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REGULAR ARTICLE

How did the ultramafic soils shape the flora of the New Caledonian hotspot?

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Abstract

Background New Caledonia is renowned as one of the world's most significant biodiversity hotpots. The nutrient-deficiency and cations imbalances of ultramafic soils, which cover a third of the island, harbor a disproportionally high proportion of the plant diversity and endemism of New Caledonia.

Scope This review explores how ultramafic soils have influenced the exceptional endemism and richness of New Caledonia trough the concomitant occurrences of habitat patchiness, climatic instability, environmental gradient, and edaphic heterogeneity of ultramafic soils. We focus on the unique 'maquis' vegetation where selective pressures by nutrient deficiency and trace element surplus are at their acme. We aim to synthesize our current understanding of diversification and speciation of lineages that have been phylogenetically studied to date.

Conclusions Fragmentation of the peridotite mantle in isolated massifs, and as such spatial heterogeneity of ultramafic soils types, appear to promote plant endemism and speciation. Repeated independent dispersal events of pre-adapted species and persistence of paleo-endemic lineages have contributed to the phylogenetic diversity and the endemism of the ultramafic flora. Finally, historical climatic instability has caused shifts of rain forest species in refugia thereby favoring the extension of maquis species.

Keywords Diversification · Endemism · Forests · Harsh edaphic conditions · Maquis · Nutritional strategies · Preadaptation · Species richness

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Introduction

New Caledonia, located in the southwestern Pacific, is renowned for its exceptional flora (Morat et al. 2012; Schmid 1981; Thorne 1965; Virot 1956) and considered one of the world's most important biodiversity hotpots, as defined by Myers et al. (2000). The total vascular flora comprises ~3370 species of which more than 74 % are endemic (Morat et al. 2012). The richness of the New Caledonian flora is attributed to the climatic, geological and topographical diversity of the archipelago (Jaffré 1993), combined with long-term isolation. The presence of old and early diverging lineages was previously considered as evidence of the Gondwanan origin

of New Caledonia (e.g. Lowry II 1998; Morat 1993) with a flora dating back to the Cretaceous (~85–65 Ma). However, recent geological studies (Pelletier 2006) and dated phylogenies (reviewed by Grandcolas et al. 2008; Murienne 2009), provided evidence for a more recent origin of the New Caledonia biota ~37 Ma, consequently implying that most plant lineages colonized the island through long distance dispersal since the Eocene. The main island of New Caledonia (Grande Terre) experienced a submersion up to the late Eocene for a period of ~20 Ma (Pelletier 2006) and has probably been almost entirely covered by a slice of oceanic lithospheric mantle during its emersion, giving rise to the ultramafic bedrock that, after erosion and fragmentation, covers about one third of the surface area today (including the Belep and Pines islands totaling ~5470 km^2). Ultramafic outcrops are found from sea level to about 1600 m on Grande Terre. These outcrops include ultramafic massifs (Fig. 1), composed of peridotites mainly overlying serpentinite bedrock, which are known as "terrains miniers" (L'Huillier et al. 2010), and serpentinite outcrops occurring in the form of veins up to 10 m wide and several kilometers long within the volcano-sedimentary formations and at the base of ultramafic massifs on the western coast up to 400-450 m. The ultramafic soils of New Caledonia are mineralogically, pedologically and chemically varied and supports diverse vegetation types (Fig. 2) and high levels of plant endemism (Jaffré 1980; Morat et al. 2012).

Edaphic endemism has been recognized as a key factor for stimulating plant diversity and endemism of several other global biodiversity hotspots, such as in California and the Mediterranean Region, the South African Cape and the Southwest Australian floras (Cowling and Lombard 2002; Hopper and Gioia 2004; Safford et al. 2005). In New Caledonia ultramafic soils have long been considered as the main causal factor of the plant richness and distinctiveness of the Island (Jaffré 1980, 1992; Pillon et al. 2010; Schmid 1982; Virot 1956). Although ultramafic plants in New Caledonia have been intensively studied, an integrated understanding, combining the current knowledge on floristic and soil diversity, habitat heterogeneity, and phylogenetic patterns of diversification and adaptation to a wide diversity of ultramafic soil properties, is lacking. Here we review the ways in which ultramafic soils have influenced patterns of plant diversity, distribution and endemism in New Caledonia. We use botanical information collected over the past decades, combined

with recent insights from molecular studies that have produced robust phylogenetic hypotheses on patterns of plant diversification, thereby progressively filling the gaps in the evolutionary history of the New Caledonian flora. We consider the relative importance of factors such as habitat patchiness, climate, complex topography and the edaphic heterogeneity of ultramafic soils, on patterns of diversification and speciation of the (ultramafic) flora of New Caledonia.

Methods and terminology

The information contained in this article is based on an updated list of the ultramafic flora (which is available upon request). The list was first compiled from the 25 volumes of the Flora of New Caledonia (Aubréville et al. 1967-) and records from the herbaria of the IRD in Nouméa (NOU), the Muséum National d'Histoire Naturelle de Paris (P), and the Missouri Botanical Gardens (MO)). An extensive survey of recent literature, herbarium records and field observations was conducted to ensure the taxon listing was as complete as possible. The recently revised checklist of the New Caledonian flora "FLORICAL" (Morat et al. 2012; www.botanique.nc/herbier/florical) was used to update the taxonomy.

To score the affinity of taxa to ultramafic soils, we used species description or occurrence localities. We assigned the category "ultramafic-obligate" ("Uo") when habitat description or localities unambiguously states that a species is ultramafic- or serpentine-specialist. The category "ultramafic-facultative" ("Uf") was assigned when adjectives such as "often", "sometimes" or "usually" were added to the description of species' soil ecology. Finally, the category other "soil-obligate" ("Oo") was assigned to species that have not been observed on ultramafic soils. We then added to the list a number of taxa that we considered to be endemic or facultative to ultramafic soils but were not indicated as such by the current literature. The final list contains a total of 3313 documented native species, i.e. 98 % of the total known flora.

Species were classified according to: (i) their status (endemic or native) and (ii) their distribution in the different vegetation types. For simplicity, the vegetation types have been treated as forest flora or non-forest flora. The ultramafic flora has been analysed in comparison to the flora occurring on all other soils.
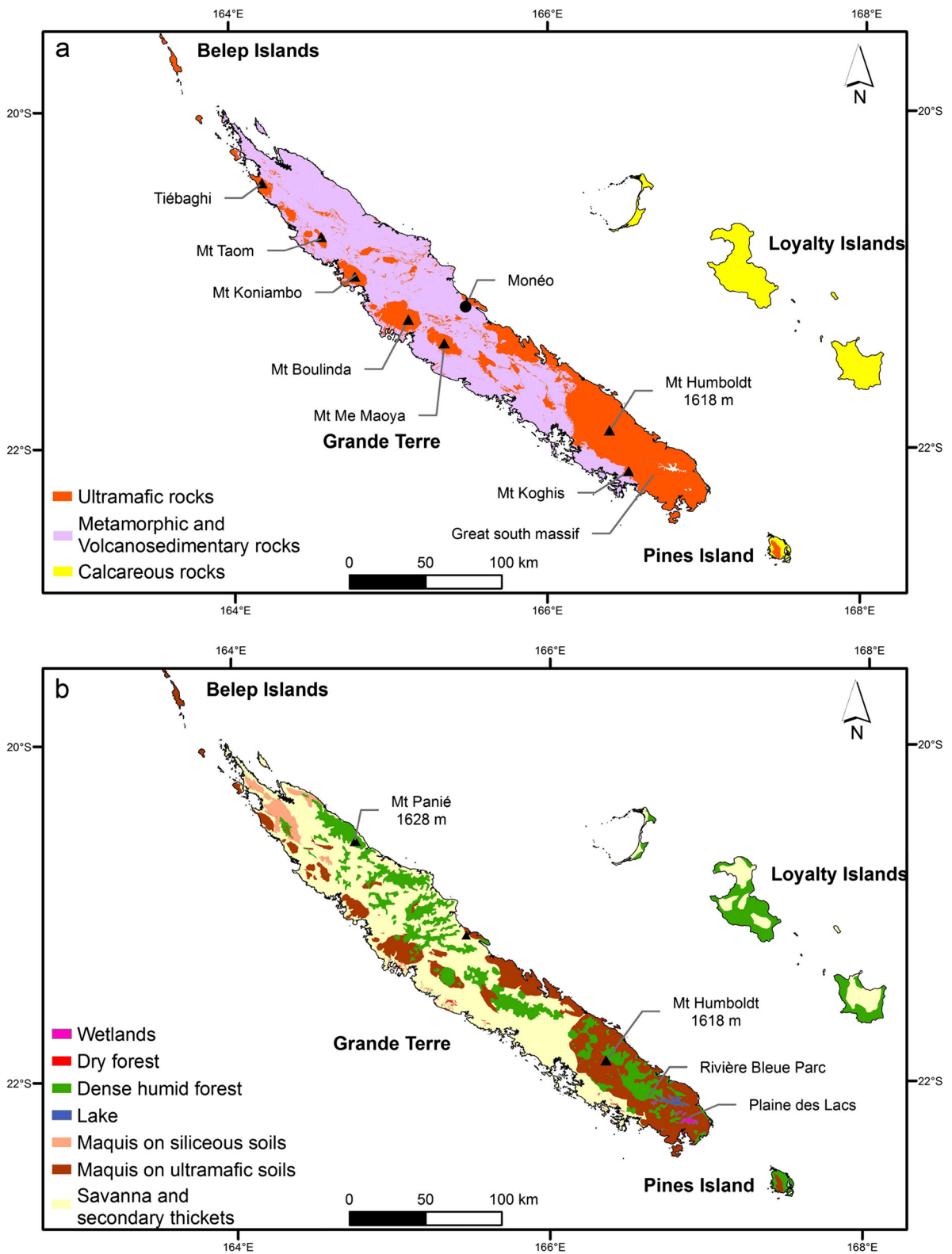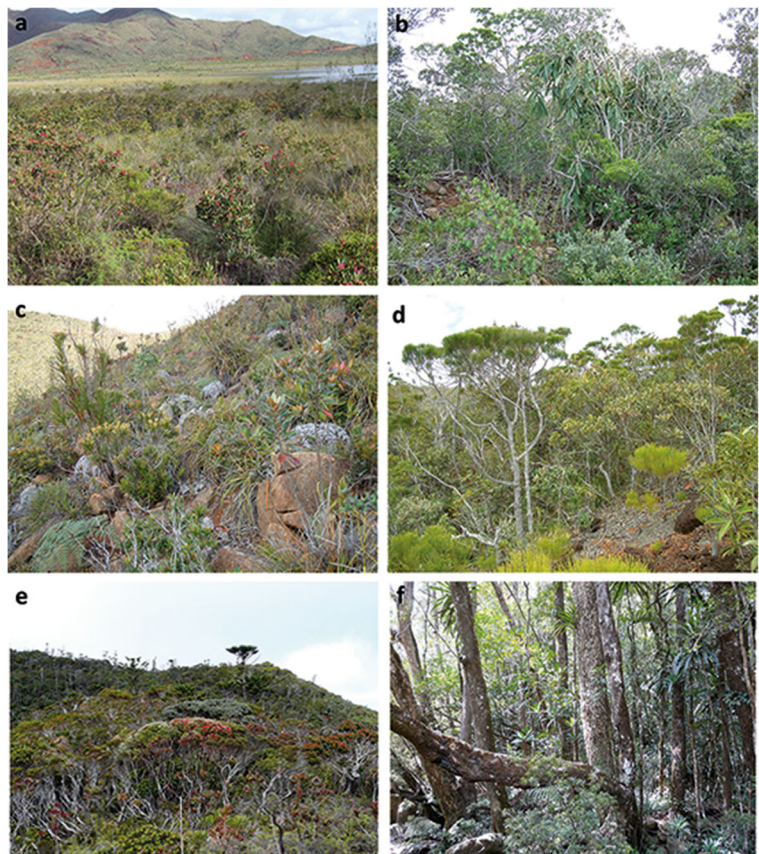
Fig. 1 Maps: **a** distribution of the main soil categories; **b** distribution of the main vegetation types

