013), a species may be considered as a hyperaccumulator of a given element if a concentration exceeding the element-specific threshold (generally set between 100 and 1000 times the concentrations in normal plants) has been recorded in the dry leaf matter in at least one specimen growing in its natural habitat. With two individual plants out of three exceeding the threshold of 1000 $\mu g\, g^{-1}$, *Ho. kanaliense* qualifies as a Ni hyperaccumulator. The concentration in all three individuals were considerably higher than that observed in other individual plants of different species in the same plot (maximum: 265 $\mu g\, g^{-1}$). Our observations are consistent with those of Purwadi et al. (2023), who based their findings on a large data set (27,000 specimens) of X-ray fluorescence measurements. They observed a bimodal distribution of Ni concentration, with Ni hyperaccumulating plants separated from normal plants by a threshold of 280 $\mu g\, g^{-1}$. *Ho. kanaliense* is also the most functionally distinct species when all elements are considered.

Manganese hyperaccumulation was also present in the plot, although it appeared less distinct. A continuum exists between the lowest and the highest Mn concentrations. Only one extensively sampled species (*Po. pancheri*, 64 individuals) has one individual value that exceeds the threshold of 10,000 $\mu g\, g^{-1}$, qualifying it as a Mn hyperaccumulator. Our observations are somewhat consistent with those of Purwadi et al. (2023) with their large data set. In their study, the Mn concentrations did not appear to exhibit a bimodal distribution, but rather exhibited a long-tailed distribution. Overall, several species in the plot displayed relatively high Mn content, suggesting that they could exudate carboxylates to acquire P (Lambers, 2022). Nevertheless, the single presumably non-mycorrhizal species sampled here (*Gr. gillivrayi*, Proteaceae) does not stand out with a particular high Mn content (contra Lambers et al., 2021), and only has the ninth highest Mn content. The observed 1000-fold variation in Mn concentrations demonstrates the diversity of strategies employed by plants to assimilate this essential element. However, this variation does not permit the separation of species into discrete nutritional strategies, including cluster roots, on the basis of Mn concentration alone.

The coexistence of diverse metal hyperaccumulators in a limited geographical area suggests that elevated Ni and Mn contents may represent distinct adaptations to identical edaphic constraints, such as ultramafic substrates. These two strategies have also been observed in different species that belong to the same genus, *Pancheria* (van der Ent et al., 2022), which are occasionally sympatric. The two metals are stored in different compartments, indicating the involvement of distinct mechanisms (van der Ent et al., 2022). The occurrence of these globally rare strategies in the plot is also consistent with an increased functional ecophysiological diversity on nutrient-poor soils (Hopper, 2009; Lambers et al., 2010). New Caledonia, in particular, is home to the second largest concentration of metal hyperaccumulators in the world (Jaffré et al., 2013; Reeves et al., 2018; Gei et al., 2020).

The vegetation of the plot consists of a heterogeneous assemblage of species, composed of abundant species with relatively distinct strategies, and rarer species with even more distinct ionomes. The nine most abundant species ($n > 10$) represent seven families. The results of the overlap analysis indicate that three to five of these species exhibit a distinct elemental hyperspace

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(sensu Garten, 1978). Four out of five species belong to the eudicots and have arbuscular mycorrhiza, namely *Alp. neocaledonica*, *C. discolor*, *Po. pancheri*, and *Xanthostemon aurantiacus*. The sixth species, *D. ramosum*, belongs to Ericaceae and has ericoid mycorrhiza. Nevertheless, some overlap has been observed between species that were expected to be functionally distinct, such as *Gr. gillivrayi* (which has cluster roots), *L. insularis* (the only abundant monocot in the plot), *T. glauca* (the only abundant ectomycorrhizal plant in the plot), and *St. cymbulae* (which has ericoid mycorrhiza). These four species were, in fact, the least functionally distinct. Conversely, the least abundant species in the plot appeared to be the most distinct functionally, as demonstrated by the Ni hyperaccumulator *Ho. kanaliense* (three individuals). The ecological space occupied by rare species within communities varies and may be redundant or original (see e.g., Walker et al., 1999; Jain et al., 2014; Leitão et al., 2016). In our study, it appears that rare species occupy niches that are left vacant by dominant species.

