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ARTICLE

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ABSTRACT

About a third of New Caledonia is covered with ultramafic soils (UM) which hosts a rich flora (endemism > 85%) threatened by mining activities. This combination makes the ultramafic vegetation a floristic hotspot within a biodiversity hotspot. UM soils are distributed from sea level to 1618 m elevation with about two-thirds forming a large continuous unit while the remaining forms numerous relatively small isolated units. Here, we provide a synthesis of the distribution of forest and tree species across 22 UM units. We compiled an extensive tree occurrence dataset (109,896 occurrences and 1,065 species) and a new expert-based forest map at a 1:3000 spatial resolution. Only 10% of these species represented more than 50% of the occurrences, while 10% of the species had only one or two occurrences. A quarter of the UM area did not contain any occurrences, and we estimated that on average a quarter of the species remained to be inventoried in the 22 units. Forest covers about one-third of the UM areas with forest coverage ranging from 1.7% to 72.3% in the different UM units. Forest coverage increased from 14.6% on sea level to 93.3% at 1,200 m of elevation. About 30% of the forest and 90% of the species were located within mining concessions, while 14.5% and 73%, respectively, were located within protected areas. We recommend setting up new protected areas on ultramafic substrate, specially in the Northern province, to protect more forest and the diversity it harbours.

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KEYWORDS
Ultramafic soils; forest cover; fragmentation; species richness; biodiversity hotspot

Introduction

Ultramafic soils cover only ~3% of the terrestrial surface but are distributed globally (Guillot and Hattori 2013; Garnica-Díaz et al. 2022). Many of the areas covered by ultramafic soils are located within Biodiversity Hotspots for biodiversity conservation (Hulshof et al. 2020). Ultramafic soils often harbour original, diverse, and threatened floras on relatively small and isolated outcrops (Garnica-Díaz et al. 2022). New Caledonia is one of the most emblematic of those Biodiversity Hotspots: it is one of the regions with the largest area of ultramafic soils (~5,500 km^2) and the greatest cover of ultramafic soils relative to its size (~30%, Isnard et al. 2016; Garnica-Díaz et al. 2022). In New Caledonia, ultramafic soils are distributed from sea level to 1618 m elevation (Mt Humboldt summit) with about two-thirds of these soils forming a large continuous unit (the Massif du Sud), while the remaining forms numerous relatively small isolated units (Jaffré 1993). Understanding how habitat and species are distributed along elevational gradients and across different isolated units is critical to improve conservation planning (e.g. Wulff et al. 2013; Birnbaum et al. 2015; Lannuzel et al. 2022).

Ultramafic soils are challenging for plants in many ways. They generally exhibit low concentration of macronutrients (N, P, and K), and high concentration of magnesium (Mg) causing calcium (Ca) deficiency (low Ca/Mg ratio) or Mg toxicity. They often exhibit high concentration of potentially phytotoxic elements such as nickel (Ni), manganese (Mn), or chromium (Cr), and are generally low in water-holding capacity, further limiting plant growth (Whittaker 1954; St-Jean et al. 2018; Kierczak et al. 2021). Consequently, the species and vegetation types growing on ultramafic soils often differ from those growing on other soils in the same region (Stevanović et al. 2003; Kazakou et al. 2008; Trethowan et al. 2021). In New Caledonia vegetation on ultramafic soils consists of a mosaic of forest and maquis, maquis being shrubland-like vegetation specific to these types of soils (Jaffré 2022).

The flora on ultramafic soils in New Caledonia is rich and highly diverse with ~2,100 species, among which 85% are endemic to the territory and 56% only grow on ultramafic soils (Isnard et al. 2016). The ultramafic flora is one of the most threatened vegetation community of New

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Caledonia mainly due to bushfire and mining activities (Curt et al. 2015; Ibanez et al. 2019).

Despite its relatively small size, New Caledonia is one of the top nickel-producing territories in the world (Maurizot et al. 2020). Mining concessions cover nearly 50% of New Caledonian ultramafic areas. This coverage has increased over the past 20 years (Ibanez et al. 2019) and should further increase in the future due to the global increase in nickel demand for electric vehicles, which is expected to be multiplied by almost 30 by 2040 (Castelvecchi 2021). The impacts of mining are dramatic as the vegetation and topsoil are removed to access the nickel-enriched ore.

It is assumed that before the arrival of humans in the archipelago, New Caledonian landscapes were largely dominated by forest with maquis restricted to high elevations or areas with the harsher soil conditions (Jaffré 1980, 2022; L'huillier et al. 2020). Since the establishment of Melanesian (~3000 years ago) and European (~200 years ago) populations, forest has been largely pushed back by land clearing, fires, and mining activities (Jaffré et al. 1987; Garnica-Díaz et al. 2022). Today, most landscapes on ultramafic soils are largely dominated by maquis, especially at low and middle elevation where forest is very fragmented and often restricted to gullies (e.g. Ibanez et al. 2017; Blanchard et al. in press). Furthermore, because of harsh soil conditions and resulting slow growth rates, forest recovery is very long. For instance, in the absence of fires, the secondary succession leading to the reconversion of maquis into forest takes hundreds of years (Jaffré et al. 1997; McCoy et al. 1999). Following mining activities and soil removal, forest recovery might take thousands of years (L'huillier et al. 2020; Amir et al. 2014; Román-Dañobeytia et al. 2015).

Here, we provide a synthesis of the distribution of forest and tree species on ultramafic soils in New Caledonia. We used a new expert-based forest map and compiled an extensive tree occurrence dataset from various sources to analyse how forest coverage and tree species are distributed along elevational gradients and across the isolated ultramafic units. Based on the compiled tree occurrences, we measured floristic similarities between ultramafic units and estimated the number of species that have yet to be inventoried in each of those units. We also analysed the distribution of forest cover and tree species within mining and protected areas and discussed how the system of protected areas could be improved to meet the conservation challenges (Jaffré et al. 1987; Ibanez et al. 2019).