Fig. 2 Main vegetation type on ultramafic soils: **a** Hydromorphic vegetation; **b** bushy maquis on serpentinite; **c** ligno-herbaceous maquis; **d** shrubby to bushy maquis; **e** shrubby to bushy altitudinal maquis; and **f** rain forest

Characteristics of soils derived from ultramafic rocks in New Caledonia

All soils derived from ultramafic rocks in New Caledonia, as in other parts of the world (Bani et al. 2014; Brooks 1987; Cheng et al. 2011; Garnier et al. 2009; van der Ent et al. 2016; Walker 1954), are diverse but characterized by low fertility (low phosphorous (P), potassium (K), and calcium (Ca), high exchangeable magnesium/calcium (Mg/Ca) ratio and high concentration of the trace elements nickel (Ni), cobalt (Co), chromium (Cr) and manganese (Mn). Two main types of ultramafic soils have been described from New Caledonia: "Brown Hypermagnesian soils" (Jaffré and Latham 1974) also classified as Magnesic Cambisols (Fritsch 2012), and "Ferritic Ferralitic soils" (Latham 1975) also classified as Ferralsols (Fritsch 2012). Various processes resulting from the tectonic history, relief re-organization, and climatic changes (Chevillotte et al. 2006; Trescases 1975) have resulted in the formation of: (i) eroded Ferralsols; (ii) colluvial Ferralsols (iii) gravelly or

indurated Ferralsols; and (iv) hydromorphic colluvio-alluvial Ferralsols (Table 1). The main chemical characteristics of soils derived from ultramafic rocks found in low sclerophyll evergreen scrublands (also called "maquis") are given in Table 1. Soils in rainforest differ in their thicker litter layer, higher rates of decomposition and higher nutrient concentrations. A comparison of the mineral composition of Ferralsols under adjacent maquis and rainforest is provided in Table 2.

The ultramafic soils of New Caledonia are immensely varied, as such represent a powerful useful models to study plant- soil relationships. Magnesic Cambisols on serpentinite, while representing only a small fraction of soils in New Caledonia, are equivalent to the "serpentine soils" which have been extensively studied (see Brady et al. 2005 for a review). Ferralsols are widespread in New Caledonia, and are more diversified than in many other regions due to their variation in depth (up to 30 m), pH (3.25–6), concentrations in Mg and in available Mn and Ni (Becquer et al. 1995, 2002; L'Huillier 1994). Ferralsols can be assimilated within laterites but lack

Table 1 Main chemical characteristics of soils derived from ultramafic rocks in the maquis of New Caledonia

| | Magnesic Cambisols ($n = 80$) | Ferralsols | | | |
| | | Eroded on slope ($n = 43$) | Colluvial ($n = 44$) | Plinthic (gravelly or indurated) ($n = 55$) | Hydromorphic colluvio-alluvial ($n = 4$) |
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
pH (H_2O)	6.81 (0.45)	5.96 (0.32)	5.25 (0.50)	4.69 (0.39)	6.00 (0.20)
Org. Matter (%)	13.66 (4.35)	14.17 (1.64)	14.45 (1.71)	14,26 (4,32)	–
N (mg/kg)	1390 (990)	610 (520)	750 (480)	720 (920)	1100 (300)
C/N	14.40 (3.41)	16.65 (7.93)	18.37 (6.57)	21.81 (10.47)	12.90 (4.42)
Exch. cations (cmol$_c$/kg)					
Ca^{++}	2.35 (2.31)	0.93 (0.96)	0.63 (0.88)	0.60 (0.65)	1.75 (0.20)
Mg^{++}	33.50 (15.00)	2.04 (1.54)	0.70 (1.11)	0.52 (0.52)	9.62 (2.61)
K^+	0.22 (0.17)	0.06 (0.04)	0.06 (0.05)	0.08 (0.12)	0.20 (0.10)
Na^+	0.35 (0.19)	0.08 (0.07)	0.05 (0.04)	0.08 (0.08)	0.25 (0.5)
CEC	40.90 (18.20)	8.15 (6.15)	6.03 (4.69)	7.65 (6.48)	24.40 (7.00)
Total elements					
P (mg/kg)	108 (89)	83 (47)	151 (48)	185 (117)	–
SiO_2 (%)	30.2 (9.4)	5.2 (6.4)	2.81 (2.30)	1.37 (2.40)	5.90 (1.80)
Al (%)	1.84 (1.19)	2.63 (1.13)	3.43 (1.13)	3.00 (1.43)	–
Fe (%)	17.30 (7.75)	42.50 (9.84)	46.58 (5.88)	46.50 (4.60)	17.40 (2.80)
Mn (%)	0.43 (0.38)	0.47 (0.28)	0.56 (0.30)	0.46 (0.36)	–
Ni (%)	0.60 (0.27)	0.94 (0.26)	0.66 (0.24)	0.26 (0.11)	0.91 (0.02)
Cr (%)	1.20 (1.37)	2.11 (1.46)	2.51 (1.45)	4.24 (2.82)	–
Co (%)	0.06 (0.05)	0.09 (0.03)	0.08 (0.05)	0.03 (0.03)	–

Sampling depth: 0–20 cm. Organic Matter determined by loss on ignition. CEC: cation exchange capacity measured in 0.5 m NH_4Cl. Data from Jaffré 1980; Jaffré and L'Huillier 2010; L'Huillier and Edighoffer 1996

kaolinite clays and consequently have a low ion exchange capacity.

"Non-ultramafic soils" are mostly associated with volcano-sedimentary rocks along the central chain of Grande Terre and metamorphic rocks in northeastern Grande Terre (Fritsch 2012). These soils generally have an acidic pH and contain high concentrations of aluminium (Latham et al. 1978). The western coast of Grande Terre is characterised by schist, limestone or basalt rocks with higher fertility than in other soils (Latham 1981).

Contribution of the ultramafic flora to the diversity and endemism of the New Caledonian flora

Plant species richness and endemism

The ultramafic and non-ultramafic floras of New Caledonia have an equivalent number of species, with ~2100 species found on either (Table 3). Thus, despite covering less than a 1/3 of the surface area (~5500 km^2), ultramafic soils harbor a disproportionally high fraction of the total flora.

