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## Infertile landscapes on an old oceanic island: the biodiversity hotspot of New Caledonia

Yohan Pillon<sup>1</sup>, Tanguy Jaffré<sup>2,3</sup>, Philippe Birnbaum<sup>2,3,4</sup>, David Bruy<sup>2,3</sup>, Dominique Cluzel<sup>5</sup>, Marc Ducouso<sup>1</sup>, Bruno Fogliani<sup>5</sup>, Thomas Ibanez<sup>6</sup>, Hervé Jourdan<sup>7</sup>, Louis Lagarde<sup>8</sup>, Audrey Léopold<sup>4</sup>, Jérôme Munzinger<sup>2</sup>, Robin Pouteau<sup>2</sup>, Jennifer Read<sup>9</sup> & Sandrine Isnard<sup>2,3</sup>

<sup>1</sup>LSTM, IRD, INRAE, CIRAD, Institut Agro, Univ Montpellier, Montpellier, France

<sup>2</sup>AMAP, Univ Montpellier, IRD, CIRAD, CNRS, INRAE, Montpellier, France

<sup>3</sup>AMAP, IRD, CIRAD, Herbier de la Nouvelle-Calédonie, Nouméa, New Caledonia

<sup>4</sup>Institut Agronomique Néo-Calédonien (IAC), équipe SolVeg, Nouméa, New Caledonia

<sup>5</sup>ISEA, Université de la Nouvelle-Calédonie, Nouméa, New Caledonia

<sup>6</sup>Department of Biology, University of Hawai'i at Hilo, Hilo, HI, USA

<sup>7</sup>IMBE, Aix Marseille Université, CNRS, IRD, Avignon Université, Nouméa, New Caledonia

<sup>8</sup>TROCA, Université de la Nouvelle-Calédonie, Nouméa, New Caledonia

<sup>9</sup>School of Biological Sciences, Monash University, Victoria, Australia

Corresponding author: yohan.pillon@ird.fr

## ABSTRACT

The OCBIL theory comprises a set of hypotheses to comprehend the biota of old, climatically buffered, infertile landscapes (OCBILs). Here, we review evidence from the literature to evaluate to what extent this theory could apply to the biodiversity hotspot of New Caledonia. We present geological, pedological and climatic evidence suggesting how the island may qualify as an OCBIL. The predictions of OCBIL theory are then reviewed in the context of New Caledonia. There is indeed evidence for a high rate of micro-endemism, accumulation of relict lineages, a high incidence of dioecy, myrmecochory, and nutritional specializations in plants. New Caledonian vegetation also exhibits several types of monodominant formations that reveal the importance of disturbances on the island. Fires and tropical storms are likely important factors that contribute to the dynamic of New Caledonian ecosystems. Although naturally infertile, there is archaeological evidence that humans developed specific horticultural practices in the ultramafic landscapes of New Caledonia. Further comparison between New Caledonia and other areas of the world such as South Africa and Southwest Australia are desirable, to develop and then test the OCBIL theory into a more robust and general framework, and determine the most efficient strategies to preserve their outstanding biodiversity.

**KEYWORDS:** cyclone, dispersal, metal hyperaccumulation, mycorrhiza, monodominance

## INTRODUCTION

The archipelago of New Caledonia in the Southwest Pacific is acknowledged as one of the world's biodiversity hotspots (Myers *et al.*, 2000; Lowry *et al.*, 2004). Although the smallest in area (ca. 19,000 km<sup>2</sup>), this hotspot hosts a rich flora of over 3,400 native vascular plants, characterized by a high level of endemism (74.7%, Morat *et al.*, 2012; Munzinger *et al.*, 2020), while over 70% of the natural vegetation has been lost (Sloan *et al.*, 2014). The flora has high endemism at higher taxonomic levels (genus, family and even order), including a wide range of gymnosperms and "basal" angiosperms and has even been treated as a floristic subkingdom (Takhtajan, 1969). The supposed archaism of the biota has often been interpreted as a Gondwanan heritage (Holloway, 1979; Morat, 1993) after the island drifted away from Australia and the rest of the Gondwana supercontinent at c. 80 Ma (Aronson & Tilton, 1971; Uruski & Wood, 1991; McLoughlin, 2001). Geological evidence nevertheless points to a likely submersion after the divergence from Australia (Pelletier, 2006) which would imply that the biota of New Caledonia is entirely the result of long-distance dispersal (Grandcolas *et al.*, 2008), and the island could thus qualify as a "Darwinian island" (*sensu* Gillespie & Roderick, 2002). The exact age of the biota is unclear, there is good evidence for submergence between 75 and 60 Ma and for continuous emergence since 25 Ma, but there is an interval without any geological record between 34 and 25 Ma (Maurizot & Campbell, 2020). In addition, some landmasses may have emerged a few hundred km to the west between 45 and 50 Ma (Sutherland *et al.*, 2020). All endemic plant lineages investigated so far have a crown age that is no older than 25 Ma (Pillon, 2012; Nattier *et al.*, 2017), while a few arthropod clades are older and some can be considered as discordant with the geological history (Giribet & Baker, 2019).

Beside its intriguing biogeography, New Caledonia has also long been considered as unique among islands because of its large exposure of ultramafic substrates that probably had a profound influence in shaping the flora (Virot, 1956; Jaffré, 1980; Isnard *et al.*, 2016). Ultramafic soils offer challenging conditions to plant growth and are often covered by a distinctive vegetation (Proctor, 2003; Kazakou *et al.*, 2008). In New Caledonia, this includes a diverse sclerophyllous scrub-heath vegetation locally known as "maquis minier" or "maquis" (L'Huillier, Jaffré, & Wulff, 2010, pp. 65-80) that resembles the South African fynbos or the Southwest Australian kwongan (Read *et al.*, 2007). Inspired by the latter ecosystems, Hopper (2009) developed the OCBIL theory to explain the high diversity and ecological uniqueness of these very old, climatically buffered, infertile landscapes (OCBIL), as opposed to the young, often disturbed, fertile landscapes (YODFEL) that cover most of Europe and North America. In this article, we aim to address to what extent the landscapes of New Caledonia may be considered as old, climatically-buffered and infertile. We will then discuss how its unique flora and ecosystems may satisfy the seven main OCBIL predictions formulated by Hopper

(2009). We will then present the special cases of monodominant formations that are common on the island, and three major disturbance factors that may have played an important role in shaping New Caledonian ecosystems. The Loyalty Islands (offshore islands east of the main island), due to their Pliocene emergence (< 5 Ma, Maurizot & Campbell, 2020) and mostly calcareous substrate, will not be discussed here.

#### HOW OLD, CLIMATICALLY BUFFERED AND INFERTILE ARE NEW CALEDONIAN LANDSCAPES?

**The formation of New Caledonian landscapes through the Cenozoic**—Since its oldest geological record during the Carboniferous to Early Cretaceous (300 Ma to 95 Ma), New Caledonia was almost continuously separated from Gondwana and marked by prominent endemism shared with New Zealand (Maurizot & Campbell, 2020). During the mid-Cretaceous, the geodynamic setting changed into a passive margin extensional regime. Coniacian-Santonian (90-84 Ma) rifting and finally Paleocene oceanisation isolated continent-size areas of thinned continental crust termed Zealandia (Luyendyk, 1995; Mortimer *et al.*, 2017) ; meanwhile, the Norfolk Ridge was totally drowned.

A new NE-dipping subduction started at ca. 56 Ma (Cluzel *et al.*, 2006) and consumed the oceanic crust generated to the East of Norfolk Ridge during the Late Cretaceous. When the previously thinned continental crust of the Norfolk Ridge reached the trench, it emerged temporarily in the fore-arc bulge and finally jammed the subduction and resulted in obduction. Marine sedimentation continued in the south of the island until the latest Eocene (34 Ma) (Cluzel, Chiron, & Courme, 1998), before it was overthrust by peridotites. Peridotites are upper mantle rocks mostly composed of olivine and pyroxene and termed ultramafic because of their chemical composition: low in SiO<sub>2</sub> (<45%) and high in FeO + MgO (>40%). As a consequence, New Caledonia hosts one of the largest ultramafic terranes in the world, termed Peridotite Nappe (Avias, 1967), that covers at present about one third of the surface of the island and its insular extensions (Belep Islands, Isle of Pines). However, the occurrence of peridotite remnants throughout New Caledonia (Maurizot & Vendé-Leclerc, 2012) signals the existence of a complete ultramafic cover at the time of obduction.