Materials and methods

Ultramafic units

We downloaded the peridotite massif layer at a 1:1,000,000 scale provided by the French and New Caledonian geological surveys (BRGM, SGNC) and the department of industry, mines and energy of New Caledonia (DIMENC) on the New Caledonian governmental geographic information system (Géorep, https://georep.nc/). Peridotite massifs cover an area of 5,985 km^2 (i.e. 32.6% of the New Caledonian territory) located in the North and South province but not in the Loyalty Islands province, which consists of raised coral limestone. We merged all continuous polygons from the peridotite massif layer before removing polygons smaller than 10 km^2 and scattered serpentinite nappes. The resulting layer consisted of 22 ultramafic (UM) units organised around isolated mountains on the northern west coast, the mountain range on the south of the east coast, or as small islands surrounding the main island.

Forest map

Forest vegetation was mapped by digitization at a 1:3,000 scale from a mosaic of satellite images (Sentinel 2, Quickbird, Pléiades) and aerial photographs provided by the department of infrastructure, topography and land transport (DITTT) on Géorep (Birnbaum et al. 2022). Satellite images and aerial photographs were taken between 2009 and 2021 with a maximal spatial resolution of 0.5 m. We interpreted vegetation as forest when trees (that should be taller than 5 m) formed a continuous canopy cover, hiding the soil surface on a minimum of 0.5 ha (FAO 2020) regardless of floristic composition. We excluded mangroves and plantations easily detectable through their homogeneous canopy structure. The forest map covered the main island, Grande-Terre, and all smaller islands with UM areas (Ile Ouen, Ile Yande, Ile Art, Ile Pott, and Ile des Pins).

Tree species list

A list of New Caledonian tree species was produced in two steps. First, we computed a list of all taxa (including trees, tree palms, tree ferns, and *Pandanus*) with at least one individual occurring with a diameter at breast height (DBH at 1.3 m) ≥10 cm in the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN) or in the Herbarium of New Caledonia database (NOU) (Birnbaum et al. 2015; Bruy et al. 2021). Next, we submitted this list to a panel of five experts of the New Caledonian flora for validation. If there was any doubt on whether or not a species can be arborescent, the species was removed from the species list. The resulting tree species list encompassed 1,176 species belonging to 93 families and 285 genera. These species represent more than a third of the 3,424 native vascular plant species currently listed in FLORICAL (http://publish.plantnet-project.org/project/florical), the database of taxonomic names of the New Caledonian flora (Morat et al. 2012; Munzinger et al. 2022).

Tree species occurrences

The occurrences of all tree species were compiled from several datasets: (i) the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN), (ii) herbarium specimens hosted in Nouméa (NOU), (iii) the Global Biodiversity Information Facility (GBIF, mostly occurrences from herbarium specimens from Paris and Missouri Botanical Garden), (iv) the Red List Authority hosted by Endemia, a non-profit association (see https://endemia.nc/) and (v) other observations from different unpublished inventories (see Birnbaum et al. 2015 for further details). Species names were searched in major taxonomic databases (IPNI, POWO, TROPICOS, and TAXREF) by programmatically querying application programming interfaces (APIs) to retrieve the corresponding accepted name in the taxonomic repository for the New Caledonian Flora (FLORICAL). The compiled occurrence dataset included 169,376 unique georeferenced occurrences (i.e. unique combination of accepted species name, longitude, and latitude).

Conservation status and threats

We downloaded the map of mining concessions provided by the DIMENC (Géorep, https://georep.nc/). Since protected areas are under provincial jurisdiction in New Caledonia, we used the boundaries of reserves provided by the environmental services of the North and South provinces. Finally, the Red List conservation status of tree species was provided by the local Red List Authority (RLA) accredited by the IUCN to identify threats to the flora of New Caledonia (Meyer et al. 2021). Currently, the group has assessed more than 1,800 taxa and all species assessments are published both on the Global Red List website (www. iucnredlist.org) and on the Endemia website (www.endemia.nc).

Analysis

We analysed forest coverage, occurrences, and tree species diversity at three different spatial scales, (i) at the New Caledonian scale (all 22 UM units pulled together), (ii) at the UM unit scale (each UM unit separately), and (iii) within UM units using a 2×2 km grid (i.e. 4 km^2 cells). This 2×2 km grid is used by the IUCN species survival commission group New Caledonia Plant Red List Authority (Meyer et al. 2021). A total of 1,934 grid cells intercepted the 22 UM units but only 882 cells were fully included in the 22 UM units. We only considered the 1,368 cells with at least 50% of their area included within one of the 22 UM units to perform the grid-scale analyses. We also analysed the distribution of the forest coverage, the number of occurrences, and the number of tree species within mining or protected areas within 100-m elevation bands along the elevation gradient from a 50-m resolution digital elevation model (DTSI 2012). We assessed the total portion of forest and species that was included in mining or protected areas. We counted the number of red-listed species included either in each UM unit and each grid cell.

Tree diversity

We computed the observed number of species at both the UM unit and grid cell scales. We then used the bias-corrected Chao2 estimator to estimate the expected number of species (i.e. including those that have not been inventoried so far) in each UM unit. The bias-corrected Chao2 estimator (Chao 1984) was computed with the "SpadeR" package (Chao et al. 2016). It provides a robust estimator of the minimum expected species richness of a given area (i.e. here each UM unit) based on the number of species occurring in only one sample (i.e. here one grid cell) and the number of species occurring in only two samples (i.e. here two grid cells). The difference between the observed number of species and the expected number of species provided a conservative estimate of the number of species that have yet to be inventoried in future surveys.