The ultramafic-obligate flora, represents over 1200 species and ~50 % of the endemic flora of New Caledonia, and makes a major contribution to distinctiveness of the Island (Table 3). The ultramafic obligate flora is remarkable by its very high endemism (96.7 %), which is higher than the endemism of the non-ultramafic obligate flora (58 %). For comparison, Kinabalu Park in Sabah, renowned for its ultramafic vegetation, consists of over 1500 species on ultramafic soils (UM), with relatively few soil-endemics (van der Ent et al. 2014). Whereas the Californian flora consists of about 1410 species endemic to the state, only ~180 species are ultramafic-endemic (Safford et al. 2005). Further, the ultramafic outcrops in Western Australia harbours 1355 taxa of which only 14 are known to be soil-endemic

Table 2 Comparison of ultramafic soil mineral properties according to vegetation type (from Read et al. 2006a)

Soil properties	Forest ($n=3$)		Maquis ($n=4$)	
	Mean	SE	Mean	SE
pH	5.3	0.1	4.8	0.0
Total elements				
N (mg/kg)	2390	100	1130	170
C/N	16.8	0.9	19,500	1100
P (mg/kg)	123	50	84	33
K (mg/kg)	147	65	72	23
Mg (mg/kg)	11,470	4840	5360	1480
Ca (mg/kg)	700	225	92	15
Fe (mg/kg)	396,000	6300	435,000	37,000
Cr (mg/kg)	91,400	46,900	61,900	17,500
Ni (mg/kg)	5200	1690	4780	920
Al (mg/kg)	37,200	12,600	37,100	8400
Extractable elements				
P ($\mu g\ g^{-1}$)	0.9	0.3	0.4	0.1
K ($cmol_c$/kg)	0.38	0.07	0.26	0.07
Mg ($cmol_c$/kg)	2.72	0.79	0.29	0.10
Ca ($cmol_c$/kg)	1.85	0.41	0.22	0.06

Sampling depth: 0–10 cm

(van der Ent et al. 2015a). The Queensland ultramafic flora is comprised of 553 species, of which only 19 are soil-endemics (Batianoff and Singh 2001). Finally, in New Zeeland, ultramafic outcrops host 34 soil-endemic taxa from a flora consisting of 2066 species (Lee 1992).

There is a strong disparity in ultramafic obligate endemism and species richness between lineages in New

Caledonia (Table 4). The most endemism-rich families are the Myrtaceae (112 ultramafic obligate species) and the Rubiaceae (100 ultramafic obligate species), which are also the families with the greatest number of species occurring in New Caledonia. In contrast, the Pteridophytes and Monocots make a low contribution to the ultramafic obligate flora (Table 4). Both groups are mainly represented by epiphytes and are therefore not directly associated with soils. Pteridophytes comprise about 40 % of epiphytic species, while Orchidaceae, the second largest family in New Caledonia (42 % of monocot), consists of about 45 % of epiphytes.

Most of the large families in the New Caledonian flora (i.e. those with at least 15 species) have a higher fraction of their species restricted to ultramafic soils (Fig. 3). The strong floristic affinities of New Caledonia with Australia is illustrated by families such as the Dilleniaceae, Ericaceae and Proteaceae (Morat et al. 1994; van der Ent et al. 2015a). Only 7 of the largest eudicots families of New Caledonia have a larger fraction of species occurring on other soils (Fig. 3).

Eudicot ultramafic obligate species are almost all endemic (99.3 %). Conversely, the four eudicot families with the highest proportion of obligate species on other soils have a relatively low level of endemism: Asteraceae (28.6 %), Moraceae (69 %), Malvaceae (59.6 %) and Fabaceae (62.1 %) (Morat et al. 2012). These families consist of a large number of ruderal, coastal or early successional species. The Asteraceae, which is among the under-represented families in New Caledonia (Pillon et al. 2010), is the most important family of serpentine endemic plants in California (Safford et al. 2005) and the

Table 3 Endemicity and number of species, genera and families in the different substrate-related floras

		Total*	UM Flora		Non-UM Flora			
			Uo		Uf		Oo	
			No.	%	No.	%	No.	%
Species	Total	3309	1218	36.8	877	26.5	1214	36.7
	Endemic	2492	1178	96.7 (47.3)	610	69.6 (24.5)	704	58 (28.3)
Genera	Total	795	72	9.1	426	53.6	297	37.4
	Endemic	97	36	50 (37.1)	55	12.9 (56.7)	6	2 (6.2)
Families	Total	193	8	4.1	137	71	48	24.9
	Endemic	3	0	0	2	1.5	1	2.1

Numbers in brackets are the percentage of endemic species of the total flora

Uo ultramafic-obligate; *Uf* ultramafic-facultative; *Oo* other substrate-obligate

* documented species

Table 4 Endemicity and number of species in the different substrate-related floras

| | | Total* | UM Flora | | Non-UM Flora | | | |
| | | | Uo | | Uf | | Oo | |
			No.	%	No.	%	No.	%
Ferns and Lycophytes	Total	256	36	14.1	128	50	92	35.9
	Endemic	99	22	61.1	46	35.9	31	33.7
Monocots	Total	546	131	24	205	37.5	210	38.5
	Endemic	260	117	89.3	88	42.9	55	26.2
Gymnosperms	Total	46	29	63	14	30.4	3	6.5
	Endemic	45	29	100	14	100	2	66.7
Basal angiosperms	Total	111	39	35.1	39	35.1	33	29.7
	Endemic	100	37	94.9	35	89.7	28	84.8
Eudicots	Total	2354	979	41.6	494	21	881	37.4
	Endemic	1987	972	99.3	427	86.4	588	66.7

Uo ultramafic-obligate; *Uf* ultramafic-facultative; *Oo* other substrate-obligate

* documented species

largest family in the (non-ultramafic) South African Cape flora (Cowling and Holmes 1992). It thus remains unclear whether ecological filtering of ultramafic soils is a major factor in explaining the underrepresentation of Asteraceae in the New Caledonian flora as suggested by Pillon et al. (2010). The subtropical climate could also constitute a major barrier to the diversification of Asteraceae in New Caledonia.

Despite a roughly similar number of species on ultramafic and non-ultramafic soils, the ultramafic-obligate flora is contained in a smaller number of families and genera. The distinction of floras at the generic and family levels is essentially marked by the lack of many genera and families on ultramafic soils (Table 3). Thus despite high species richness, the phylogenetic diversity of the ultramafic-obligate flora appears to be relatively low. Among the 795 genera of the New Caledonia flora, only a small proportion of them (72 genera, ~9 %) have all their species exclusively found on ultramafic soils. About a third of these genera have a wide geographical distribution (data not shown), which attests to the pivotal role played by the soil in their distribution. Endemicity at the generic level is remarkable for the ultramafic obligate flora since 36 out of the 97 endemic genera of the New Caledonian flora have their species restricted/obligate to ultramafic soils, while only 6 genera are restricted to non-ultramafic soils (Table 3). Endemic genera associated with ultramafic soils represent more than 37 % of all the endemic genera of New Caledonia, a percentage

similar to Cuba (32–33 % of endemic genera) (Borhidi 1991; Iturralde 2001). This high generic endemicity confirms the selective power of ultramafic soils that strongly favor endemism, but not necessary species richness since endemic ultramafic-obligate genera are essentially species-poor in New Caledonia. This low infra-generic endemic diversity is not a specificity of the ultramafic flora, since among the six endemic genera found exclusively on non-ultramafic soils, four are mono-specific and two genera have only two species each.

About 75 % of the families have at least one representative on ultramafic soils but only eight of them are restricted/obligate to ultramafic soils (Table 3). None of the three families endemic to New Caledonia are exclusively found on ultramafic soils, while one of them (Amborellaceae) is restricted to non-ultramafic soils (Table 3). There is a striking lack of New Caledonian mono-specific families belonging to the Trimeniaceae and Amborellaceae on ultramafic soils, while these species are relatively widely distributed in New Caledonia.

Hence, the ultramafic obligate flora has a higher level of endemism at both the species and generic level compared to the flora associated with non-ultramafic soils. The majority of the genera endemic to New Caledonia are soil-facultative which confirms that the ultramafic flora contributes to the endemicity and originality of the flora of New Caledonia, and that the juxtaposition of different substrates is an important source of diversity.
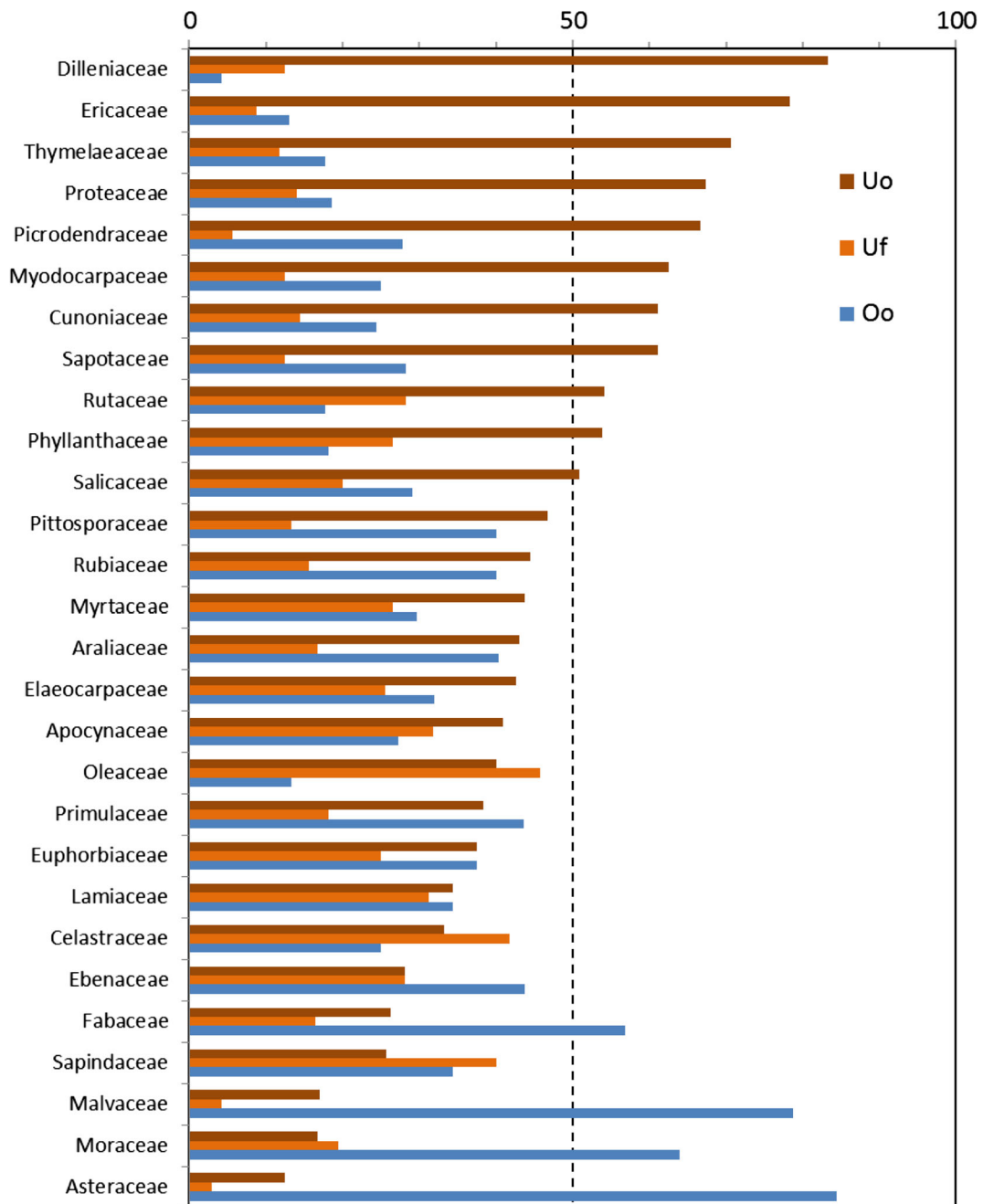
Fig. 3 Proportion of substrate-related species for eudicot families with at least 15 species in the native flora of New Caledonia. *Abbreviations: Uo* Ultramafic-obligate; *Uf* ultramafic-facultative; *Oo* other substrate-obligate