The exhumation of previously subducted metamorphic rocks started from 44 Ma to 38 Ma (Spandler, Rubatto, & Hermann, 2005) and they arrived near the surface at ca. 34 Ma (Baldwin, Rawling, & Fitzgerald, 2007). They form at present the rugged Mt Panié ridge (1,629 m a.s.l.) in the north of the island. It is likely that, in contrast with the rest of the island, the area that now corresponds to unroofed metamorphic rocks was uncovered relatively soon from the peridotites; however, this hypothesis is not yet constrained by data. Due to the absence of sedimentary record, nothing is known of the period (Oligocene) that immediately followed obduction and was probably

marked by fast uplift and intense erosion. In contrast, tropical weathering of serpentinised peridotites in a relatively smooth topography and stable environment was recorded by the development of lateritic profiles and a meandering river system prior to ca. 25 Ma (Sevin *et al.*, 2012). Therefore, the final emergence of Grande Terre is loosely time-constrained after 34 Ma (latest marine sediments underneath peridotites) and prior to 25 Ma (erosion of the earliest regolith).

After the formation of Early Miocene fringing coral reefs along the west coast, slab break-related uplift occurred at ca. 23 Ma (Sevin *et al.*, 2014); the corresponding erosion created steep slopes and re-incision of meandering valleys. As a result, the large klippe of the west coast were isolated from the main peridotite unit termed Massif du Sud (Figure 1). Meanwhile, large volumes of reworked laterite filled the former topography and created the sedimentary plateaus of the Massif du Sud (Folcher *et al.*, 2015). During the Quaternary glaciation, sea level variations repeatedly filled and re-incised the valleys without greatly changing the bulk landscape; finally, the fore-arc bulge due to the east-dipping subduction of the Australian Plate in the Vanuatu Trench (Dubois, Launay, & Recy, 1974) resulted in the moderate asymmetrical uplift (ca. 10 m) and westward tilt of southern New Caledonia from ca. 200 ka to Present.

**The low soil fertility of ultramafic and non-ultramafic substrates**—New Caledonia has a very wide diversity of soils over a relatively small area: twenty main soil types classified in eight groups following the World Reference Base (WRB) for soil resources (Fritsch, 2012). This diversity is related to the various geological substrates, relief, and variability of precipitation that have significant impacts on the vertical development of the soils (Tercinier, 1963; Latham, Quantin, & Aubert, 1978; Fritsch, 2012). Five main types of soils will be described hereafter that account for 70% of the main island area (Figure 2). The remaining 30% occur almost exclusively on the west coast and consist of a wide diversity of soil types, with principally Vertic Cambisol, Vertisol and Haplic Fluvisol. Because the natural vegetation almost completely disappeared in these areas due to human activities, these soils are not discussed here.

From the peridotite nappe (ultramafic rocks), and under a humid tropical climate, two main soil types have developed. The most widespread type consists mainly of iron oxy-hydroxide (Becquer *et al.*, 2001); these soils are ferralsol (ferritic) (IUSS Working Group, 2006, Table 1). During weathering, especially in areas having well-drained topography, silica and cations ( $Mg^{2+}$ ,  $Ca^{2+}$ ,  $K^+$ ) are exported, resulting in the accumulation of ferrous minerals in soils (Trescases, 1969, 1973; Latham, 1986). In addition, these soils do not contain clay minerals; kaolinite is notably absent due to the low aluminum content in peridotites (Latham *et al.*, 1978; Becquer *et al.*, 2001). Consequently, these soils

have a very low cation exchange capacity (CEC), mainly determined by the soil organic matter (SOM) content. The pH is very acidic and also depends on the SOM content. Total and available phosphorus concentrations are particularly low, and the low availability is accentuated by the high retention rate due to iron oxides (Dubus & Becquer, 2001; Becquer *et al.*, 2001). Total and exchangeable calcium and potassium are deficient; magnesium concentrations are low, but the soil CEC is mainly occupied by this element. In the humic horizon of the soil surface, calcium and magnesium may be in equilibrium, but in deeper horizons, magnesium is the only exchangeable cation, particularly in alluvial and colluvial soils, and in deep soils with an indured or gravelly upper horizon (Jaffré & Latham, 1974). In addition to the very low availability of key nutrients, these soils may also contain exceptionally high levels of nickel, cobalt, manganese and chromium (e.g., Lee *et al.*, 1977; Latham *et al.*, 1978). However, their bioavailability would depend on the position of soil along the toposequence and the modifications undergone by the soils (erosion, colluvium) as well as the degree of hydromorphy, oxydo-reduction and biological processes (L'Huillier & Edighoffer, 1996; Becquer *et al.*, 2001, 2006; Quantin *et al.*, 2002). The second soil type is mainly developed on peridotite massifs with high slope and serpentinite (Trescases, 1969, 1973). These soils are young with a low vertical development due to rejuvenation by mechanical erosion. Clay minerals as smectite suggest high CEC, but it is clearly saturated by magnesium. Indeed, exchangeable magnesium can occupy more than 80% of the CEC (Jaffré pers. obs. in Jaffré & L'Huillier, 2010): they are Haplic Cambisol (Magnesic, WRB classification) known as brown hypermagnesian soils (Table 1). Calcium and potassium are deficient while concentrations of metals such as nickel, cobalt and manganese are high, especially when the soils receive matter inputs from peridotites. Although their natural fertility may be considered slightly better than ferralsols, their low vertical development and chemical characteristics, particularly very high magnesium content (magnesian soils with exchangeable Ca :Mg ratio < 1) and metals, constrain the mineral nutrition of plants (e.g., Lee *et al.*, 1977).

On the other major geological substrates, from metamorphic or volcano-sedimentary origin, young soils developed in the 'Chaîne Centrale' mountain range, representing the largest set of soils in terms of land area (Table 1). These soils, classified as Ferralic Cambisol (Dystric), are characterized by very acidic pH and CEC saturation less than 20%, i.e. oligotrophic or desaturated soils. Their natural chemical fertility is considered very low because of nutrient deficiency (N, Ca, P, K), and very high acidity leading to high concentrations of exchangeable aluminum and manganese. Moreover, unprocessed illite- and vermiculite- clay minerals are present, suggesting very young soils, rejuvenated by intense gully erosion due to the slopes. On the northeast coast, soils have developed on acidic metamorphic rocks: mica-schist and gneiss. These Haplic Regosol, which are found on the



highest topography of New Caledonia, i.e. Mount Panié (1,628 m), are located on very steep slopes. They are young soils due to systematic rejuvenation, but the bedrock is deeply altered. Indeed, under a thin and humic surface horizon, a very soft and altered horizon ('C'), of more than one meter can develop. Naturally covered by montane cloud forest, their natural fertility is considered very low (Table 1). On the opposite slope, on the northwest coast of the main island, soils with a marked profile differentiation have developed: Haplic Acrisols (Albic and Rhodic) (Table 1). These soils are acidic and desaturated (saturation rate  $\leq 50\%$ ), the shallowest horizons may be bleached (Albic), while the B horizons may be enriched in illuviated clay and are reddish (rubefied) (Rhodic). Their pedogenesis tends towards podzolization, and these soils are associated with Podzol *sensu stricto* developed on phtanites (black cherts) and siliceous alluvium (Latham *et al.*, 1978). Although the soil profile is differentiated, these soils are subject to rejuvenation by mechanical erosion. Their chemical fertility is very low to nil, and clay migration (i.e. illuviation) may create a discontinuity in the soil texture that may limit or inhibit root penetration.

The soils mentioned above often have a low vertical development, mainly due to rejuvenation caused by a marked topography. Strong alteration and weathering have resulted in low chemical quality, i.e. acidic pH, low CEC, desaturation, and low nutrient concentration. In addition, the pedogenesis of peridotites and serpentinites has led to an excess in magnesium associated with a high imbalance in the Ca/Mg ratio, and to a high content of metals, particularly nickel, chromium, manganese and cobalt, whose bioavailability may be significant. Given all these constraints, the natural fertility of the main type of soils developed in the New Caledonia main island can be considered very low (Table 1).

**A tropical oceanically buffered climate**—Normal annual temperature ranges from 19.2°C in July-August to 25.9°C in February. Annual precipitation ranges from 300 mm to 4,200 mm with greater precipitation on the windward east coast (Météo-France, 2007). There are several indications of prolonged buffered climatic conditions in New Caledonia, suggesting a Pleistocene climatically stable landscape (Mucina & Wardell-Johnson, 2011). Pollen records collected from Lake Xere Wapo, in the southeast of the main island, revealed that the vegetation alternated between rainforest and maquis over the last 120 ka (Stevenson & Hope, 2005). However, in contrast to the northeast Australian records of Lynch's Crater (Kershaw, 1986), rainforest gymnosperms of the genera *Dacrydium*, *Podocarpus* and *Araucaria*, and rainforest angiosperms of the families Cunoniaceae and Myrtaceae never disappeared in sediment cores, providing evidence for the persistence of a distant source of rainforest tree pollen over time (Stevenson & Hope, 2005). Based on the present day

distribution of *Nothofagus* in the area and the prevalence of *Nothofagus* forest at ~30,000 yr BP in dated sediments from the nearby Lake Suprin (southern New Caledonia), Hope & Pask (1998) suggested that local temperatures may have been cooler by as little as 1-5 °C over this period.