We measured the floristic similarity between each pair of UM units using the Simpson dissimilarity index (β_{dissim}). For a pair of UM units 1 and 2, the florisitic diversity (β_{sim}) = 1 - β_{dissim} = $1-[\min(b,c)/[a+\min(b,c)]]$, with a being the number of shared species, b being the number of species occurring only in unit 1, and c the in unit 2 (Simpson 1943; Lennon et al. 2001). We chose this index because it describes spatial turnover in species composition without being directly influenced by differences in species richness (Baselga 2010; Castro-Insua et al. 2018). Indeed, differences in species richness were expected to have a strong influence on similarity given the large differences in the size of UM units. We then used hierarchical cluster analysis (hclust function from the vegan R package, Oksanen et al. 2022) with the Ward agglomeration method to group UM units as a function of their floristic similarity.

Data management and processing

Data management was performed with the PostgreSQL 14.5 relational database management system (PostgreSQL Global Development Group). Geographic data processing was performed using the Postgis 3.2.2 spatial base extension (The PostGIS Team) and the maps were drawn through Quantum GIS 3.26.2-Buenos Aires (Quantum GIS Development Team, 2022). Statistical analyses were performed using the R software 4.2.1 (R Foundation for Statistical Computing, Vienna, Austria).

Results

The 22 studied UM units covered a total of 5,481 km^2 (i.e.>90% of the total New Caledonian UM areas) with areas ranging from 12 to 3,426 km^2, maximum elevations ranging from 187 to 1,618 m asl, and maximum annual rainfalls ranging from 1,370 to 4,710 mm.year^{-1} with high elevation units receiving more rainfall (Figure 1). Mining concessions cover 44.1% of the UM units with a coverage ranging from less than 3% in Ouatilou up to 84.3% in Bogota (Table 1). All but two UM units (Poindas-Grandié, and île des Pins) included mining concessions. All the protected areas on UM were located in the South province, mainly on the Massif du Sud (360.6 km^2), while much smaller protected areas or portions of protected areas were located on the Me Maoya (8.1 km^2), Mt Dô (3.0 km^2), and Téné-Mé Adéo (1.1 km^2).

Forest

Forest covered an area of 5,341 km^2 on the North and South provinces (32.6% of the land area), including 3,441 km^2 of forest on non-UM soils (33.1% of non-UM areas) and 1,900 km^2 of forest on UM soils (31.7% of UM areas). The 22 studied UM units were covered by 1,747 km^2 of forest (i.e. a forest cover of 31.9%). Forest cover greatly varied between UM units and ranged from 1.7% on Poum up to 72.3% on the Poindas-Grandié unit (Table 1). The largest UM unit, i.e. the Massif du Sud, disproportionately contributed to the forest cover of the 22 UM units (71.1% of the total forest area vs. 62.5% of the total land area represented by the 22 UM units). Overall, about 30% of the forest in the studied UM units were located within mining concessions while only 14.5% were located within protected areas. The Massif du Sud, which concentrated 53.7% of the mining concessions and 96.7% of the protected ultramafic areas, exhibited the greatest proportion of forest cover located within protected areas (19.7%) in comparison with other UM units. However, this relatively high proportion of protected forest was still lower than the proportion of forest located within mining areas (25.4%).

At the grid level, more than 50% of grid cells (708), distributed over 19 UM units, had a forest cover of less than or equal to 25% (Figure 2). They totalized 278.6 km^2 of forest including 10.6 km^2 in protected areas and 145.0 km^2 in mining concessions. Contrastingly, only 7 UM units enclosed 134 cells with a forest cover ≥75% (Massif du Sud, Me Maoya, Poindas-Grandié, Téné-Mé Adéo, Tchingou, Kopéto-Boulinda and Ile des Pins). These cells accounted for 459.7 km^2 of forest, with 172.8 km^2 of forest located in protected areas and 40.4 km^2 of forest located in mining concessions. Six units (Ile Ouen, Ile Yande, Monéo, Ouala, Poum, Tiébaghi) only had forest cover cells <25% and only

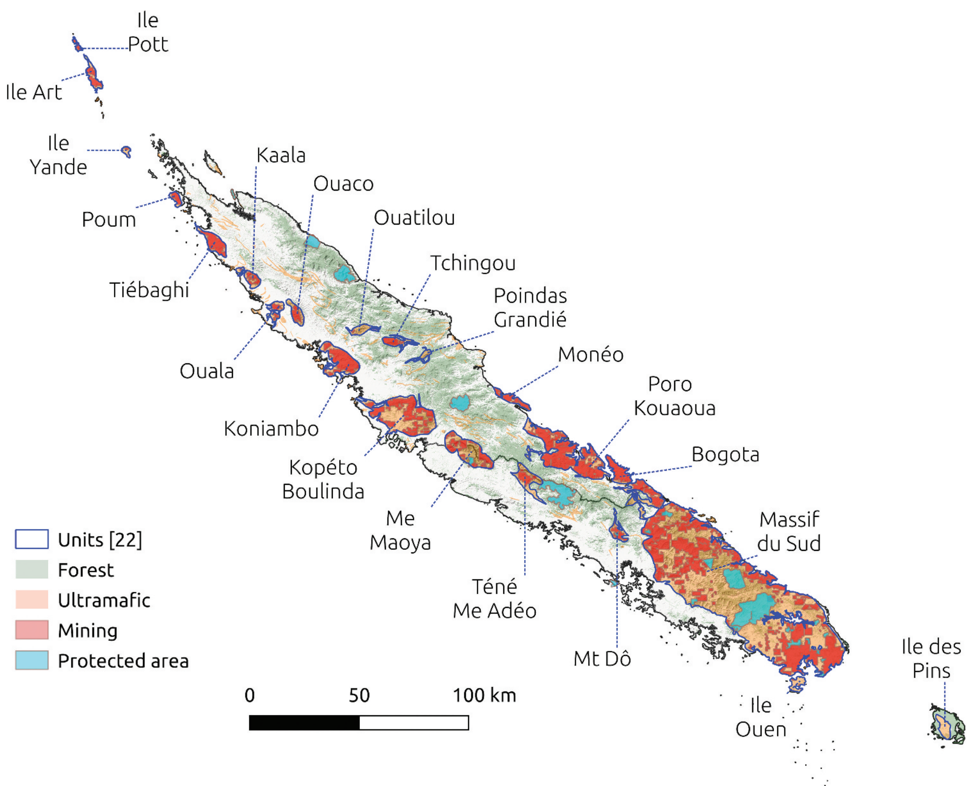

Figure 1. Location of the 22 studied ultramafic units, mining concessions, and protected areas. background colours show ultramafic and forest areas as well as elevation in transparency. toponymy was extracted from georep.Nc.