Vegetation of ultramafic soils versus other soils

As elsewhere, the vegetation on ultramafic outcrops is discernable from the vegetation on other substrates by its distinctiveness and physiognomy (Fig. 2), as illustrated by the maquis in New Caledonia that contrasts with savannas and thickets constituting the secondary vegetation on non-ultramafic soils. However, the maquis of New Caledonia are floristically and physiognomically varied, and range from shrubby, evergreen, sclerophyllous to cyperoid vegetation depending on soil properties (Jaffré 1980; van der Ent et al. 2015a). Three

main maquis types found in New Caledonia are: (i) "bushy maquis", (ii) "shrubby to bushy maquis"; (iii) "ligno-herbaceous maquis" (Fig. 2; Table 5). These vegetation types mainly result from the destruction of the initial forests by fire, although some subalpine maquis might have existed at higher elevation on the most exposed summits (Nasi et al. 2002) or at lower elevation on the dry western coast (Morat et al. 1986). Thus, most maquis is composed of fire-adapted species (Jaffré and L'Huillier 2010; Jaffré et al. 1998b; McCoy et al. 1999). The maquis also includes (i) heliophilous hydromorphic vegetation characterized by a shrubby layer along river-banks with a dense herbaceous layer (Jaffré and L'Huillier 2010); (ii) the vegetation growing on serpentinite veins, on Magnesic Cambisols, included within metamorphic or volcano-sedimentary soils, (Jaffré 1980); (iii) altitudinal maquis composed of mountain species, sometimes dominated by *Araucaria* spp. (e.g. *A. humboldtensis*). This maquis, mainly found on summits, can developed into forest once protected from wind or fire (Jaffré 1980; Nasi et al. 2002).

The maquis contains at least 840 species restricted to this vegetation type (Fig. 4). The richness of the maquis is remarkable considering the relatively small area covered by this vegetation (4300–4400 km^2) compared to the total area covered by other non-forest vegetation on non-ultramafic soils (~6000–7000 km^2) (Jaffré et al. 2009) (Fig. 1b). The maquis is particularly remarkable by its very high level of endemism (96.9 %) (Fig. 4). The families with a majority of ultramafic endemic species occur in the maquis (e.g. Dilleniaceae, Ericaceae, Proteaceae, Cunoniaceae, Myrtaceae) (Fig. 3). The non-forest vegetation on non-ultramafic soils is mainly covered by savannas or secondary thickets, which are generally species-poor. The non-forest flora exclusive of non-ultramafic is also relatively poor and consists of much fewer endemic species (14.4 % endemism). Most species occur in secondary

Table 5 Vegetation types on ultramafic and non-ultramafic rocks and their associated biotic and abiotic features

	Surface (km^2)	Soil type	Altitude	Woody stratum	Herbaceous stratum (Cyperaceae (C) or Poaceae (P))
Ultramafic rocks	5600–5700		0–1816 m		
Rain forest	1100–1200	Magnesic Cambisols, Ferralsols	>10 m	20–30 m	C, P, <10 %
Maquis	4500				
Bushy		Magnesic Cambisols	<400 m	1–6 m	C, 20–40 %
Shrubby to bushy		Plinthic (F)	0–1816 m (most often >200 m)	50 cm–5 m	C, <15 %
Ligno-herbaceous		Magnesic Cambisols (serpentinite vein)	<600 m	1–6 m	C, P, 50–100 %
Ligno-herbaceous		Eroded (F)	0–1816 m	20 cm–80 cm	C, >50 %
		Colluvial (F)	0–1800 m	1–5 m	C, >50 %
		Hydromorphic (F)	200–280 m	120-cm-2 m	C, >50 %
Maquis passing forest[a]		All non-hydromorphic soils	10–1800 m	5–7 m	C, < 50 %
Non-ultramafic rocks			0–1816 m		
Rain forest	1800 (+900)	metamorphic rocks (+ calcareous rocks[b])	>300–400 m	20–30 m	P,<10 %
Sclerophylous and mesic forest	450	Sedimentary rocks	<300 m	8–15 m	C,P,<20 %
Savanna and thicket	6000	Metamorphic, calcareous, volcano-sedimentary rocks	<600 m	6 m	P, 100 %, 10–60 % (thicket)
Wetland	1000	Freshwater and salty	<270 m	0–8 m	–
Siliceous "maquis"	600	Siliceous or acid soils, mica-schist	10–1000 m	5–6 m	C, P, <30 %

Data from Jaffré 1980; Jaffré and L'Huillier 2010; Jaffré et al. 2009

F ferralsols

[a] "Maquis paraforestier" that forms an interface with a strict maquis and comprises several distinctive species
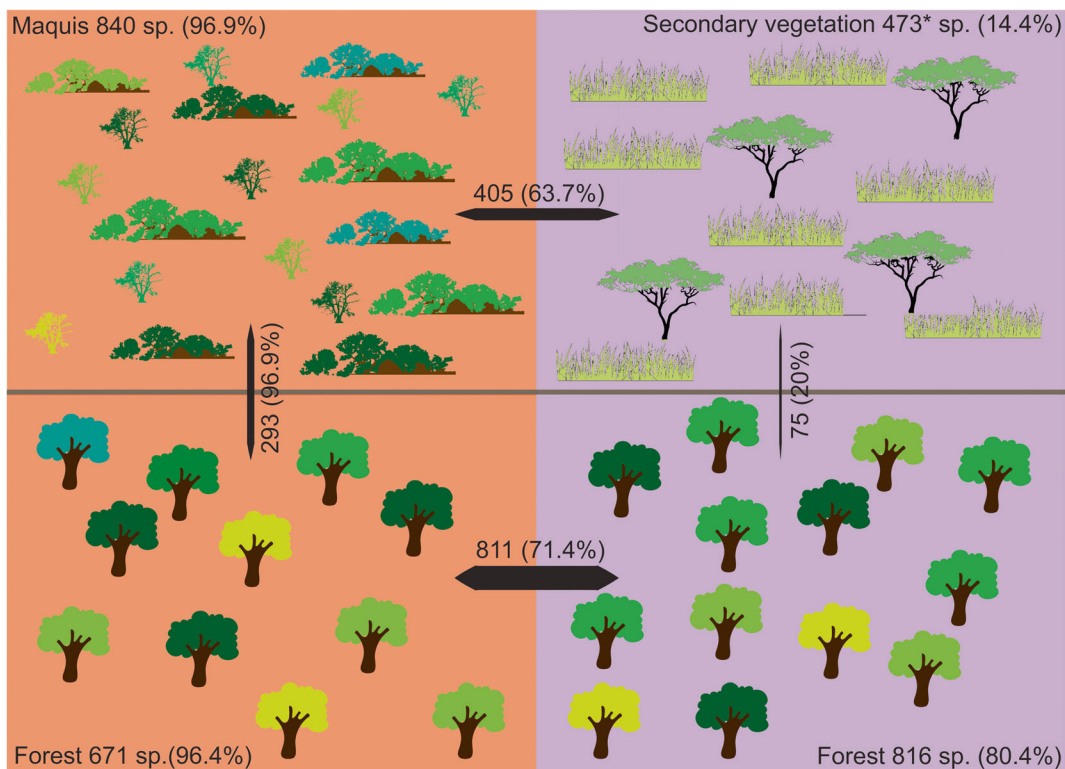
[b] Principally on the Loyalty Islands

Fig. 4 Substrate-related flora in the different vegetation types: [*top*]: non-forest vegetation; [*bottom*]: forest; [*left*]: ultramafic obligate flora; [*right*]: other-soil obligate flora. Number of species and endemism (in *bracket*). *the non-forest vegetation includes savannas, thickets on non-ultramafic or calcareous substrates, maquis on siliceous substrates and acid soils in altitude, wetland, and halophile vegetation. Note that the non-ultramafic forest flora, as treated here, includes both rainforest and dry forest. Numbers above *arrows* indicate facultative species and endemism level

vegetation on siliceous soils ("maquis on siliceous", Fig. 1b) whose floristic composition is close to the ultramafic maquis on degraded Ferralsols (Jaffré et al. 2012) (Fig. 4). This explains the relatively large number of species shared between maquis and other vegetation and attests to the selective effect of soil chemistry (i.e. acidity, low nutrient contents) in species sorting. The maquis encompass a wide spatial disparity in species richness from poor (~14 species) in the ligno-herbaceous maquis on hydromorphic alluvium to rich (~131 species) of the shrubby maquis on Magnesic Cambisols (Jaffré 1980).