Further evidence comes from spatially-explicit reconstructions of the Late Quaternary climate, which are increasingly available with the development of general circulation models. Results from these models indicate that the warm and wet climatic conditions currently found in the archipelago were less dramatically affected than those of Australia and some nearby islands during the Last Glacial Maximum (LGM), which occurred ~20,000 yr BP (Poncet *et al.*, 2013; Pouteau *et al.*, 2015). If one considers macroclimatic shifts since the LGM together with current topoclimatic gradients, the dispersal speed needed to track the mean annual change in temperature (past climate change velocity) is much higher in most parts of Australia than in New Caledonia (Figure 3).

The relative climate stability in New Caledonia is also reflected in forecasts of future climate change. Recent bioclimatic envelope modelling of species distributions has estimated that up to 15% of the 469 most widespread New Caledonian tree species will likely have no analogue habitat by 2070, and might then become extinct (Pouteau & Birnbaum, 2016). In comparison, using a similar approach based on the same envelope model, general circulation models and scenarios have found that up to 25% of *Banksia* species (100 species investigated), thought to be representative of diversity patterns of plants in general in southwestern Australia, are threatened with extinction by 2080, although the region is much larger (Fitzpatrick *et al.*, 2008). More generally, analyses of mid- (2046-2065) and long-term (2081-2100) climate projections revealed that average temperature increases in coastal and continental regions may exceed those of oceanic islands by more than 2 °C (Harter *et al.*, 2015).

The question then arises as to why the climate has been relatively stable in New Caledonia since at least the last glacial period, while a significant portion of Australia experienced dramatic climate change. One reason is certainly the lower diurnal and annual temperature amplitudes on islands compared with larger land masses because of the buffering effect of the ocean (Leuschner, 1996). In addition, Irl *et al.* (2016) and Pouteau *et al.* (2018) showed that, contrary to mainland regions, local topography prevails over regional factors in shaping the elevational distribution of montane ecosystems on relatively small islands. This finding suggests that historical global climate change likely caused less significant upslope shifts of rainforest habitats on coastal mountains found on oceanically-buffered islands than on continents. This is probably all the more the case for slopes facing trade winds throughout the year (east coast), on which orographic clouds and showers

develop more frequently, thus supporting the subsistence of locally cool and wet microrefugia during global glacial periods (Irl *et al.*, 2015).

## NEW CALEDONIA AND THE PREDICTIONS OF THE OCBIL THEORY

**1. Reduced dispersability, increased local endemism and common rarity**— Dispersal from parental habitat may be a risky strategy in OCBILs, where reduced dispersability, high numbers of localised rare endemics, and strong population differentiation, is therefore expected (Hopper, 2009). Based on observations on the southwestern Australian flora, Hopper (2009) considered that seed dispersal assisted by wind or animal, indicated by the presence of wings or fleshy arils, was uncommon in OCBILs; although this may be less true in the Cape flora. Carlquist (1974, p. 215) considered that New Caledonian Gymnosperms are not easily dispersible, and indicated *Zygogynum* (Carlquist, 1965, p. 245) and *Strasburgeria* (Carlquist, 1974, p. 481) as examples of loss of dispersibility. However he considered this phenomenon as an insular syndrome.

Several census of dispersal syndromes have been published for the ultramafic flora of New Caledonia, covering rainforest (Carpenter, Read, & Jaffré, 2003; Ibanez *et al.*, 2017) or maquis and its interface with rainforest (Ititiaty *et al.*, 2020). The dominant means of dispersal were animals (55-72% of the plant species), followed by wind (14-23 %) and gravity (7-31 %). The proportion of taxa dispersed by animals increases along the ecological succession (Ititiaty *et al.*, 2020), with more animal-dispersed species found in the maquis-forest edge (64.7%) than in maquis (41.8%). The paucity of vertebrates (particularly mammals) in New Caledonia probably has an impact on dispersal syndromes and could explain the relatively high representation of wind-dispersed species compared with similar vegetation in the world, as in lowland rainforest of Malaysia, North Queensland and Costa Rica (Webb & Tracey, 1981; Levey, Moermond, & Denslow, 1994; Seidler & Plotkin, 2006). This is especially the case in maquis, which is open vegetation known to comprise a larger proportion of wind-dispersed species (Duncan & Chapman, 1999). The patchy distribution of habitats and the rugged topography of New Caledonia would, however, suggest that these wind-dispersed seeds (with wings, hairs, etc.) are generally not dispersed over a very long distance. This is further attested by many rainforest species that exhibit a strong spatial aggregation (Birnbaum *et al.*, 2015). Long-distance dispersal is probably an uncommon phenomenon in New Caledonian rainforests and may only be attributed to *Ducula goliath* (Barré *et al.*, 2003), a large pigeon (600-720 g) that can swallow large fruits (> 2 cm); and fruit bats (Muscarella & Fleming, 2007), which likely swallow only small seeds (e.g., *Ficus*). Most small to medium size (< 2 cm) fleshy fruits are probably dispersed by small

frugivorous birds, but lizards (mostly diplodactylid geckos and a few skinks) are not insignificant dispersers in New Caledonia (Sadlier *et al.*, 2014), both being mainly short-distance dispersers.

Some seeds may be dispersed over short distances by invertebrates as a high level of myrmecochory (dispersal by ants) was found in the New Caledonian flora, potentially in 8% of plant species, i.e. 300 species, among which 113 have already been confirmed to possess an elaiosome (lipid rich appendage, which attract ants). In particular, 72% of the confirmed myrmecochorous species are ultramafic obligates, in both forest and maquis (Le Yannou-Cateine, 2017), in line with a high level of myrmecochory observed on nutrient-poor soils in Australia or South Africa (Westoby *et al.*, 1991; Mucina & Majer, 2012). Indeed, elaiosomes are less costly dispersal attributes compared with fleshy fruits and may be promoted in infertile or fire-prone landscapes, although dispersal distances may only be a few meters (Orians & Milewski, 2007).

Models of costs and benefits of dormancy predict that non-dormant seeds should be favored under a scenario of long-term climatic stability (Dayrell *et al.*, 2017). Accordingly, the dormant/non-dormant ratio found for campo rupestre (an OCBIL in Brazil, Hopper, Silveira, & Fiedler, 2016) is the lowest for any vegetation type on Earth (62.5% non-dormant) (Dayrell *et al.*, 2017). For 332 ultramafic species examined in New Caledonia, 38% were confirmed by experimentation as non-dormant and a further 20% could be so (already identified within the same genus), suggesting that up to 50% of the examined species could be non-dormant (Ititiaty *et al.*, 2020).

Micro-endemism is a well-known feature of the New Caledonian flora (Wulff *et al.*, 2013) and fauna (Caesar, Grandcolas, & Pellens, 2017). Based on literature and herbarium specimens, Wulff *et al.* (2013) estimated that 635 of the 2930 plant species assessed are narrow endemic species, i.e. known from no more than three locations separated by more than 10 km (Figure 4). 309 species were recorded from a single location. The rate of micro-endemism was higher on ultramafic substrates, with 228 species. The few population genetics studies published on New Caledonian plants have revealed well-differentiated populations, e.g., in *Amborella* (Poncet *et al.*, 2013), *Araucaria* (Kettle *et al.*, 2007; Ruhsam *et al.*, 2016), and *Santalum* (Bottin *et al.*, 2005). The micro-endemic *Scaevola coccinea*, is an extreme case with four genetic groups within its range of 12 × 6 km (Wulff *et al.*, 2017), although its pollination system is specialized for small nectarivorous birds (Wulff, 2012).