It is not clear how the community is structured, although root symbioses, botanical families and larger clades could be considered as a priori groups. In the phylogenetic PCA, Cunoniaceae stand out due to their higher concentration of catalytic metals (Ni, Co) involved in redox and hydrolytic reactions (da Silva & Williams, 2001). Cunoniaceae, along with *Ho. kanaliense* (Salicaceae, Malpighiales), belongs to the malvid clade (sensu Zuntini et al., 2024) which accounts for a significant proportion of Ni hyperaccumulating species worldwide (Pillon et al., 2010; Jaffré et al., 2013). They may represent specialized strategies for metalliferous substrates. The phylogenetic PCA also indicates a convergence toward low concentrations of elements with structural (N, P, Ca) and electrochemical functions (Na, K) (da Silva & Williams, 2001) in Ericaceae and Myrtaceae. The first family comprises three species of ericoid mycorrhiza, while the second includes three species with ectomycorrhiza and two species with arbuscular mycorrhiza. The lower demands in macronutrients of those two families are consistent with the prevalence of these two symbiotic types in nutrient-poor soils (Read, 1996; Lambers et al., 2008). On the other hand, Araliaceae species (Apiales) have higher concentrations of macronutrients, which along with their lower wood density (Ibanez et al., 2017) fits more a competitive strategy. Further plot-based studies of community ionomics in other vegetation types, substrates and biogeographic settings would be desirable to identify other functional guilds.

It remains unclear how species interact within the plot; their interactions probably include both competition and facilitation. The apparent partition of the ionomic space and the co-occurrence of strategies that tends toward stress tolerance (e.g., Ericaceae) or competitiveness (e.g., Araliaceae) (Grime, 1977) suggest that competition plays an important role. However, experimental studies have demonstrated a complex interplay of positive and negative feedbacks between different functional groups of species in the southwest Australian flora (Teste et al., 2017). Among the most abundant species here, plants with arbuscular mycorrhiza exhibited more distinct ionomic hypervolumes than plants with distinct root strategies. This counterintuitive observation may be attributed to the leaching of nutrients. For example, plants with cluster roots, such as non-mycorrhizal Proteaceae, have the capacity to mobilize phosphorus sorbed to soil particles, which can benefit neighbouring plants (Lambers et al., 2018). This phenomenon has also been observed in other elements, including manganese (Staudinger et al., 2024). A nitrogen-fixing plant such as *Gym. deplancheanum* enriches the soil with nitrogen, which benefits the entire community. Non-mycorrhizal plants may be more susceptible to soil pathogens, whereas mycorrhizal plants benefit from the protection provided by symbiotic fungi (Lambers et al., 2018). For now, the role of the soil microbiota (from symbiotic to pathogenetic) in plant interactions has been largely overlooked and understudied. Further research may assist in the identification of complementary species groups and their associated microbiota that could be employed for the ecological restoration of metalliferous ecosystems, which are currently under significant pressure from mining activities (Ibanez et al., 2019).

AUTHOR CONTRIBUTIONS

Vanessa Hequet and Yohan Pillon performed the sampling the field, Karine Gotty and Sandrine Chay conducted the chemical analyses, Audrey Léopold interpreted the soil data, Juliette Hocedez and Stéphane Dray analyzed the ionomic data. Yohan Pillon, Juliette Hocedez, Audrey Léopold, Stéphane Dray wrote the first draft and all authors edited the last version.

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CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare.

DATA AVAILABILITY STATEMENT

The raw ionomic data are openly available in DataSuds repository (IRD, France) at https://doi.org/10.23708/OJGC5S. Data reuse is granted under a CC-BY license.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Photograph of the plot.

Figure S2. Phylogenetic tree of the 37 species represented in the plot.

Figure S3. Spatial variation of each element measured in *Dracophyllum ramosum*.

Figure S4. Distribution of the nine most abundant species across the plot.

Figure S5. Between-class analysis of all species.

Figure S6. Overlap between the hypervolume of the nine most abundant species.

Figure S7. Functional distinctiveness.

Figure S8. Phylogenetic variation of elemental concentrations.

Table S1. Main physico-chemical characteristics of soil sample.

Table S2. Spatial autocorrelation in leaf mineral concentrations of *Dracophyllum ramosum*.

Table S3. Phylogenetic signal for each element studied.

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