The high distinctiveness of the maquis versus other non-forest vegetation, contrasts with the forests that does not differ physiognomically from one edaphic condition to another. The structure of New Caledonian rainforest is characterized by a high density of small diameter stems regardless of the soil type (Ibanez et al. 2013). Secondary forest on Ferralsols is highly distinctive, often dominated by *Nothofagus* spp.

(Nothofagaceae) (Read et al. 2000), *Arillastrum gummiferum* (Myrtaceae) (Jaffré 1980), *Gymnostoma* spp. (Casuarinaceae) (Jaffré et al. 1994; McCoy et al. 1999) or *Cerberiopsis candelabra* (Apocynaceae) (Read et al. 2008). The flora is less rich in the ultramafic forest (Fig. 4) and roughly similar in plots of the southern massif on ultramafic soils (on Ferralsols) and on the whole main island on acid soils (i.e. non-ultramafic) (Ibanez et al. 2014; Jaffré and Veillon 1995). Thus, despite covering a smaller area (Table 5), ultramafic forests have slightly lower plant diversity than forests on non-ultramafic soils. Endemism is noticeably higher in ultramafic forest, reaching levels comparable to the maquis (Fig. 4). The relatively low level of endemism of the forest flora occurring exclusively on non-ultramafic soils can however be explained by the low level of endemism in dry forests (59.2 %, Morat et al. 2012) and rainforests on calcareous soil (52 %, Morat et al. 2001). Both forest types are strongly disturbed by repeated fire or invasive species. Rainforest on other soils

contains a quite high number of endemics (83 %, Morat et al. 2012). Soils clearly constitute an ecological barrier, since 65 % of forest species are confined to one type of substrate (Fig. 4). Forests nevertheless share a higher percentage of soil-facultative species than the total flora. This floristic affinity is possibly higher for large rainforest trees (DBH ≥10 cm) (Birnbaum et al. 2015). Tree species have also been suggested to be less soil-specialized in Sabah (van der Ent et al. 2015b). The rainforests on both soil types are similar in their structure and diversity (Ibanez et al. 2014; Jaffré and Veillon 1995). The soil affinity is a reduced barrier in rainforest, allowing more species overlap. Rainforest conditions, i.e. canopy and litter make water and nutrient less limiting irrespective of the soil type or lithology (Table 2), reducing the soil-related competitive exclusion. The largest areas of rainforest on ultramafic soils are located in the southern massif (Fig. 1), where rainfall is the highest even at low elevations. This geographical isolation and reduce water deficit could explain the high level of endemism found in ultramafic rainforest.

Several families under-represented on ultramafic soils mainly occurr in forests (e.g. Malvaceae, Moraceae). Few families are exclusively found in rainforest (e.g. Nothofagaceae, Paracryphiaceae, Phellinaceae) and have a strong affinity for ultramafic soils. Basal angiosperms, mainly occurring in rainforest (Pouteau et al. 2015) are equally represented on ultramafic and non-ultramafic soils (Table 4). Niche modeling of 60 basal angiosperm species showed a higher species overlap on non-ultramafic soils and suggests that, rather than an affinity for a particular soil type, the distribution of basal angiosperms is mainly driven by a preference for rainforest habitats (Pouteau et al. 2015). Similar climate-driven distribution pattern was suggested for palms, the substrate being subordinate to climate (Pintaud et al. 2001).

Conversely, non-forest dominant families such as the Poaceae are predominantly restricted to non-ultramafic soils, and a very low proportion (~6 %) is restricted to ultramafic soils. The vast majority of species in the Poaceae occur in contact zones at the base of ultramafic massifs and on serpentinite veins surrounded by savanna. The presence of ultramafic ecotypes, i.e. populations locally adapted to specific soils, as found in other areas worldwide (Burgess et al. 2015; Chathuranga et al. 2015; Kruckeberg 1984; O'Dell and Rajakaruna 2011) have not been investigated.

It seems obvious that the non-forest vegetation, which results mainly from repetitive fires on both ultramafic (Jaffré et al. 1998b; McCoy et al. 1999) and other soils (Ibanez et al. 2013), increases the differences between the ultramafic and the non- ultramafic floras. This was also suggested by Proctor (2003) for the vegetation on ultramafic soils in Malaysia and the Philippines.

Plant adaptations to ultramafic soils

Adaptation to ultramafic soils is widely proposed to be related with physiological prerequisites (Cecchi et al. 2011). The "serpentine syndrome" is related to adaptation to dry soil and nutrient limitation, which are major sources of stress in ultramafic environments (Kazakou et al. 2008). In New Caledonia, the disharmony of the flora, as commonly observed on islands, is mainly driven by pre-adaptation to ultramafic soils while dispersal limitation played a less important role (Pillon et al. 2010). Most of the over-represented lineages would have benefited from pre-adaptation to ultramafic soils that favored settlement and diversification (Jaffré et al. 1987; Pillon et al. 2010). This hypothesis is further supported by recent studies where ultramafic tolerance was reconstructed as plesiomorphic in some clades (Barrabé 2013; De Kok 2002; Pillon et al. 2009). The question, however, arises as to what traits facilitate colonization onto ultramafic soils, since plants found on ultramafic soils have to adapt to both drought and soil chemical stresses (Brady et al. 2005), but also bare soils (Cacho and Strauss 2014).

Tolerance to nutrient-poor and harsh environments

The ability of some lineages to grow on ultramafic soils is related to their tolerance for low nutrient conditions as shown by the low concentration of these elements in their leaves, especially the maquis species (Table 6). For example, P-concentrations are extremely low in all ultramafic soils (Table 1), and consequently at very low foliar concentrations (90 % have <0.05 % P) in the shrubby species of the maquis (Jaffré 1980). Conifers too have low foliar P and K, as well as a low capacity to limit the uptake of Mn and Ni (Jaffré 1995). The dominance of conifers growing on ultramafic soils was also reported in California (Kruckeberg 2002) and Sabah (van der Ent

Table 6 Foliar concentrations (dry mass basis) of major elements in three categories of maquis on ultramafic soils (Jaffré 1980)

		N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Mg/Ca
Maquis on Magnesic Cambisols ($n = 100$)	Mean	1.03	0.034	0.81	1.04	0.51	0.65
	Range (90 % of sp.)	0.55–1.39	0.014–0.053	0.26–1.54	0.35–1.55	0.14–0.84	0.33–5.00
Maquis on eroded Ferralsols ($n = 58$)	Mean	0.82	0.032	0.69	1.08	0.36	0.48
	Range (90 % of sp.)	0.48–1.04	0.011–0.044	0.18–1.30	0.35–1.85	0.10–0.70	0.29–1.67
Maquis on Plinthic Ferralsols ($n = 100$)	Mean	0.91	0.032	0.59	1.10	0.24	0.27
	Range (90 % of sp.)	0.48–1.39	0.014–0.041	0.15–1.10	0.25–2.05	0.06–0.60	0.14–1.25

et al. 2014). Despite very high soil Mg concentrations in Magnesic Cambisols, Mg is often found at normal concentration in the leaves of shrubby species from the maquis, and an unbalanced Mg/Ca has been little recorded in plants growing on these soils (Jaffré 1980).

Sclerophylly and microphylly

Low leaf nutrient concentration in plants from the maquis reflects a high degree of scleromorphic adaptations, with vegetation described as 'sclerophyll' (Jaffré 1980) or xerophyll (Virot 1956). There is, however, a long-term debate as to whether sclerophylly is an adaptation or a consequence of seasonal water deficit or to soil nutrient deficits (Kruckeberg 1954; Lamont et al. 2002). By comparing leaf mechanical properties, as a proxy for sclerophylly, in two contrasting environments (i) maquis on nutrient-deficient (Magnesic Cambisols) but moist conditions and (ii) dry forest in higher-nutrient soils but drier sites, Read et al. (2006b) found that maquis leaves were on average more "sclerophyllous" than those in dry forest. It was however noted that despite higher rainfall, maquis plants are facing water deficits in the dry season (Read et al. 2006b). Another study showed that leaf physical traits of maquis species in wet conditions in New Caledonia did not significantly differ from those of species in Mediterranean climate *kwongan* on low-nutrient soils in southwestern Australia (Read et al. 2007). This is suggestive of a stronger influence of soil-nutrient properties than rainfall on sclerophylly; nevertheless, these studies suggested that sclerophylly is a complex phenomenon where mechanical properties reflect both an adaptive response and a by-product of anatomical adaptation to a stressful environment. Sclerophylly is a syndrome resulting from adaptive responses to various stresses. For instance, leaf strength and toughness are also associated with herbivory stresses that increase in bare environments, as in some maquis. In New Caledonia, the shrubby to bushy maquis on deep Ferralsols in areas receiving high rainfall (2000–4000 mm) may be used to study the effect of water deficits on sclerophylly. Low concentrations of N and P, in these deep Ferralsols, appear to be important together with the effects of intensive solar radiation (Jordan et al. 2005). Whatever the ecophysiological significance of sclerophylly, the strong floristic affinities of the New Caledonia maquis flora with that of Australian "heathlands" on poor soils, is suggestive of pre-adaptation of sclerophyllous species that colonized the maquis in New Caledonia (Morat et al. 1994, 1986). In California, drought-related leaf traits were present in the ancestors of chaparral lineages, before the advent of Mediterranean-type climate (Ackerly 2004).