**2. Accentuated persistence—old lineages, old individuals**—If natural selection has favoured limited dispersability of sedentary organisms in OCBILs, elevated persistence of lineages and long-lived individuals should be expected (Hopper, 2009). New Caledonia is rich in relict lineages such as its

iconic bird, the kagu (*Rhynochetos jubatus*). New Caledonia surpasses all other Pacific islands by the number of endemic genera of vascular plants, between 62 and 91 depending on taxonomic concepts (Pillon, Barrabé, & Buerki, 2017), and three endemic plant families: Oncothecaceae, Phellinaceae, and Amborellaceae (endemic order Amborellales), the sister group to the rest of the angiosperms (Qiu *et al.*, 1999). Most of these endemic taxa are monotypic or species-poor and may often represent relict lineages rather than offspring of adaptive radiation (Pillon *et al.*, 2017). Conifers are also particularly diverse with almost half the diversity of the world's Araucariaceae, as well as the ANA grade (Amborellales, Nymphaeales, Austrobaileyales), Chloranthales and Magnoliids (Poureau *et al.*, 2015). Some of these lineages are particularly ancient, e.g., the stem age of *Amborella* is between 140 and 256 My (Poncet *et al.*, 2019), that of the conifer *Austrotaxus* between 90 and 145 My (Leslie *et al.*, 2012), and the fern *Stromatopteris* c. 90 My (Pryer *et al.*, 2004). They are clearly older than the emergence of New Caledonia and are evidence of the mismatch between the age of endemics and the age of islands/ecosystems (Pillon & Buerki, 2017). The majority of the endemic genera (59–85) are found on ultramafic substrates and 25–36 of the endemic genera are restricted to them (or almost so), whereas only three to six avoid them (Pillon *et al.*, 2017); conifers also have a strong bias for ultramafic substrates (Jaffré, Munzinger, & Lowry, 2010). “Basal” angiosperms, on the other hand, seem to prefer the wettest areas, also putative climatic refugia (Figure 4) (Poureau *et al.*, 2015; Trueba *et al.*, 2017). The flora of New Caledonia is largely woody with a limited diversity of herbaceous (short-lived) species, besides the families Orchidaceae, Cyperaceae and Poaceae. Some tree species can be particularly long-lived with slow growth, e.g., *Agathis ovata* (> 700 years old, perhaps up to 1500, Figure 5C, Enright, Miller, & Perry, 2003), *Araucaria goroensis* (650 years, as *A. muelleri*, Enright *et al.*, 2014). Lifespan in many species is further increased by resprouting after fire (Jaffré, Rigault, & Dagostini, 1998b). On the other hand, *Cerberiopsis candelabra* is a long-lived pioneer monocarpic tree that can reach 20-30 m in height and 40-60 cm in diameter (Veillon, 1971), whose lifespan is determined by flowering.

**3. The James Effect**—The James Effect has been defined as the “natural selection for genetic, cytogenetic, or phenotypic adaptations that conserve heterozygosity in the face of inbreeding due to small population size” (Hopper, 2009). Adaptations to avoid inbreeding in the flora of New Caledonia may include pollination by strong-flying animals. In their study of 123 rainforest tree species, on ultramafic substrates, Carpenter *et al.* (2003) reported that 6% were pollinated by birds. Kato and Kawakita (2004), found 12% of 95 indigenous species from diverse vegetation types were bird-pollinated, a value close to the Southwest Australian Floristic Region, which has the highest proportion of plants pollinated by vertebrates in the world (15%, Hopper & Gioia, 2004). There are

six species of honeyeaters in the archipelago (mostly represented by endemic subspecies), and some species are very common in the maquis, where the single Barred Honeyeater (*Glycifohia undulata*) visits at least 26 species, including several Proteaceae (Barré, Chazeau, & Jourdan, 2010). Other vertebrates could also be pollinators. Little is known about diplodactylid geckos and skinks (locally diverse), but they have been observed visiting flowers, especially in maquis (e.g., Bauer & Sadlier, 2000; Barré *et al.*, 2010), and some gecko gut contents showed anthers and stamens (Bauer & Sadlier, 1994), while bats can also visit some flowers, such as those of *Geissois* (Cunoniaceae, Hopkins *et al.*, 2015).

Another way to increase heterozygosity is through sexual systems such as dioecy. Indeed, New Caledonia has the highest percentage of dioecious species in the world (21%, Figure 5B, Schlessman *et al.*, 2014). It thus substantially surpasses other OCBILs: Southwest Australian Floristic Region (4%, McComb, 1966), Gran Sabana of the Pantepui (4.5%, Ramirez, 1993), Cape Flora (6.6%, Steiner, 1988) have values lower than, or comparable to, the global average percentage for angiosperms (6%, Renner & Ricklefs, 1995). Other floras with a high incidence of dioecism are New Zealand (12-13%, Godley, 1979) and Hawaii (14.7%, Sakai *et al.*, 1995), both dominated by YODFELs. Insularity and wet forest habitat are probably confounding factors that promoted dioecy in New Caledonia.

**4. Prolonged speciation at the margins**—Hopper (2009) predicted recurrent speciation events in semi-arid areas adjacent to the climatically stable OCBIL. There is no semi-arid region in New Caledonia that would be comparable to South Africa and Southwest Australia. Nevertheless the western coast of New Caledonia is much drier (<1,200 mm of annual precipitation) and once harboured large areas of tropical dry forest that have largely vanished today (Bouchet, Jaffré, & Veillon, 1995). This vegetation has many endemic species, but lower endemism (65%). It is lacking unique endemic genera and is depauperate in relict lineages including Gymnosperms or Magnoliids. This flora seems rather derived from the local rainforest lineages (e.g., *Diospyros*, Paun *et al.*, 2016). The biodiverse main island of New Caledonia also served as a stepping-stone into the Pacific where some of its unique lineages dispersed and gave rise to endemic species. For instance, peripheral speciation is observed on the nearby Loyalty Islands, that are more recent (<5 Ma) low coralline islands. Their biota is largely borrowed from the main island with a small number of endemic species (see Schmid, 1969; Sadlier & Bauer, 1997; Barré *et al.*, 2006 for the flora, herpetofauna and avifauna respectively). Several lineages also dispersed and speciated on the volcanic islands of Vanuatu and

Fiji: e.g., *Macadamieae* (Mast *et al.*, 2008), *Geissois* (Pillon *et al.*, 2014) and *Oxera* (Barrabé *et al.*, 2015).

**5. Nutritional and other biological specialisation**—To cope with infertile lands, plants in OCBLs are expected to display special nutritional and other biological traits (Hopper, 2009). The flora of New Caledonia is indeed remarkable in the diversity of root symbioses represented. Ectomycorrhizal plants are particularly diverse (Table 2) and often locally dominant in maquis, rainforest (on ultramafic substrates), and savanna ; they are associated with a high fungal diversity (Carriconde *et al.*, 2019). At least nine species of Cyperaceae (in five genera) can produce dauciform roots (Lagrange *et al.*, 2011), which are structures that are involved in P-acquisition strategy based on carboxylate release in some Australian species (Playsted *et al.*, 2006; Shane *et al.*, 2006). Although this family is predominantly non-mycorrhizal, evidence of root colonization by arbuscular mycorrhizas have been found in nine species (Lagrange *et al.*, 2011), with at least some cases of infection in the dauciform roots. Cyperaceae are also associated with beneficial rhizospheric bacteria (Bourles *et al.*, 2020) and often dominate the herbaceous strata in maquis. The family Proteaceae, which are mostly non-mycorrhizal but produce cluster roots to acquire phosphorus (Lambers *et al.*, 2011), are species-rich (ca. 50 species, all endemics, in nine genera) and present in most ecosystems. Ericaceae (particularly subfamily Epacridoideae, 20 endemic species), with their specific ericoid mycorrhizas, are abundant in maquis. Although under-represented on the island (Pillon *et al.*, 2010) and specifically on ultramafic substrates (Pillon *et al.*, 2019), the nitrogen-fixing Fabaceae (associated with symbiotic proteobacteria such as *Rhizobium*) are represented by over 90 species, but may be ecologically displaced by actinorhizal Casuarinaceae (nitrogen-fixing species associated with symbiotic *Frankia*, Navarro *et al.*, 1999) that can be locally dominant. Casuarinaceae are either ectomycorrhizal (genus *Casuarina*) or form peculiar mycorrhizal nodules (*Gymnostoma*), involving *Glomus* fungi (Duhoux *et al.*, 2001). Interestingly, the most widespread, ecologically labile, and often locally dominant legume species is *Acacia spirorbis*, one of only two native Fabaceae that are ectomycorrhizal (Houlès *et al.*, 2018) with a strong ability to fix nitrogen (Vincent *et al.*, 2018). The phylogenetic and species diversity of Santalales is high on the island: four families, 12 genera, 19 species, with a varying degree of parasitism, including two endemic achlorophyllous genera (*Daenikera* and *Hachettea*). The rainforests of New Caledonia are also home to the only known parasitic Gymnosperm, *Parasitaxus usta* (Feild & Brodribb, 2005). Terrestrial carnivorous plants are represented by *Drosera neocaledonica*, *Nepenthes vieillardii*, mainly on ultramafic substrates. This diversity of nutrient acquisition strategies could be important in maintaining high local species richness ( $\alpha$ -diversity) as suggested elsewhere (Teste *et al.*, 2017; Tedersoo, Bahram, & Zobel, 2020).