Table 1. Summary of the land and forest variables for the 22 UM units.

	Land					Forest				
UM Unit	Max. elevation (m)	area (km^2)	contribution (%)	mining area (%)	protected area (%)	area (km^2)	contribution (%)	coverage (%)	mining area (%)	protected area (%)
Bogota	612	77.8	1.4	84.3	-	6.8	0.4	8.8	80.4	-
Ile Art	288	51	0.9	60.3	-	7	0.4	13.8	73.1	-
Ile des Pins	259	46.1	0.8	-	-	9.9	0.6	21.4	-	-
Ile Ouen	326	35.2	0.6	5.8	-	4.6	0.3	13.1	13	-
Ile Pott	185	11.7	0.2	80.1	-	2	0.1	17	93	-
Ile Yande	302	13	0.2	9.7	-	0.5	0	3.9	5.7	-
Kaala	1075	52.7	1	41.6	-	9.3	0.5	17.7	50.7	-
Koniambo	934	169.4	3.1	70.5	-	19.4	1.1	11.5	81.3	-
Kopéto-Boulinda	1330	423.1	7.7	49.3	-	106.8	6.1	25.2	42.5	-
Massif du Sud	1618	3426.4	62.5	37.9	10.5	1242.1	71.1	36.2	25.4	19.7
Me Maoya	1501	209.4	3.8	43	3.9	110.3	6.3	52.7	28	6.9
Monéo	419	51.2	0.9	76.3	-	3	0.2	5.9	48.5	-
Mt Dô	1025	48.6	0.9	44.7	6.2	17.2	1	35.4	29.1	6.7
Ouaco	1073	50.9	0.9	45.3	-	24.6	1.4	48.3	50.6	-
Ouala	853	46.3	0.8	33.3	-	1.7	0.1	3.7	31.6	-
Ouatilou	1168	41	0.7	2.9	-	17.3	1	42.1	0	-
Poindas-Grandié	948	23.8	0.4	-	-	17.2	1	72.3	-	-
Poro – Kouaoua	1089	449	8.2	73	-	79	4.5	17.6	70.1	-
Poum	401	24	0.4	70.8	-	0.4	0	1.7	84.1	-
Tchingou	1381	50.7	0.9	53.9	-	27.9	1.6	55	51.1	-
Téné-Mé Adéo	1098	98.3	1.8	30.5	1.1	37.8	2.2	38.4	28	0.9
Tiébaghi	599	81.2	1.5	83.1	-	2.1	0.1	2.6	93	-
All	1.618	5480.8	100	44.1	6.8	1746.8	100	31.9	30.2	14.5

two units (Tchingou and Poindas-Grandié) had forest cover cells > = 25%. Surprisingly, the large units of Poro-Kouaoua (449 km^2) and Koniambo (169 km^2) did not have forest cover cells > = 75%.

Forest cover of the UM units increased with elevation, from 14.6% below 100 m up to 93.3% between 1,200 and 1,300 m before decreasing at higher elevations (cf. SOM1). Although 45.3% of the land was located below 300 m elevation, only 29.3% of the forest was located below this threshold. On the contrary, while 3.4% of the land was located above 1,000 m elevation, almost 7.7% of the forest was located above this elevation. The proportion of forest located within mining concessions decreased with elevation while the proportion of forest located within protected areas increased. Below 800 m of elevation, there was