Nutritional strategies in nutrient-deficient soils

Fewer studies have been conducted on nutrient-acquisition strategies in New Caledonian plants, compared to other ultramafic regions (e.g. Europe, California, Australia), but a wide array are currently known. Ectomycorrhizal symbioses are found in Nothofagaceae and some Myrtaceae (Leptospermoïdeae) (Perrier et al. 2006), N_2-fixing symbiosis occurs in the Casuarinaceae (Gauthier et al. 1999) and in the Fabaceae (Chaintreuil et al. 2007). Mycorrhizal symbioses are known to enhance P-acquisition from low-P soils by "scavenging strategies" (Lambers et al. 2008; Smith and Read 2008). For the vast majority of maquis species, the acquisition of P is favoured by symbiotic associations with arbuscular mycorrhizal fungi (AM) and with ectomycorrhizal fungi (ECM) for a smaller number of species (Amir et al. 2013). Leaf N concentrations of shrubby species in the

maquis are low, less than 1 % in >60 % of species (Jaffré 1980). Foliar N-concentrations >2 % are uncommon and mainly recorded in the Fabaceae (*Acacia*, *Archidendropsis, Serianthes* and *Sophora*, whose roots form nodules with symbiotic N-fixing *Rhizobium*. Some non-mycorrhizal species display specialized root-adaptations such as cluster roots in the Proteaceae or dauciform roots (i.e. carrot-shaped) reported in some tribes of the Cyperaceae (Shane et al. 2006). These specialized roots are known to facilitate P-acquisition through the release of carboxylates (Lambers et al. 2014). Several species belonging to the genera *Costularia* and *Schoenus* (Cyperaceae) are pioneer species on mining substrates (Jaffré 1977a). These species have been recommended for restoration of mining sites (Wulff et al. 2010).

The vast majority of studies dealing with the role of nutrition-acquiring strategies in plant ecology in New Caledonia focus on mono-dominant and gregarious species. Mycorrhizal symbioses are known to confer a competitive advantage to such species by enhancing their growth rate and their ability to access soil nutrients, especially P. *Acacia spirorbis* (Mimosaceae) is known to exhibit a gregarious behaviour at low elevation on both ultramafic and non-ultramafic soils, and has ectomycorrhizal symbiosis (Jourand et al. 2014). The different species of *Gymnostoma* (Casuarinaceae) growing in mono-specific stands have a pioneer behaviour in the maquis (McCoy et al. 1999). The N_2-fixing ability of root-bacteria (*Frankia*) in pioneer species of *Gymnostoma* enables faster growth to colonize bare or degraded soils (Reddell et al. 1986). While all *Gymnostoma* species in New Caledonia show a strong affinity for one soil type (Jaffré et al. 1994), no strict specific genotype of *Frankia* strain isolated from the root nodules of various species was associated with a specific host-plant (Navarro et al. 1999). Nevertheless several *Frankia* strains were exclusively associated with ultramafic soils (Navarro et al. 1999). The presence of ectomycorrhizal symbioses was also revealed in the genus *Nothofagus*, in several *Tristaniopsis* species (Perrier et al. 2006) and in *Arillastrum gummiferum* (Myrtaceae) (F. Carriconde, pers. comm.). The mono-dominance of *Nothofagus* in rainforest on ultramafic soils may result from a higher capacity to tolerate low nutrient conditions compared to co-occurring species (Read et al. 2002). The same hypothesis could apply for *Tristaniopsis* species that form monospecific stands in shrubby to bushy maquis and in margin forest

vegetation, as for *Arillastrum gummiferum* which dominates the canopy of some rain forests on Ferritic Ferralsols.

Hyperaccumulation of trace elements

Plants with anomalous concentrations of particular trace elements (Ni or Mn) (e.g. >1000 µg g^{-1} Ni and 10 000 µg g^{-1} Mn) are called "hyperaccumulators" (Jaffré et al. 1976; van der Ent et al. 2013). Concentration of these elements (Ni and Mn) in leaves of shrubby species growing on ultramafic soils is highly variable between species. On the 445 species tested in New Caledonia the mean foliar Mn concentration was ≤500 µg g^{-1} for 66.5 and ~22 % had 1000–10,000 µg g^{-1} (Jaffré 1980). Foliar Mn concentrations 1.0–5.5 % occur in 11 species (Losfeld et al. 2015). In contrast, of the about 500 plant species tested from New Caledonia, 67 % had leaf Ni concentration ≤100 µg g^{-1} and 27 % had 100–1000 µg g^{-1} (Jaffré 1980). Manganese hyperaccumulation occurs in various families and genera (e.g. *Alyxia* (Apocynaceae), *Denhamia* (Celastraceae), *Garcinia* (Clusiaceae), *Gossia* (Myrtaceae) and *Polyscias* (Araliaceae)) (Losfeld et al. 2015), with, a high proportion of Mn accumulating species in the Proteaceae (Jaffré 1979), clearly succeeding on ultramafic soils as shown by their over-representation of ultramafic obligate species. Manganese accumulation by some species growing on Magnesic Cambisols, with a basic pH constraining Mn uptake, is remarkable (Jaffré 1977b). In contrast, an acidic soil pH facilitates Mn acquisition (Fernando et al. 2008), and specialized root adaptations found in Proteaceae, which facilitate P-acquisition through the release of carboxylates, might also mobilize Mn (Lambers et al. 2015).

Strong variations in floristic richness in response to ultramafic-derived soil chemistry has been reported for New Caledonian rainforest (Jaffré and Veillon 1991). The depletion of species richness on alluvial Ferralsols, associated with modification of floristic composition, has been attributed to the high concentration of available Ni in the soil (Jaffré and Veillon 1991). Similar trends were observed for the ultramafic flora in Queensland where species richness was negatively correlated and endemism positively correlated with the available Ni concentrations in the soil (Batianoff and Singh 2001). Low species richness on sites with high Ni concentration might also be accentuated by allelopathy occurring under the canopy of Ni hyperaccumulator trees or

shrubs. Nickel concentrations in both litter and topsoil can affect both germination and development of some seedlings providing a competitive advantage to Ni hyperaccumulator plants (Boyd and Jaffré 2001). Most of the research on the phenomenon of hyperaccumulation has focussed on Ni (Proctor 2003). In New Caledonia a total of 65 Ni-hyperaccumulators (foliar Ni concentrations >1000 μg g^{-1}) have been reported to date (Jaffré et al. 2013). Fifteen of these species have Ni concentrations ≥10,000 μg g^{-1} and may be called hypernickelophores (Boyd and Jaffré 2009; Jaffré and Schmid 1974).

Together with Cuba, with a reported ~140 hyperaccumulator species (Reeves et al. 1996; 1999), New Caledonia is a global hotspot of Ni hyperaccumulator plants with. 65 species belonging to 12 families and 20 genera (Jaffré et al. 2013). Most of the Ni-hyperaccumulator plants are ultramafic-obligates and occur in rainforest. The main families in which Ni hyperaccumulator plants occur in New Caledonia belong to the Order Malpighiales (Jaffré et al. 2013; van der Ent et al. 2015a). The large Cunoniaceae family (Oxalidales) has numerous Ni hyperaccumulator species in three genera. The Malpighiales and Oxalidales contain 54 hyperaccumulator species in New Caledonia, with the remaining 11 species spread over 10 genera, 7 families and 7 Orders (Jaffré et al. 2013). Even though the hyperaccumulator species of New Caledonia are taxonomically diverse, they cluster phylogenetically (Jaffré et al. 2013; Pillon et al. 2010). The reasons for the observed phylogenetic clustering remains unknown, but the time of exposure is probably important for the evolution of ultramafic endemics and hyperaccumulators. This can be illustrated by Cuba where the majority of hyperaccumulators are endemic to the oldest serpentine soils (Reeves et al. 1996, 1999). The fact that numerous hyperaccumulator species are found in ultramafic obligate-rich lineages could simply result from the greater chance for species to evolve hyperaccumulation. Examples include the genera *Codia, Pancheria* and *Geissois* (Cunoniaceae), the genus *Pycnandra* (Sapotaceae), the genus *Phyllanthus* (Phyllanthaceae), and the genera *Xylosma* and *Homalium* (Salicaceae).

High soil Ni concentration correlate with the occurrence of hyperaccumulator plants in Sabah, Malaysia (Van der Ent et al. 2016). In New Caledonian, hyperaccumulator plants in "Parc de la Rivière Bleue" occur on alluvial Ferralsols with high Ni concentrations

(Jaffré and Veillon 1991). Nickel accumulation was shown to be negatively correlated with habitat-specialization in Cuba (Borhidi 2001), which could help explain the lack of hyperaccumulator plants in the maquis of New Caledonia. A number of families overrepresented on ultramafic soils that are mostly ultramafic-obligate (which occur on maquis) do not have any Ni hyperaccumulator species, for example the Ericaceae and Dilleniaceae.