Plants in New Caledonia also differ in their ways of dealing with the high concentrations of metals (Ni, Co, Mn, Cr) found in ultramafic soils. The majority of plants are metal excluders, i.e. they maintain a low and relatively constant concentration of metals in their biomass over a wide range of soil concentration (Baker, 1981). A few plant species and genotypes have however evolved toward hyperaccumulation of specific elements, i.e. they accumulate high concentrations of metals in their shoots (Baker & Brooks, 1989). Hyperaccumulation is a mechanism involving an enhanced rate of loading and translocation and sequestration of metal in the leaves (Clemens, Palmgren, & Krämer, 2002). Current estimates suggest that hyperaccumulation occurs in less than 0.2% of angiosperms (Cappa & Pilon-Smits, 2014; Reeves *et al.*, 2018) and in 1–2% of the ultramafic flora (van der Ent *et al.*, 2015). New Caledonia hosts a particularly rich and phylogenetically diverse set of hyperaccumulator species, second only to Cuba (Reeves *et al.*, 1999), with 99 hyperaccumulators of Ni, and 74 of Mn, 34 of Co, and 10 of Zn (Jaffré *et al.*, 2013; Losfeld *et al.*, 2015; Gei *et al.*, 2020). Hyperaccumulator species occur in both maquis and rainforests and are predominantly endemic to ultramafic soils. The longtime of exposure and the extent of ultramafic substrate are considered as important factors explaining the high incidence of hyperaccumulation in the flora (Isnard *et al.*, 2016), as suggested for Cuba (Reeves *et al.*, 1999). Species within the same genus can have contrasting behavior regarding nutrients and metals and these different strategies can evolve relatively quickly (Pillon *et al.*, 2014). The selective advantages of hyperaccumulation are uncertain and probably diverse: chemical defense (Martens & Boyd, 1994; Boyd & Martens, 1998), disposal (Baker, 1981), drought resistance (Bhatia *et al.*, 2005), allelopathy (Boyd & Jaffré, 2001), or a 'side effect' of a carboxylate releasing P-acquisition strategy (Lambers *et al.*, 2015; DeGroot, McCarthy, & Pollard, 2018).

**6. Adaptation to saline soils**—A diverse halophytic flora is observed on saline palaeoriver systems of the Southwest Australian flat landscapes, but Hopper (2009) expected that this feature would not apply to other OCBILs. New Caledonia has large areas of mangroves, which, however, mostly comprise limited assemblages of widely distributed species, to which the endemic flora makes little if any contribution (Munzinger & Lebigre, 2006).

**7. Special vulnerability and enhanced resilience**—OCBIL organisms are expected to have an enhanced ability to survive and persist in small fragmented populations, and to be vulnerable to soil removal (Hopper, 2009). The current fragmentation of New Caledonian forests at low- and mid-elevation principally results from a combination of anthropogenic impacts, very intense at low and



medium altitude (Jaffré, Bouchet, & Veillon, 1998a; Ibanez *et al.*, 2017), and natural topographic and edaphic ruptures due to a sharp relief and a complex geology over relatively short distances (Jaffré, 1993). Fragmentation is also an intrinsic feature of tree populations in New Caledonia where rainforest trees showed high spatial species turnover not correlated to the geographical distance (Ibanez *et al.*, 2018). On mountain tops, temperatures are lower, rainfall and runoff are higher, insolation is reduced, light is enriched with UV-B and relative humidity decreases above 1,200 m (Nasi, Jaffré, & Sarrailh, 2002). At this elevation, the climatic conditions prevailing inside and outside the forest do not differ significantly. In particular, because the moisture of the air remains saturated in both cases, the vegetation does not undergo water stress. On the contrary, the closed canopy of mid-elevation rainforests sharply dampens the atmosphere, by reducing the temperature and increasing the relative humidity, so that the Vapour Deficit Pressure (VPD) is 0.35 kPa lower than outside (P. Birnbaum, unpublished data). Thus by considering only the micro-climate, we can expect a low edge effect at low and high rainfall where forests are more structurally heterogeneous (Harper *et al.*, 2005; Oliveira *et al.*, 2013) and, a maximum effect at the mid-climatic domain, which also hosts the most diversified forests (Birnbaum *et al.*, 2015; Chao, Chiu, & Jost, 2016). However, fragmentation leads to numerous other effects unrelated to climate (Laurance *et al.*, 2018) as a lower immigration rate that leads to a slow shift in tree communities by filtering species according to their dispersal ability (Halley, Sgardeli, & Triantis, 2014; Figueiredo *et al.*, 2019). In addition, the anthropogenic activities concentrated at low elevation, induce additive effects such as fire and exotic organisms, at the edge of the driest forest (Malcolm, Valenta, & Lehman, 2017; Blanchard *et al.*, 2019).

On the ultramafic substrates exploited for nickel, the reconstitution of plant cover after mining is difficult and slow (Jaffré, Latham, & Schmid, 1977). Sensitivity to topsoil removal is suggested by the slower growth of plantlets measured in controlled conditions in soils from mine tailings compared with soil taken from pristine maquis (Houlès, 2017, p. 131). There are numerous invasive alien plant species in New Caledonia (Meyer *et al.*, 2006). However, they currently cover relatively small areas and much of them appear to be the passengers of human-induced disturbances (e.g. roads, agriculture, forestry) rather than the drivers as very few alien species are invasive in non-anthropogenic habitats, especially those on ultramafic substrates (with the notable exception of *Pinus caribaea*, an ectomycorrhizal tree naturally present on these substrates in its native range). This mirrors the high resilience of New Caledonian forests, which include a number of "aggressive" pioneer native species (e.g. *Acacia spirorbis*, *Cordia* spp., *Melaleuca quinquenervia*), and the high biotic resistance of these forests due to their high diversity that offers few niche opportunities for alien species.

## THE SPECIAL CASE OF MONODOMINANT FORMATIONS

A particular feature of New Caledonian landscapes is the extent and diversity of monodominant vegetation. Monodominance, where one species contributes  $\geq 50\%$  to the canopy (Connell & Lowman, 1989), has been reported in other tropical regions, often over extensive areas (Connell & Lowman, 1989; Hart, 1990; Torti, Coley, & Kursar, 2001; Peh, Lewis, & Lloyd, 2011). However, New Caledonia may be unusual in the number of taxa from diverse families that form monodominant canopies. Monodominance occurs in maquis and forest, including by *Gymnostoma* spp. (Casuarinaceae, Jaffré & Latham, 1974; McCoy *et al.*, 1999; Navarro *et al.*, 1999), *Tristaniopsis* spp. (Myrtaceae, Jaffré & Latham, 1974), *Codia* spp. (Cunoniaceae, Jaffré, 1980; Ibanez & Birnbaum, 2014), *Acacia spirorbis* (Fabaceae, Jaffré & Latham, 1974), and *Araucaria* spp. (Araucariaceae, Rigg *et al.*, 2010), predominantly on, but not limited to, ultramafic soils. Perhaps its most striking manifestation is in species-rich rainforests of the ultramafic massifs of the main island. Some monodominant rainforests have relatively low species richness, but often the dominant species forms an uppermost canopy over a species-rich lower canopy and understorey that is comparable to that of nearby mixed-canopy rainforests (Read *et al.*, 2000; Demenois *et al.*, 2017). The monodominant species that are best documented, *Arillastrum gummiferum* (Myrtaceae, Demenois *et al.*, 2017), *Cerberiopsis candelabra* (Read *et al.*, 2008), *Nothofagus* spp. (Nothofagaceae, Read *et al.*, 2000; Read & Jaffré, 2013) and *Codia mackeeana* (Ibanez & Birnbaum, 2014), are somewhat diverse in their functional traits. In common, they appear to be non-persistent (Connell & Lowman, 1989) or transient (Newbery *et al.*, 2013) dominants, achieving dominance after large-scale disturbances such as fires and cyclones; their comparatively poor capacity to regenerate in the shaded understorey makes progress to mixed-canopy rainforests likely in the absence of further disturbance, at least at low to mid-elevations (Read *et al.*, 2008; Read, McCoy, & Jaffré, 2015; Read & Jaffré, 2013; Ibanez & Birnbaum, 2014; Demenois *et al.*, 2017). Multiple and divergent traits may contribute to dominance by these species, as suggested for persistent monodominance (Torti *et al.*, 2001; Peh *et al.*, 2011). Unfortunately, the bulk of the literature from elsewhere focuses on persistent monodominance (but see Newbery *et al.*, 2013), so comparisons with New Caledonia are limited. At least some of those persistent monodominant forests are potentially in OCBILs (Woolley, Henkel, & Sillett, 2008; Fonty *et al.*, 2011). The high incidence of fires and cyclones in New Caledonia (Hope & Pask, 1998; Jaffré *et al.*, 1998b; McCoy *et al.*, 1999; Read *et al.*, 2011; Demenois *et al.*, 2017) has probably contributed to the number of taxa of non-persistent monodominants and the extent of monodominant vegetation. Low soil fertility may interact with the disturbance regime to increase the extent of monodominant vegetation, since slow growth potentially reduces the rate of successional

change, increasing the likelihood of interruption by large-scale disturbance (Read *et al.*, 2006b). Equally, this disturbance regime probably reduces the likelihood of persistent monodominance.