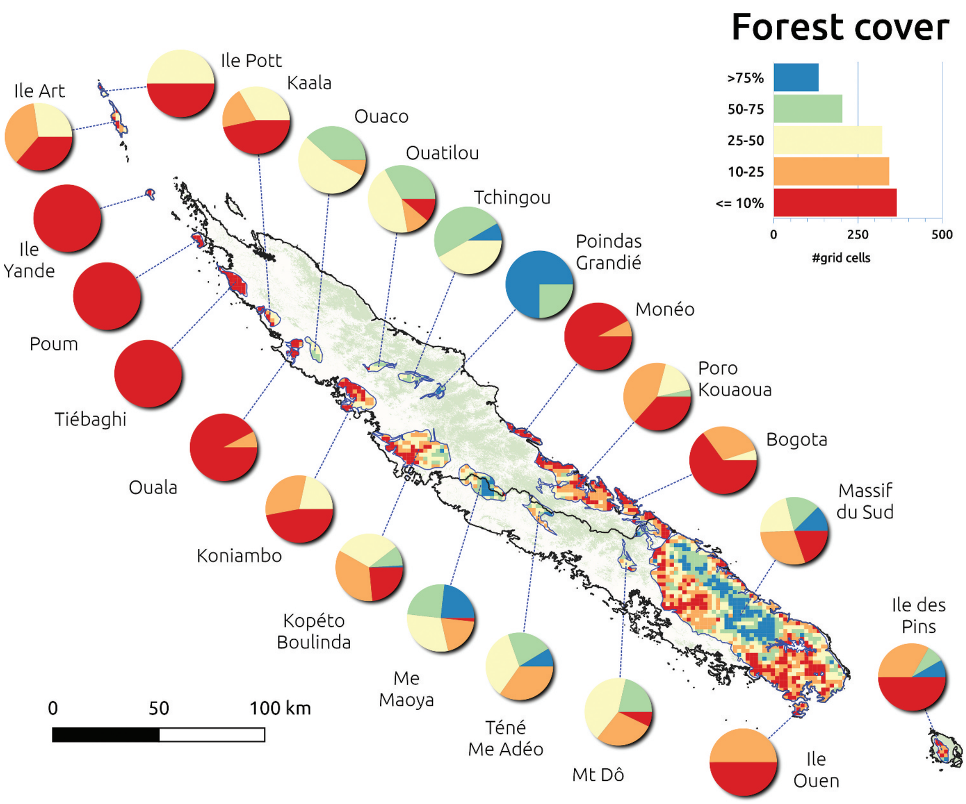

Figure 2. Geographical distribution of the UM units forest cover over a 2 × 2 km grid (bar plot) and for the 22 UM units (pie charts).

more forest area in mining concessions than in protected areas, while at higher elevation, the reverse pattern was observed.

Trees

Occurrences and species distribution

About two-thirds of the total tree occurrences compiled at the NC scale occurred on the 22 UM units, representing a total of 109,896 unique occurrences (Table 2). A total of 1,065 tree species (1020 Angiosperms, 36 Gymnosperms and 9 Pteridophytes), belonging to 279 genera and 93 families occurred at least once in one of the 22 UM units (cf. SOM2). Most of these species were endemic to NC (90.8%), 474 (44.5%) have been assessed by the IUCN Red List Authority, 147 species were classified as threatened (CR, EN, or VU), and 66 species as near threatened (NT). Only 62 species were restricted to UM but 303 species (28.4%) had more than 90% of their occurrences on UM. The top 10% of species, each with more than 250 occurrences, accounted for more than 50% of total occurrences.

More than a third of species only occurred in one or two UM units, 13.6% of the species occurred in only one or two 2 km x 2 km grid cells, and 9.9% of the species had only one or two occurrences (cf. SOM3). Only two species, *Styphelia cymbulae* (Ericaceae) and *Austrobuxus carunculatus (Picrodendraceae)*, occurred in all UM units. *Styphelia cymbulae* was particularly frequent with more than 2,000 occurrences distributed over 483 grid cells (out of the 1,368 grid cells).

The distribution of occurrences was also unevenly distributed among and within UM units. Higher number of occurrences were gathered in larger units (Rho spearman = 0.84, $P < 0.001$). For instance, the Massif du Sud represented 59.1% of the occurrences while the contribution of Ile Ouen was less than 0.1% (Table 2). Overall, 75.8% of grid-cells contained at least one occurrence and 19 units had empty grid cells (Figure 3). More than a third of the grid cells of the Poindas-Grandié, Ile Ouen and Tchingou units contained no occurrences. On average, a cell contained 32 species, while the median was only 13 species per cell. However, two grid cells in the Massif du Sud contained more than 2,000 occurrences each, 12 units had cells with 100 or more species, while 50 grid cells contained only one occurrence. The richest cell (332 species for 1,063 occurrences) was located in the massif du Sud.

Four UM units included protected areas. Despite representing a low proportion of occurrences (17.1%) over a small area (6.8% of UM land areas, i.e. 50.4 occurrences/km^2), these protected areas included at least one individual of nearly three quarters of the total number of tree species (72.8%) and 54.4% of the threatened species (Table 2). Mining concessions included 57.2% of the occurrences (i.e. 26.0 occurrences/km^2), including nearly 90% of species (with 13 species occurring exclusively in mining areas) and over 81% of the threatened species.

The number of occurrences and species decreased with elevation with a maximum of 837 species located in the range 100–200 m and only 66 species at highest elevation (cf. SOM1). The species density slowly increased from less than 2 species/km^2 in the range 0–800 m to 162 species/km^2 above 1,600 m on Mt Humboldt. Occurrences and species densities were higher in protected areas than in mining areas. However, in the lowest band (0–100 m), we accounted for a total of 743 species of which 613 were located in mining concessions, while only 14 were included in protected areas.

Diversity

The number of inventoried species ranged from 27 on the Ile Ouen to 898 in the Massif du Sud unit and was strongly correlated with the number of occurrences (Rho = 0.92, $P < 0.001$). The differences between the observed number of species and the Chao2 estimator (Table 2) suggested that on average about one-quarter of the species had yet to be inventoried in the different units. About 90% (between 87.4% and 95.9%, 95% CI) of the species would have been already inventoried in the Massif du Sud, while between 34.6% and 53.0% (95% CI) of the species would have yet to be inventoried in the Téné-Mé Adéo unit. Five units (Ile Ouen, Ile Pott, Ile Yande, Ouatilou, Poindas-Grandié) did not have enough data to compute the Chao2 estimator.

Similarity

Hierarchical cluster analysis using Simpson similarity index (βsim) identified three different groups of units (Figure 4, cf SOM4). The largest and more heterogeneous group (βsim ranging from 1.00, i.e. all species that occurred in Ile Ouen also occurred in the Massif du Sud, to 0.22) included the Ile Ouen, the southern UM units of the Grande Terre up to Me Maoya, as well as the three units located in the centre of the northern part of the Grand Terre (Ouatilou, Tchingou, and Poindas-Grandié). In this group, the three units located in the center of the east coast (Poro – Kouaoua, Bogota, and Monéo) formed a sub-group. A smaller and more homogeneous group (βsim ranging from 0.95 to 0.54) included all the UM units located along the Northwestern coast from Kopéto-Boulinda to Poum plus the Ile Yande. Finally, a third group included the Ile des Pins in the south and the Ile Art and Pott in the North with the two later units forming a sub-group.

Discussion

Forest distribution

Estimates of forest coverage in New Caledonia largely varied over the last decades depending on the

Table 2. Summary of tree species occurrence dataset for the 22 ultramafic units.