New Caledonia phylogenetically diverse set of Ni hyperaccumulator plants offers opportunities to advance the knowledge of the molecular mechanisms involved with Ni hyperaccumulation (Callahan et al. 2012; Perrier et al. 2004). The identification of genes involved in Ni accumulation (Merlot et al. 2014) will be especially critical for identifying mechanisms involved in Ni hyperaccumulation and adaptations to ultramafic soils. Nickel absorption is affected by rhizosphere processes such as root physical characteristics, rhizosphere chemistry, and rhizosphere microorganisms (reviewed by Alford et al. 2010). Several studies conducted in New Caledonia have shown that bacteria were abundant and diverse, with some strains exhibiting high levels of Ni-tolerance (Gonin et al. 2013; Guentas et al. 2016; Hery et al. 2003). Similarly, mycorrhizas forming symbiotic associations with some species were found to have a high Ni-tolerance (Amir et al. 2013; Amir et al. 2007; Jourand et al. 2010).

Occupation of bare habitats

The bareness associated with some ultramafic sites in New Caledonia may represent a selective force for some habitat specialist plants. In California, adaption to microhabitat bareness was more conserved across clades than soil properties (Mg, Ni, Ca/Mg ratio), and taxa from bare environments were also less competitive in greenhouse experiments (Cacho and Strauss 2014). Such a phylogenetic signal suggests that the ability to occupy bare environments might precede immigration onto ultramafic soils.

Competitive exclusion

The low number of species shared between maquis and other non-forest vegetation (savanna and secondary thickets) that together cover >95 % of the non-forest vegetation of New Caledonia, results from the strong selective pressures imposed by ultramafic soils. Slow-

growing stress-tolerant species are less competitive and the edaphic barrier is well illustrated by changes in the flora at the base of ultramafic massifs on the west coast of Grande Terre (Jaffré and L'Huillier 2010). Similar distribution patterns have also been reported elsewhere on ultramafic-non-ultramafic geological boundaries (Brooks 1987; Kruckeberg 2002). In New Caledonia, many maquis species have been shown to grow in auto-ecological condition on other soils (Jaffré 1980), but they are likely excluded from these sites by interspecific competition. Competitive exclusion is widely known to limit ultramafic-tolerant species to ultramafic soils because of their slow growth rate and their inability to compete in less stressful environments (Anacker et al. 2011; Brady et al. 2005; Kruckeberg 1954). This exclusion then leads to species becoming restricted (endemic) to ultramafic sites.

In virtue of their high richness and local abundance in some forests and maquis on ultramafic soils, conifers are emblematic of this substrate in New Caledonia. New Caledonia hosts 7 % (45 species) of the worldwide conifer flora, and conifers are known to be highly efficient at outcompeting angiosperms in unproductive sites where water and/or nutrients are limiting (Brodribb and Hill 1998; Brodribb et al. 2012; Enright and Hill 1995). With the exception of a few shade-tolerant Podocarp species, most of the species belonging to *Araucaria, Podocarpus*, *Dacrydium* and *Callitris* genera are light-demanding, often growing on steep slopes of the ultramafic massifs (Jaffré 1995). Under these ecological conditions, conifers are able to overtop forest/maquis canopy and resist high wind exposure during the cyclone season. Studies on the ecology and population dynamics of *Araucaria* (Enright et al. 2014, 2001; Rigg et al. 2010) and *Agathis* (Enright et al. 2003) have shown their ability to grow in harsh environments on Ferralsols. The most extreme case of tolerance is *Araucaria muelleri* growing on Ferralsols. This species has a slow stand-dynamics, characterized by low recruitment and one of the lowest growth rates ever reported for any tree species worldwide (e.g. average stem diameter increase ranging from 0.1 to 0.3 mm per year) (Enright et al. 2014).

The ecological barrier imposed by ultramafic soil is also highlighted by the scarcity of introduced species. Approximately 500–600 naturalized species are found on non-ultramafic soils in New Caledonia (Hequet and Le Corre 2010; Meyer et al. 2006) while only about 10 species occur on ultramafic soils. These species persist (with a few exceptions such as *Pinus caribaea*) only in mixed zones or on sites strongly affected by human activities. The initial flora on non-ultramafic soils (metamorphic, volcano-sedimentary and calcareous) has been largely replaced by common and widespread species with pan-tropical or pan-pacific distribution, after clearings and repetitive fires.

Factors influencing species richness and endemism on ultramafic soils

Extend and age of ultramafic crops

The number of ultramafic endemics in the regional flora appears to be related to the percentage of the land area made up of ultramafic soils, simply because a large area provides more chances for species to adapt and become restricted (Anacker 2011). Among the other endemism hotspots, Cuba and California with respectively ~27 % (Anacker 2011) and 12.5 % (Safford et al. 2005) of their species endemic to ultramafic soils, New Caledonia has a substantially higher proportion of endemic species (47.3 %), while the areal extended is smaller (compare to Cuba with 7500 km^2 of ultramafic soils). This may be explained by other factors that contribute to the very high level of ultramafic endemism in New Caledonia, including the age of ultramafic exposure and fragmentation of the peridotite mantle in isolated massifs across the Island. Age of ultramafic exposure is a predominant factor of soil-endemism and diversity in Cuba (Reeves et al. 1996, 1999).

Patchiness and environmental gradients

The range of soil types on ultramafic lithologies (Tables 1 and 5), some of the most varied globally, has been particularly important in the maquis, considering the high diversity of soil chemistry and physics (structure and depth) and isolation of ultramafic patches. As a consequence of the fragmented distribution, ultramafic outcrops are isolated 'edaphic islands' across the New Caledonian landscape. For example, "serpentine veins" typically form small isolated patches in non-ultramafic environments. This type of "patchiness" causes two ecologically important factors: environmental gradients and habitat discontinuity. When de-coupled from environmental gradients, patchiness affects floristic dissimilarity with extinction and colonization acting

differentially among sites (Harrison 1997). In California patchiness strongly affects regional diversity through edge-effects (Harrison 1997). Whittaker (1954) reported greater changes in community composition along an elevation gradient for an ultramafic flora compared to a non-ultramafic flora. This may be explained by a stronger response of ultramafic endemic species to climatic conditions (precipitation) compared with non-endemic species (Harrison and Inouye 2002). The complex topography and climatic gradients in New Caledonia cause a wide diversity of habitats is an important driver for plant speciation, especially in the maquis. The maquis of New Caledonia range from low elevation (<10 m) to the summit of Mont Humboldt (1816 m) and is coupled with a edaphic heterogeneity (Table 5) enhancing patchiness and between-site diversity.

Vegetation

Although the forest flora on ultramafic soils has a greater total number of species compared to the maquis, the maquis harbors more habitat-specialised species. The maquis develops from forest impacted by fire and presents a harsh environment for species to persist. Though, maquis on poor soils are species poor but harbor a distinctive and endemic-rich flora. Tree cover has a significant impact on species composition through improvement of soil fertility, leading to a reduction of endemic species by the spread of competitive species (Chiarucci et al. 2001). In New Caledonia, the over-representation of some floristic groups is frequently related with occurrence in maquis. Lineages currently associated with maquis may have spread during the Pleistocene rainforest regression, and may have coincided with Pleistocene aridification, which has stimulated diversification in the (non-ultramafic) South African Cape flora (Richardson et al. 2001). As such, a drier climate may have opened ecological niches favorable to the extension of species adapted to dry forest (on non-ultramafic soils) and maquis (on ultramafic soils). Diversification rates in New Caledonia have been the fastest in the youngest clades of the genus *Dracophyllum* (Ericaceae) which is restricted to maquis (Pillon 2012). This study however includes a single maquis-restricted lineage (*Dracophyllum*). More research is needed to highlight the role of in situ diversification (neo-endemism) on maquis endemism.

The distribution of rainforest lineages appears less influenced by soil types, as gauged by the even distribution of forest-affiliated groups in both edaphic compartments (e.g. basal angiosperms, palms, etc.). The current over-representation of basal angiosperms arose from the persistence of rainforest on the main island despite global Quaternary fluctuations that have affected regional floras (Pouteau et al. 2015). As such, rainforest species may have persisted in refugia, thus explaining the current disjointed distribution of some taxonomic groups. The disjointed distribution of many closely-related rainforest species is suggestive of fragmentation of a once continuous lowland rainforest that is likely to have persisted only in the northeast and south of Grande Terre during glacial maxima (Pintaud et al. 2001; Pouteau et al. 2015). The relatively large fraction of ultramafic-obligate species (293 spp.) shared between forest on ultramafic substrate and maquis could result from maquis species persisting in closed forest and forest species persisting after fire on bare ultramafic soils.