## MAJOR DISTURBANCE AFFECTING NEW CALEDONIAN ECOSYSTEMS

**Cyclones**—Among the regions with significant areas of OCBILs identified by Hopper *et al.* (2016), New Caledonia and Madagascar (and to a lesser extent, forests of eastern Australia and the Western Ghats/Sri Lanka) are affected by recurrent tropical storms and cyclones (on average 3-4 events per year over the last 40 years in New Caledonia). These events bring strong winds (up to 300 km h<sup>-1</sup>) and heavy rainfall. Recurrent cyclonic winds likely shape the structure of New Caledonian forests, which exhibit high stem density and low canopy height (Ibanez *et al.*, 2019a). Although little is known about potential adaptation of plants to cyclone regimes in New Caledonia (e.g., Read *et al.*, 2011), trees may disproportionately invest in radial growth compared to height growth to increase mechanical stability (Blanchard *et al.*, 2016). The recurrent convergent evolution of small, unbranched trees (i.e. monocaulous, Figure 5A), particularly preponderant in forest understorey, has been, at least partially, attributed to the peculiarity of forest structure and recurrence of cyclones (Bruy, 2018). Heavy rains brought by tropical storms and cyclones also affect ecosystems through the effect of erosion and nutrient leaching. Leaching can be particularly important on burned areas (e.g., Gay-des-Combes *et al.*, 2017) and most cyclones occur in February-March, i.e. a few months after the end of the fire season (September-December).

**Fire**—New Caledonia, as for most of the regions with significant OCBIL areas identified by Hopper *et al.* (2016), exhibit recurrent fires. The importance of fires relative to soil and climate in shaping plant functional traits and plant communities in these areas has emerged as one of the most controversial points in the OCBIL theory (e.g., Mucina & Wardell-Johnson, 2011; Hopper *et al.*, 2016).

Since Melanesian (~3,000 years ago) and European (1774) arrivals, fire has contributed to the conversion of forests into open vegetation, i.e. mostly into maquis on ultramafic and siliceous substrates and into savannas on non-ultramafic substrates (Morat *et al.*, 1981; Jaffré *et al.*, 1998b). Also, palaeoecological records (e.g., charcoal) support the view that natural fires (i.e. initiated by lightning) shaped New Caledonian landscapes long before human arrival, but human arrival coincides with dramatic changes in fire regime and vegetation (see review by Cabioch *et al.*, 2008). Fire is today recognized as one of the major threats to New Caledonian flora (Viot, 1956; Jaffré *et al.*, 1998a;

Ibanez *et al.*, 2019b). Each year, about 1-2% of the land of New Caledonia burns and 68% of the currently 502 Red Listed plant species are threatened by fire (Endemia & RLA Flore NC, 2019).

According to Whittaker's (1975) 'ecosystems uncertain' definition, climate (mean annual temperature and precipitation) can equally support savannas, maquis, or forests on about 45% of New Caledonia (excluding Loyalty Islands, see Figure 6). The vast majority of these New Caledonian 'ecosystems uncertain' are no longer covered by forests and constitute 'black world' where savannas and maquis (depending on substrate) are maintained by recurrent fires (Bond, 2005). Most maquis and savannas are expected to burn at least once every 50 years in New Caledonia (Curt *et al.*, 2015) which is frequent enough to maintain these vegetations.

The areas of savannas and maquis extend far beyond the 'ecosystems uncertain' climatic envelope and cover today about 75% of New Caledonia. The difference between the observed vegetation and the potential vegetation predicted from climate may be partially explained by flaws in bioclimatic envelope definitions and global climatic datasets. However, feed-backs between soil, vegetation and fire frequency are also very likely to play an important role (Bowman & Perry, 2017). Low soil fertility and water availability promote more open vegetation and higher fire frequency, which in turn promotes run-off and nutrient-leaching. These processes may be particularly important in extending 'black world' outside its climatic envelope on ultramafic substrates and/or on slopes and ridges (Morat *et al.*, 1981; McCoy *et al.*, 1999; Ibanez *et al.*, 2013a). Whether or not fire has been an evolutionary force shaping New Caledonian ecosystems remains an open question. To date the longest palaeoecological record suggests that more than 50,000 years ago fire contributed to maintaining diversity in New Caledonian landscapes (Stevenson & Hope, 2005). Only 13.5% of the species occurring in savannas are endemic to New Caledonia (Morat *et al.*, 2012). The savanna tree layer is dominated by *Melaleuca quinquenervia*, which is native to New Caledonia, but was likely restricted to swampy areas before the arrival of humans on the island. The dominance of *M. quinquenervia* results from high resistance and resilience to fires supported by a thick, multi-layer spongy bark and high resprouting capacity (from epicormic buds in both roots and shoots) as well as high fire-induced seed release (Serbesoff-King, 2003). In contrast to savannas, more than 95% of the species occurring in ultramafic maquis are endemic to New Caledonia (Isnard *et al.*, 2016), and natural maquis was likely present before human arrival (Jaffré *et al.*, 1998a). In both maquis and savannas, most native or endemic species are able to resprout from lignotubers (woody species) or rhizomes (herbaceous species) after being top-killed by fires (Jaffré *et al.*, 1998b), but only a few species are currently known to exhibit other potential adaptations to fire such as thick bark or resprouting from epicormic buds (Jaffré *et al.*, 1998b; McCoy *et al.*, 1999; Ibanez, Curt, & Hely, 2013b). Resprouting from lignotuber may be a mode of persistence that evolved in response to

disturbance (e.g., drought and winds), and site productivity (e.g., infertility) (Bellingham & Sparrow, 2000), and would then rather be an exaptation in fire-prone vegetation (Bradshaw *et al.*, 2011; Pausas *et al.*, 2016). Many species growing on ultramafic substrates occur in both fire-prone maquis and forest (~300 species), but a larger set of species (840 species) is known only from maquis (Isnard *et al.*, 2016). More research is needed to assess the importance of *in situ* diversification to maquis endemism. New Caledonian *Dracophyllum*, mostly found in maquis, is a recent clade (crown age of 5.2 Myr [2.6–7.2], Wagstaff *et al.*, 2010; Pillon, 2012), but elements to date this ecosystem are scarce.

**Low pressure from large herbivores**—New Caledonia, in contrast to most of the OCBILs identified to date (Hopper *et al.*, 2016), lacked large herbivores. In particular, long-term isolation has preserved the territory from colonization by large herbivorous mammals (Pascal *et al.*, 2006). In other island systems, other groups, particularly now extinct giant flightless birds, filled the niche of large herbivores: e.g., Moanalos in Hawaii (Olson & James, 1991), Moas in New Zealand (Worthy & Holdaway, 2002). This does not seem to have been the case in New Caledonia, where the only giant bird identified (*Sylviornis neocaledoniae*, Poplin & Mourer-Chauviré, 1985), also extinct, was probably not a browser nor a grazer (Worthy *et al.*, 2016). Current knowledge suggests that the only large herbivore in New Caledonia would have been the extinct horned terrestrial turtles (Meiolaniidae), whose distribution would have been limited to the coastal plains (Anderson, Petchey, & Worthy, 2010). Among the only 15 plant species presenting prickles, thorns or spines native to New Caledonia, two thirds are present in dry and coastal forests and 10 are climbers (Bruy *et al.*, 2017, D. Bruy, pers. obs.). In addition, heteroblasty (pronounced difference between juvenile and adult foliage), suggested to evolve in response to herbivory (Greenwood & Atkinson, 1977; Givnish *et al.*, 1994), is not a widespread feature of the New Caledonian flora. Of the 14 species identified by Burns & Dawson (2006) as presenting leaf heteroblasty, more than half occur in dry forest in lowland coastal areas. In addition, the authors noted that the transition from juvenile to adult foliage occurs around 1 m high on the plant, which corresponds to the estimated height of the horned turtles (White *et al.*, 2010). Thus, coastal vegetation is the only type to retain cues of ghosts of extinct herbivores (anachronisms, Galetti *et al.*, 2018). The dramatic habitat loss of these ecosystems (less than 1% of the original dry forest areas remaining, Bouchet *et al.*, 1995) may bias our interpretation of the apparent naivety of the New Caledonian flora to large herbivores.