	Tree												
UM Unit	Nb. Occurrences	Occurrences density (#/km^2)	Contribution (%)	mining area (%)	protected area (%)	Nb. Species	mining area (%)	protected area (%)	Red List Assessed Species	Red List Threatened species	mining area (%)	protected area (%)	Richness Chao2 [95%CI]
Bogota	688	8.8	0.6	96.2	-	168	97.6	-	65	6	100	-	238 [204–297]
Ile Art	777	15.2	0.7	62	-	187	73.8	-	63	7	100	-	247 [215–307]
Ile des Pins	563	12.2	0.5	-	-	174	-	-	57	5	-	-	232 [208–274]
Ile Ouen	34	1,0	0	0	-	27	0	-	13	1	0	-	-
Ile Pott	163	13.9	0.1	66.9	-	76	89.5	-	19	1	100	-	-
Ile Yande	182	14,0	0.2	12.1	-	73	27.4	-	18	1	0	-	-
Kaala	1504	28.5	1.4	62.7	-	189	85.2	-	73	16	81.3	-	224 [205–262]
Koniambo	6958	41.1	6.3	80.9	-	316	81.6	-	118	17	82.4	-	380 [348–435]
Kopéto-Boulinda	9492	22.4	8.6	80.5	-	568	82.6	-	232	49	81.6	-	587 [555–639]
Massif du Sud	64919	18.9	59.1	42.7	27.2	898	83.6	83.5	399	99	75.8	74.7	971 [937–1027]
Me Maoya	1834	8.8	1.7	46.3	25.5	397	61	45.8	169	26	61.5	38.5	530 [484–598]
Monéo	414	8.1	0.4	81.2	-	117	88	-	54	9	77.8	-	154 [128–208]
Mt Dô	1085	22.3	1	54.7	51.3	234	79.1	71.8	98	12	75	66.7	290 [266–330]
Ouaco	966	19,0	0.9	51.1	-	194	69.1	-	77	8	62.5	-	266 [226–336]
Ouala	538	11.6	0.5	71.4	-	135	77	-	49	9	55.6	-	178 [154–224]
Ouatilou	378	9.2	0.3	3.2	-	136	7.4	-	62	4	0	-	-
Poindas-Grandié	323	13.6	0.3	-	-	140	-	-	62	3	-	-	-
Poro – Kouaoua	11287	25.1	10.3	92.4	-	566	76.5	-	255	51	56.9	-	756 [689–854]
Poum	1150	47.9	1	94.6	-	162	95.7	-	50	11	81.8	-	171 [153–206]
Tchingou	972	19.2	0.9	97.5	-	237	97.9	-	111	15	100	-	310 [280–359]
Téné-Mé Adéo	1037	10.5	0.9	28.1	13.3	376	63.3	17	166	21	57.1	28.6	668 [575–800]
Tiébaghi	4632	57,0	4.2	92.1	-	288	96.5	-	105	18	94.4	-	359 [327–418]
All	109896	20.1	100	57.2	17.1	1065	89.7	72.8	474	147	81.6	54.4	-

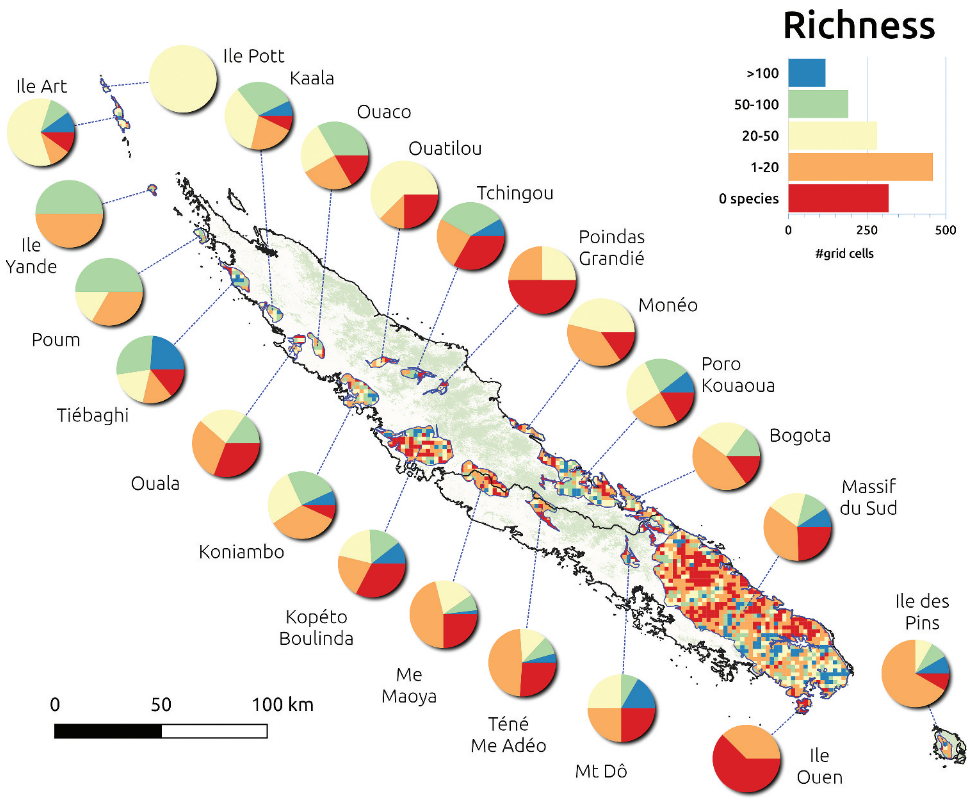

Figure 3. A) geographical distribution of tree richness over a 2 × 2 km grid (bar plot) and for the 22 UM units (pie charts).