Diversification and endemism through the prism of ultramafic soils

Lack of large radiation

In New Caledonia, adaptions to ultramafic soils have evolved independently in a wide range of different plant groups. The evolutionary origin is highly labile, as has been shown by mapping tolerance over phylogenies in California (Anacker 2011), and as was shown for Palms (Pintaud and Jaffré 2001), for the genus *Psychotria* (Rubiaceae) (Barrabe et al. 2014) and *Polyscias* (Araliaceae) (Eibl et al. 2011). Widespread adaptive radiation in the New Caledonian flora appears rare, however (Pillon 2012) and have been little studied within ultramafic clades. The largest known radiation in the New Caledonian flora, which has occurred in the clade NC2 of the genus *Psychotria* (Rubiaceae), is not strictly associated with habitat specialization on ultramafic soils but has diversified on various types of soils (Barrabé 2013). More than 30 % of *Psychotria* species are ultramafic endemics but no phylogenetic signal could be detected for ultramafic tolerance (Barrabé 2013). In the genus *Pycnandra* (Sapotaceae), the largest endemic plant genus of New Caledonia (Morat et al. 2012), 60 % of the 66 species are ultramafic obligates and

adaptive radiation on ultramafic soils does not appear to have occurred (Swenson et al. 2008). In the genus *Geissois* (Cunoniaceae) the radiation of 13 species from a single colonist results from rapid diversification on contrasting soil substrates (Pillon et al. 2014). Concluding, the current phylogenetic pattern in the largest genera of the New Caledonian flora favor polyphyletic origins of ultramafic tolerance which suggest that ultramafic tolerance is evolutionary labile. This pattern is also congruent with the idea that shifts in soil preference, rather than radiation on a single soil type, is a main driver for diversification. This is confirmed by high endemicity, but low diversity, of soil-obligate genera, while species-rich genera are soil-facultative in New Caledonia. Elsewhere, despite the strong selective pressure on ultramafic soils which promotes adaptations, soil endemism is also not associated with adaptive radiation in California (Anacker 2011, 2014; Anacker et al. 2011; Schnitzler et al. 2011).

New Caledonian old communities and recent colonization events

The New Caledonian flora is distinct from other super-species rich floras associated with edaphic conditions, such as the South African Cape *fynbos* and the *kwongan* of Southwestern Australia, neither of which are ultramafic, where large (explosive) radiations represent a large proportion of the flora (Hopper and Gioia 2004; Richardson et al. 2001). The old age of New Caledonian flora may explain the low rates of diversification found in several New Caledonian lineages (Pillon 2012). Extinction events over the Island's geological history could further increase its phylogenetic isolation of numerous taxa (Pillon 2012). This appears to hold for habitat specialist endemic species with low infra-generic and infra-family diversity. Most of the Uo genera number <5 species and 20 of these genera are mono-specific. There are eight Uo families that are mono-generic and contain less than five species each. The low diversity of ultramafic obligate genera or families may also be explained from extinction events inside formerly diverse clades. This relictual diversity is illustrated by several putative paleo-endemic lineages, such as the mono-generic *Strasburgeria* which is thought to have been widely distributed in Antarctic region in the early Eocene (Contreras et al. 2013). Other putative paleo-endemic lineages include the endemic mono-specific genera *Paracryphia* (Paracryphiaceae) and

Nemuaron (Atherospermataceae), and the endemic family Phellinaceae that dates back to mid to late Cretaceous (Bremer et al. 2004). There are currently no known examples of old diversification in New Caledonia, instead groups such as *Araucaria* or *Nothofagus* are of recent origin (Grandcolas et al. 2008). Furthermore, multiple dispersal events have occurred in numerous groups (Barrabe et al. 2014; Bartish et al. 2005). New immigrants that colonized the Island had to compete with older lineages, potentially preventing widespread radiation to occur. For more recently diversified lineages, low species richness could reflect lower diversification of habitat specialist lineages compared to generalist lineages, as in the Californian flora (Anacker et al. 2011). As such, both extinction and competition might explain why adaptive radiation is not observed today (Pillon 2012). More studies are needed to elucidate the diversification age and rates of the New Caledonian relictual lineages.

Edaphic islands

Few studies have focused on the role of ultramafic soils in promoting the levels of endemism in New Caledonia. In contrast, in California, the pivotal role of edaphic factors and habitat patchiness in promoting plant speciation and endemism have been well-studied (Kay et al. 2011; O'Dell and Rajakaruna 2011; Rajakaruna 2004; Rajakaruna and Baker 2004). In other regions, such as Southeast Asia (Chathuranga et al. 2015; Rajakaruna and Baker 2004; van der Ent et al. 2015b), in Europe (Cecchi et al. 2011; Cecchi et al. 2010; Mengoni et al. 2003; Stevanović et al. 2003) and in South Africa (Schnitzler et al. 2011) similar studies have already been undertaken. These studies stress that patchiness of soils is likely to contribute to the geographic isolation of populations, through so called "edaphic islands" (Kruckeberg 1991; Rajakaruma and Boyd 2008; Rajakaruna 2004). In New Caledonia, ultramafic-endemic genera and families combine both edaphic and geographic isolation in the mountainous cordillera of Grande Terre and wetlands of the "Plaine des Lacs". The distribution of several hyper-endemic plant species on isolated massifs supports allopatric speciation as a most common mode for speciation in New Caledonia (Mouly and Jeanson 2015). In the genus *Geissois*, species growing on ultramafic soils are weakly ecologically differentiated (concentration of elements: Al, Ca, Cr, Fe, Mg, Ni, P) and are thought to have radiated through

allopatric speciation (Pillon et al. 2014). Similarly, an allopatric model of speciation was proposed for some species of *Polyscias* (Araliaceae) occurring on ultramafic soils (Eibl et al. 2011). Further evidence for allopatric speciation on isolated massifs is provided in Wulff et al. (2013).

The few zones where different edaphic conditions are in close proximity might also have been important in providing evolutionary opportunities for adjacent populations. For instance, the parapatric distribution of several species belonging to *Burretiokentia* (Arecaceae), in the narrow contact zone, suggests a potential case of parapatric speciation. *Burretiokentia vieillardii* has a wide geographic distribution and occurs on both metamorphic rocks and Ferralsols, while its two sister species, *B. dumasii* and *B. koghiensis,* are found on two isolated ultramafic massifs (Me Maoya and Mont Koghis) of which only on Magnesic Cambisols (Pintaud and Jaffré 2001). These two species that are adapted to the distinctive Magnesic Cambisols represent possible cases of adaptive radiation (Pintaud and Jaffré 2001) and may have descended from the more widespread species *B. vieillardii*. On Mont Koghis, which consists of a complex matrix of different soils (Ferralsols, Magnesic Cambisols and sedimentary soils), mixes species that elsewhere do not co-occur. This site may have permitted hybridization for at least one endemic Cunoniaceae (*Cunonia koghicola*) (Pillon et al. 2008).

Conclusions

The flora of New Caledonia is typified by the occurrence of ultramafic outcrops that disproportionally contributes to the high levels of plant diversity and endemism on the Island. The so-called maquis vegetation, which has evolved relatively recently, as a result of repetitive fires and climatic fluctuations, is the main contributor to the distinctiveness of the ultramafic flora. Rainforest on ultramafic soils, though less exposed to harsh environments, also harbors an original and rich flora that is currently threatened by anthropogenic activities causing rainforest regression that will lead to the loss of many soil-endemic species. The edaphic heterogeneity of ultramafic soils is combined with a complex topography and severe isolation of ultramafic patches constituting edaphic islands known as drivers of plant speciation and endemism. The ultramafic flora exhibits a range of nutrient-acquisition strategies and other adaptive traits (trace element hyperaccumulation, sclerophylly). Ultramafic soils are arguably an efficient ecological barrier against plant colonist and might thus have efficiently protected New Caledonia flora against exotic plant species. Attributes of invasive exotic plants strongly differ from attributes required to grow in harsh environment. The richness of the ultramafic flora diversity is likely to have resulted from repeated independent dispersal events of pre-adapted species, rather than in situ radiation on this substrate. Paleo-endemic lineages, illustrating the relatively old age of New Caledonian flora and regional climatic events that occurred during Pleistocene, further add to phylogenetic distinctness and endemism. These factors may explain the low number of genera and families observed in many ultramafic obligate lineages and the disjoint distribution of many closely-related species. This hypothesis however, remains to be tested and involves detailed phylogenetic studies especially on maquis species. In the future, we plan to perform meta-analyses on our extensive dataset to unravel the relationships between geographical and soil factors and possible the correlations to patterns of endemism and species richness.

The extended of forest has been greatly reduced due to repeated fires since human settlement ~3300 years ago (Ibanez et al. 2013; Perry and Enright 2002). More recently, the vegetation on ultramafic soils is under acute threat by nickel mining activities (Jaffré et al. 1998a; L'Huillier et al. 2010; Wulff et al. 2013). Today, forests are restricted to mountainous locations (mainly on Ferralsols above 850–1000 m asl), on alluvial soils along rivers, in thalwegs on rock slides, and in valleys as scattered relicts protected from fire and mining activities (Jaffré et al. 2010). Only a few relict patches of forest (each <1 ha) remain on Magnesic Cambisols at the base of massifs in the more arid zone. The vulnerability of the ultramafic flora is illustrated by the conifers, of which 23 species of 41 occurring on ultramafic soils are now threatened (5CR, 12 EN, 6VU) (Jaffré et al. 2010). Of 95 hyper-endemic species occurring on mining sites, 80 have been evaluated as threatened (18CR, 41EN, 21VU) by the local Read List Authority (RLA-NC). This assessment is in progress and does not include all hyper-endemic species affected by mining activities. Habitat fragmentation exacerbates further biodiversity loss due to the low genetic diversity of small-sized populations of many endemic plant species (Honnay and Jacquemyn 2006; Kettle et al. 2007). The integral

protection of all remaining forest on ultramafic soils, and that of some maquis on Magnesic Cambisols, should be a priority. The ultimate effects of climate change are currently unknown, but expected to pose a threat to many habitat specialist plant species in New Caledonia. Specific vulnerability also comes from low dispersal ability, the restricted area for migration, the small population size and the high proportion of habitat specialists (Harter et al. 2015; Taylor and Kumar 2016). The dual insularity syndrome of the New Caledonian ultramafic flora involved further vulnerability to climate changes.

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