Some plant life forms encountered in New Caledonia differ markedly from what is expected under high herbivory regimes. Indeed there is a large proportion of woody, large leaved and poorly

branched species and a very low number of herbaceous or divaricated woody species (Veillon, 1976; Bruy, 2018). In particular, monocaulous (unbranched) species (Figure 5A), represented by 182 species in 30 families, are presumably highly sensitive to large herbivores, because of their unique meristem. Nutrient-poor scleromorphic leaves are expected to have low palatability (Orians & Milewski, 2007). In New Caledonia, sclerophylly is associated with stressful abiotic conditions, e.g., dry forest and maquis, and may in part be related to protection from invertebrate herbivores, enhancing leaf longevity and long-term carbon-gain efficiency (Read *et al.*, 2006a). However, overall, herbivores have probably not been a major factor in the maintenance of open vegetation such as maquis in New Caledonia ('Brown world', Bond, 2005).

#### ARCHAEOLOGICAL REMAINS IN ULTRAMAFIC ENVIRONMENTS

The absence of large native mammals has also shaped the human relation with New Caledonia's ultramafic environments. Thus, contrary to the behavior observed in other OCBILs such as southwestern Australia (Lullfitz *et al.*, 2017), environmental impact which facilitated hunting was unnecessary. However, other means of human niche construction could have existed. To this extent, ferrallitic plateaus bear traces of human activity, starting with surface material such as stone tools and pottery sherds – which at least indicate regular crossings of the island's mountainous central range in pre-European times.

Geologist Jacques Avias was the first to identify stone cairns, low-rising walls or zoomorphic motifs made on the ground surface with large ferrallitic fragments (Avias, 1949). Subsequent archaeological surveys and inventories led over the past two decades on several mining sites have confirmed the recurring presence of such structures (several thousand stone cairns have been identified in Bogota Peninsula, near Canala, for example). They have also allowed the identification of other types of archaeological remains: rockshelters, funerary deposits, sacred sites, and earthmounds, which may have been used for funerary practices (Lagarde, in press; Sand *et al.*, 2012).

During the last millenium, large horticultural structures became widespread throughout the main island, with the construction of irrigated terraces (mainly for taro, *Colocasia esculenta*) and of elongated earthmounds (for yam, *Dioscorea* spp.). In ultramafic environments, specifically on slopes where slightly more favorable physicochemical soil conditions are present (L'Huillier *et al.*, 2010 p. 44), these types of structures have been observed, albeit seldomly (Figure 7). Stone terraces or earthmounds encircled by walls (on Isle of Pines), cultivation pits on seashore plains (in Ouinné valley), or stone walls to change water courses and irrigate the plains (in Yaté) form past marginal horticultural experiments in these rather hostile environments (Sand & Ouétcho, 1991; Lagarde &

Ouétcho, 2016). One of the main differences from the other horticultural systems in place in other more favorable parts of Grande Terre is the presence of walls encircling small gardens. While the walls have been considered as evidence of land delimitation, it is probable that they were rather attempts to limit evaporation. Associated with mulching practices, it was perhaps a way to get slightly better results than in open fields.

## CONCLUSIONS

Most ecosystems in New Caledonia may be considered as infertile and climatically buffered, but because of its dynamic geological history and steep slopes, the landscapes are unlikely to be ancient and surface rejuvenation is still ongoing. While the flora of New Caledonia does conform well to some expectations of the OCBIL theory (micro-endemism, relict lineages, nutritional specialization), others need to be further tested, e.g., limited seed dispersal, increased vertebrate pollination, and resilience to fragmentation. The OCBIL predictions seem to work better on maquis (on ultramafic substrates), but they do apply to some extent to the rainforest and other substrates. Although the contrasts between maquis and rainforest, ultramafic and non-ultramafic substrates are quite strong, evolutionary transitions from one compartment to the other have been common (Pillon *et al.*, 2009; Paun *et al.*, 2016; Barrabé *et al.*, 2019). Rainforest structure does not seem to depend on substrate (Ibanez *et al.*, 2014), and scrub vegetation very similar to maquis is observed on siliceous substrate (Bradford & Jaffré, 2004; Isnard *et al.*, 2016). Fire and cyclones have probably been important factors in maintaining non-forest ecosystems and monodominant vegetation. On the other hand, the lack of native mammalian herbivores probably had some effects on the flora that are not yet fully understood. The floristic affinities between the Southern landmasses have often been attributed to their shared geological history (i.e. Gondwana), but may be better explained by similarities in their ecological settings and niche conservatism (Crisp *et al.*, 2009). Although infertile, the ultramafic landscapes of New Caledonia have been exploited by humans since ancient times, and are today intensively exploited for nickel mining. The territory currently faces a huge challenge to preserve its unique biodiversity, including important efforts in ecological restoration of landscapes damaged by nickel extraction and wildfire, while its network of protected areas is still considered inadequate (Ibanez *et al.*, 2019b). Hopper (2009, see his Table 7) formulated a number of strategies to conserve OCBIL biodiversity (minimizing soil removal, minimizing removal of long-lived adult plants, plant local seeds, etc.) that should be urgently considered to preserve this unique natural and cultural heritage.

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**Table 1.** Principal soil types of New Caledonia. \* WRB classification (2006), \*\* in percentage of the surface of the main island, data adapted from Latham et al. (1978), \*\*\*this area also includes Petroplinthic plinthosol described by Fritsch (2012).

Soil type*	Surface (%)**	Main substratum**	Characteristics	Main constraints		Fertility definition**	Fertility score**
				Chemical	Physical		
Ferritic ferralsol	19.9***	ultramafic, peridotites	no clay mineral, dominance of oxy-hydroxide minerals, acidic pH with pH KCl > pH water, high anion retention rate, CEC related to soil organic matter content	acidic pH / low CEC / phosphorus deficiency / imbalance in the Ca:Mg ratio / low nutrient content / high metal content	-	very low fertility to infertility	V
Haplic Cambisol magnesian	14.0	ultramafic, serpentinites	high CEC saturated by Mg, neutral to slightly basic pH, rich in 2:1 smectite-clays (ferrous smectite)	phosphorus deficiency / strong imbalance in the Ca:Mg ratio / low nutrient content / high metal content	low vertical development	very low fertility	IV
Ferralic cambisol	26.9	various volcano-sedimentary origin	CEC saturation < 20%, Ca, K and P deficient, acidic pH, kaolinite clay dominant clay mineral but presence of unprocessed illite and vermiculite	acidic pH / high exchangeable Al and Mn / phosphorus deficiency / low CEC / desaturation of CEC	rejuvenation by mechanical erosion	low fertility	III
Regosol	6.2	metamorphic, mica-schist and gneiss	thin and humic surface horizon, very soft and altered 'C horizon' (more than one-meter depth)	phosphorus deficiency	very low vertical development / rejuvenation by mechanical erosion	very low fertility	IV