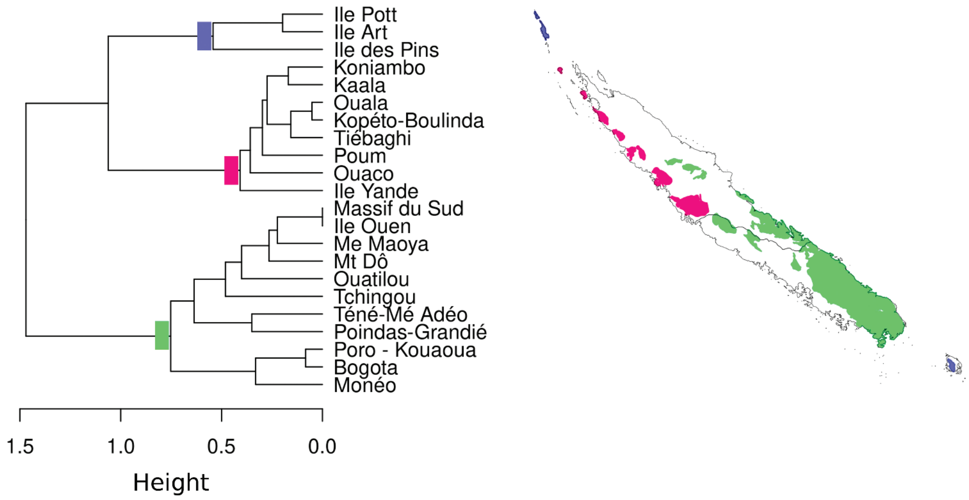

Figure 4. Hierarchical cluster analysis using Simpson dissimilarity index and ward's grouping method.

definition of the forest and the methods used to delineate forest. For instance, using an expert photo-interpretation at a 1:1,000,000 spatial resolution, Morat et al. (1981) found forest covered 21.6% of New Caledonia but Myers (1988) considered that less than half of that was actually "primary" forest. More recently, using Global Land Cover data (Bontemps et al. 2011) and after removing forest patches too small (<1 km^2) and too close to sources of disturbances (e.g. roads, villages, burned areas), Sloan et al. (2014) estimated that "natural" forest covered 17.5% of the territory.

Here we provide a new accurate estimate of forest cover based on the FAO definition (FAO 2020). We estimated that forest covers 32.6% of the South and North provinces of New Caledonia and that forest coverage was only slightly lower on ultramafic (31.7%) than on non-ultramafic soils (33.1%). This coverage is consistent with global estimates that forest covers about one-third of global land area (FAO 2020; Liang and Wang 2010). We found 1,750 km^2 of forest on the 22 ultramafic (UM) units. The Massif du Sud which covers 62.5% of the UM land areas harbours 71.1% of the forest located on UM. The Me Maoya also contributes disproportionately to forest coverage as it covers only 3.8% of the UM land areas but harbours 6.3% of the forest located on UM.

Previous studies conducted in the Massif du Sud showed that edges affect the structure and composition of forest up to 100 m and more inside forest fragments (Ibanez et al. 2017; Blanchard et al. in press). If we remove the forest within 100 m of the nearest edge, then only half of the forest area remains within the 22 UM units, with half of the UM units losing more than 70% of the original forest area. This highlights the high level of fragmentation of the New Caledonian forest. Fragmentation should result in profound changes in the structure and diversity of that forest through edge effects (Laurance et al. 2002; Smith et al. 2018; Blanchard et al. 2020). Beyond the conservation of the existing forest fragments, significant measures of forest restoration should be undertaken in the UM units with low forest coverage (e.g. in units with less than 10% forest coverage: Île Yande, Ouala, Poum, Tiebaghi, Bogota, and Monéo).

The flora

While the occurrence dataset analysed here is three times larger than previously compiled by Birnbaum et al. (2015), the frequency of occurrence remains highly unbalanced between species at all studied spatial scales. For instance, 10% of species account for 50% of the total occurrences across the 22 UM units, while 10% of the species had only one or two occurrences. Furthermore, only two species (*Styphelia cymbulae* and *Austrobuxus carunculatus*, which are common as shrubs in maquis) occurred in all UM units, while 375 species only occurred in one or two UM units and 135 occurred in only one or two 2 km × 2 km grid cells. Such patterns of rarity (Rabinowitz 1981) highlight narrow endemic species (Wulff et al. 2013; Lannuzel et al. 2022), which can be threatened or endangered when they are located outside protected areas.

Among the 1,065 tree species occurring in the 22 UM units, 303 species (28.5%) had at least 90% of their occurrences on UM but only 62 species (5.8%) were restricted to UM. The latter figure is low compared to the 36.8% of species that only grow on UM soils according to herbarium vouchers for the whole New Caledonian flora (Isnard et al. 2016). This difference can be explained by errors in species identification, geolocation, or imprecise estimates of the peridotite layer (Lannuzel et al. 2022). Most of the species with only one or two occurrences in the 22 UM units are actually quite frequent on non-UM soils. Those species that usually grow on non-UM soils are likely able to grow on UM soils in forest because of deep soil and thick litter that buffer the challenging UM soil conditions (Isnard et al. 2016). Moreover, forest areas often extend beyond the limits of UM soils so that species transgressions are possible at the boundary between the UM and non-UM soils. Such transgressions might be more likely at high elevations where more similar tree communities have been observed (Ibanez et al., 2014).

Species richness

Despite our large dataset, the estimated species richness still depends on the number of species occurrences per spatial unit. We estimate that on average a quarter of the species remained to be inventoried in the 22 units, whereas in total 23% of the 2 km × 2 km grid cells still did not contain any occurrences. Collection effort is unbalanced. While some units have been highly collected (e.g. Tiébaghi, Poum, and Koniambo) others are under-surveyed (e.g. Monéo, Me Maoya, Bogota) and several do not have enough occurrences in enough 2 km × 2 km grid cells to estimate the expected richness (Ouatilou, Poindas-Grandié, Ile Ouen, Ile Pott, Ile Yande). In addition, there are more than three times as many occurrences in mining areas than in protected areas but the number of occurrences by unit of area is higher in protected areas than in mining areas. Nevertheless, it is outside the protected and mining areas that collecting is the weakest. While occurrences in protected areas are likely to well reflect the current distribution of species, this is much more uncertain for occurrences in mining areas as many of these occurrences were gathered during mandatory impact studies prior to mining (Lannuzel et al. 2022). As a result, the observed richness is probably closer to the current value in protected areas than in mining areas where a number of species might have locally disappeared. Finally, considerable collecting efforts should be deployed to draw a complete picture of the current distribution of tree species in New Caledonia and help to plan adequate conservation measures (Ibanez et al. 2019; Meyer et al. 2021). For instance, the Ouatilou and the Poindas-Grandié units, which are among the most forest-covered units, have been under-surveyed because these units not covered by protected areas and barely or not covered by mining areas are then difficult to access. As a result, we were not able to estimate species richness in these units. Surveying these units should help to precise their floristic affinities with the other units. Another candidate for more collection is the Téné-Mé Adéo unit that has large areas of forest that remain largely under-surveyed with more than 40% of the species of this unit that remain to be inventoried.

Recommendations for new protected areas

Mining areas are prevalent in all but two units and contain most of the forest occurrences and threatened species. Proportionately to their area, protected areas contain more forest, occurrences and species than mining areas, but their cover and spatial distribution are still insufficient to guarantee conservation of tree species and forest habitat. Only four UM units include protected areas, and almost 30% of species and 50% of threatened species do not occur in these protected areas, suggesting that the current system of protected areas not only fails to capture the full species diversity but also does not integrate species distribution across the different orographic units. Importantly, there are still no protected areas on UM soils in the North province.

We identified three groups of UM units based on their floristic similarities. Currently, two of these groups do not have any formal protection. One of these two groups is the second largest floristic group (8 UM units, 860.6 km^2) and is located along the Northwestern coast from Kopéto-Boulinda to Poum plus the île Yande. Entirely located in the North province, this floristic complex that has long been identified as a priority for conservation (Jaffré et al. 1987) includes a series of isolated orographic massifs known to host many micro-endemic and threatened species (Wulff et al. 2013; Meyer et al. 2021; Lannuzel et al. 2022). Among the units of this group, the Kopéto-Boulinda is a suitable candidate with more than 100 km^2 of forest, less than 50% covered by mining concessions, 568 known tree species and a recognized peculiar flora (Jaffré et al. 1987; Barrabé et al. 2011). The other group consists of islands (Ile Pott, Ile Art, Ilde des Pins) located relatively far from the main island. Although covering a smaller area (3 UM units, 108.8 km^2) these islands host a threatened flora and only few remaining forest patches that also urgently need protection (Wulff et al. 2013; Gâteblé et al. 2018). Furthermore, some units such as Tchingou, Ouatilou and Poindas-Grandié, which have both high forest cover, high elevation and no active mining concessions could be suitable sites for the establishment of protected areas on UM soils in the North province. They would make a northern extension to the network of protected areas within the largest floristic group (11 UM units for 4,511.4 km^2) which extends the Massif du Sud unit. The system of protected areas should also be extended to lower elevation as there are only little areas protected below 300 m while remaining forest is very scarce at this elevation (<25% coverage). As suggested by Wolf (2001) and enhanced by the OCBIL theory (Hopper 2009; Pillon et al. 2021), we recommend developing an ultramafic forest conservation strategy that takes into account the fragmentation and spatial heterogeneity of floristic richness. For this, systematic conservation planning can rely on criteria-base approach (e.g. Important Plant Area criteria, Darbyshire et al. 2017) and powerful algorithms to propose protected areas adapted to such fragmented environments (Thorne et al. 2011; Justeau□allaire et al. 2021).

Forest cover increases with elevation, from ~15% below 100 m to 93% between 1200 and 1300 m. In the units located in the South province, the forest is subject to several human activities including mining and fires at low altitudes (0–300 m), while at higher altitudes, the coverage of protected areas is maximum. In the North province, mining is maximum at high altitude and there are no protected areas. Considering that a hundred new mining concessions were issued and the rate of nickel extraction has doubled in only 20 years (Nakajima et al. 2017), we expect the threat to forest and the biodiversity increases, resulting in a harsh environmental filter to the benefit of tree species that tolerate both open habitats and soil toxicity. In parallel, fragmentation could amplify the dominance of a few species tolerant to the microclimatic conditions at the forest edge to the detriment of the less tolerant species (Blanchard et al. 2020; Blanchard et al. in press). The combination of deforestation of lowland forest, high density of endemic species, and impacts of global warming on the summit forest (Pouteau and Birnbaum 2016) suggests that forest on ultramafic substrate, including many endemic tree species, is seriously threatened in New Caledonia.

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P.B. conceived the study, managed the database, compiled the datasets, led the forest digitizing, proceeded with the GIS-analysis, and led the writing of this article. T. I. conceived the study, led the statistical analyses. G. B. actively contributed to the data acquisition and the writing. D.J.-A. actively contributed to the data acquisition and the writing. V.H. was involved in the collection of many tree species occurrences used in this article. N.E. was involved in the collection of many tree species occurrences used in this article. G.V. reviewed the final manuscript. N.B. reviewed the final manuscript. R.B. was involved in the collection of many tree species occurrences used in this article. D. B. curator of the herbarium of New Caledonia provided numerous data used in the dataset and actively contributed to the writing

Data availability statement

The data that support the findings of this study result from a compilation of open data available online (GBIF, Nou-Herbarium, and NC-PIPPN) and data submitted by mining companies or environmental managers, which are hosted by endemia as the New Caledonia red list authority. The dataset is available on request from the corresponding author [PB] subject to the underlying agreement of all parties.

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