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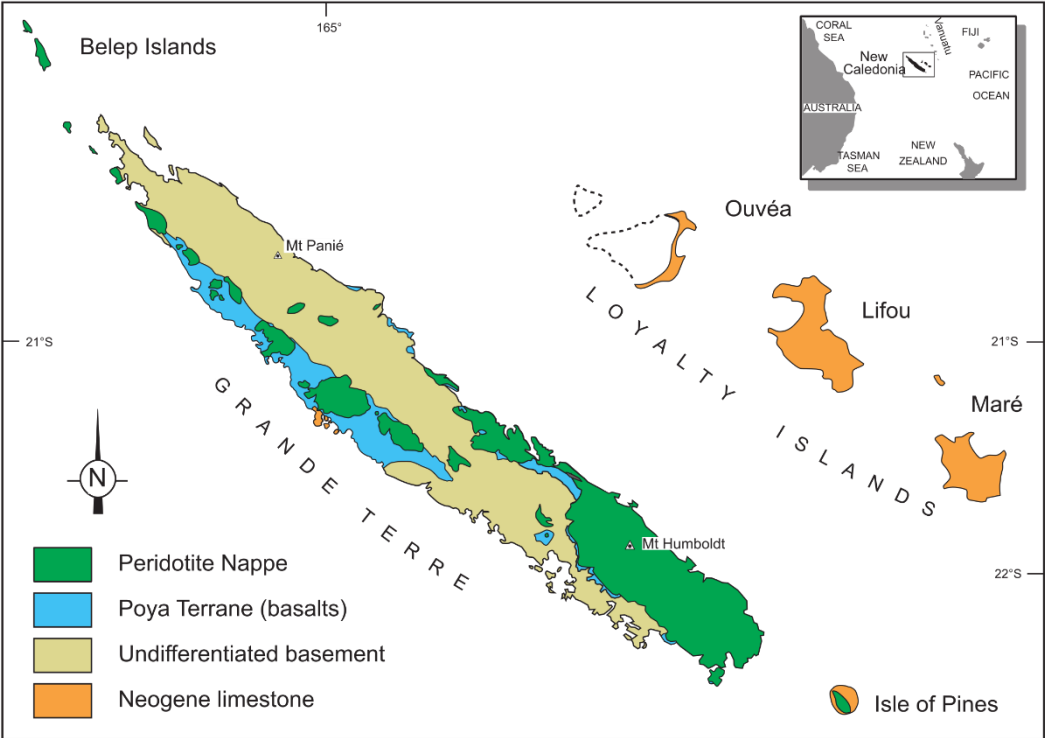
Haplic Acrisols rhodic and albic associated with podzol	3.5	siliceous rocks, notably phtanites	acidic pH, CEC desaturation, marked profile differentiation, bleaching of soil surface horizon, illuviated and rubefied B horizon, kaolinite clay dominance	very acidic pH / phosphorus deficiency	rejuvenation by mechanical erosion / textural discontinuity adverse to root penetration	very low fertility to infertility	V
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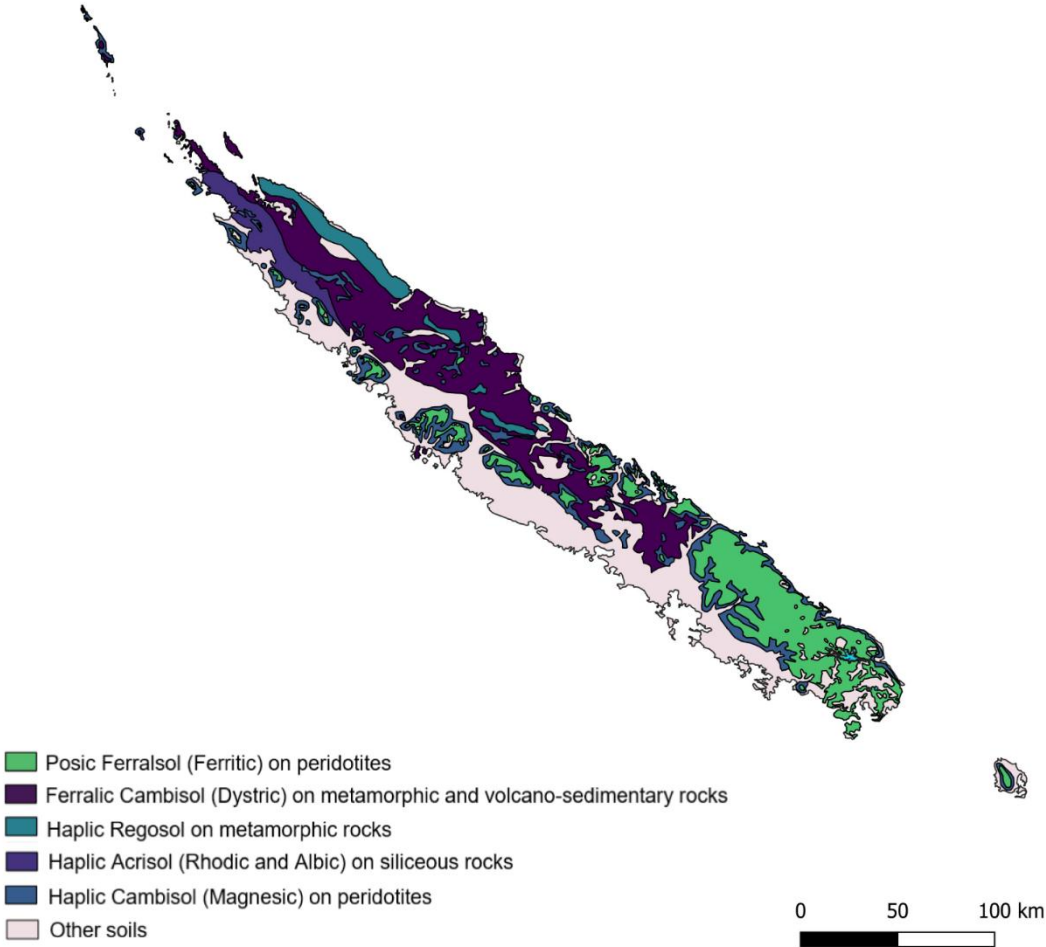
**Table 2.** List of native ectomycorrhizal species from New Caledonia. UM = ultramafic, NUM = non-ultramafic. Some doubts exist about the possible occurrence of ectomycorrhiza in some Myrtaceae genera: *Eugenia*, *Metrosideros*, *Syzygium*, and *Xanthostemon*. \*on siliceous substrate. \*\*a single location (Col des Roussettes).

Family	Species	Substrate	Main ecology
Casuarinaceae	<i>Casuarina collina</i>	UM + NUM	riparian, coastal, pioneer
Casuarinaceae	<i>Casuarina equisetifolia</i>	NUM	coastal
Fabaceae	<i>Acacia spirorbis</i>	UM + NUM	pioneer
Fabaceae	<i>Intsia bijuga</i>	NUM	forest
Myrtaceae	<i>Arillastrum gummiferum</i>	UM	rainforest, maquis
Myrtaceae	<i>Melaleuca quinquenervia</i>	mostly NUM + UM	savanna, swamp
Myrtaceae	<i>Melaleuca</i> spp. (7 species)	UM	maquis, riparian
Myrtaceae	<i>Sannantha</i> spp. (4 species)	UM + NUM	maquis, riparian, pioneer
Myrtaceae	<i>Tristaniopsis</i> spp. (13 species)	UM (rarely NUM*)	maquis, forest
Nothofagaceae	<i>Nothofagus</i> spp. (5 species)	UM (rarely NUM**)	rainforest

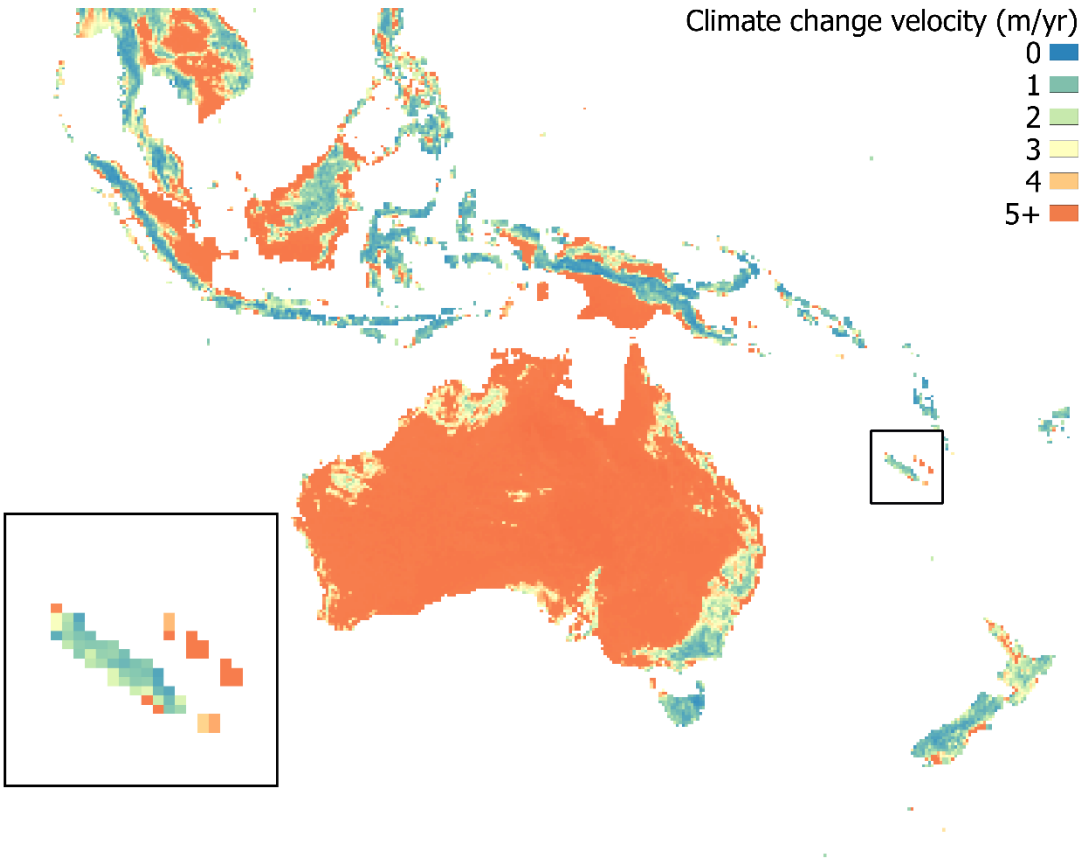
Figure 1. Simplified geological map of New Caledonia.



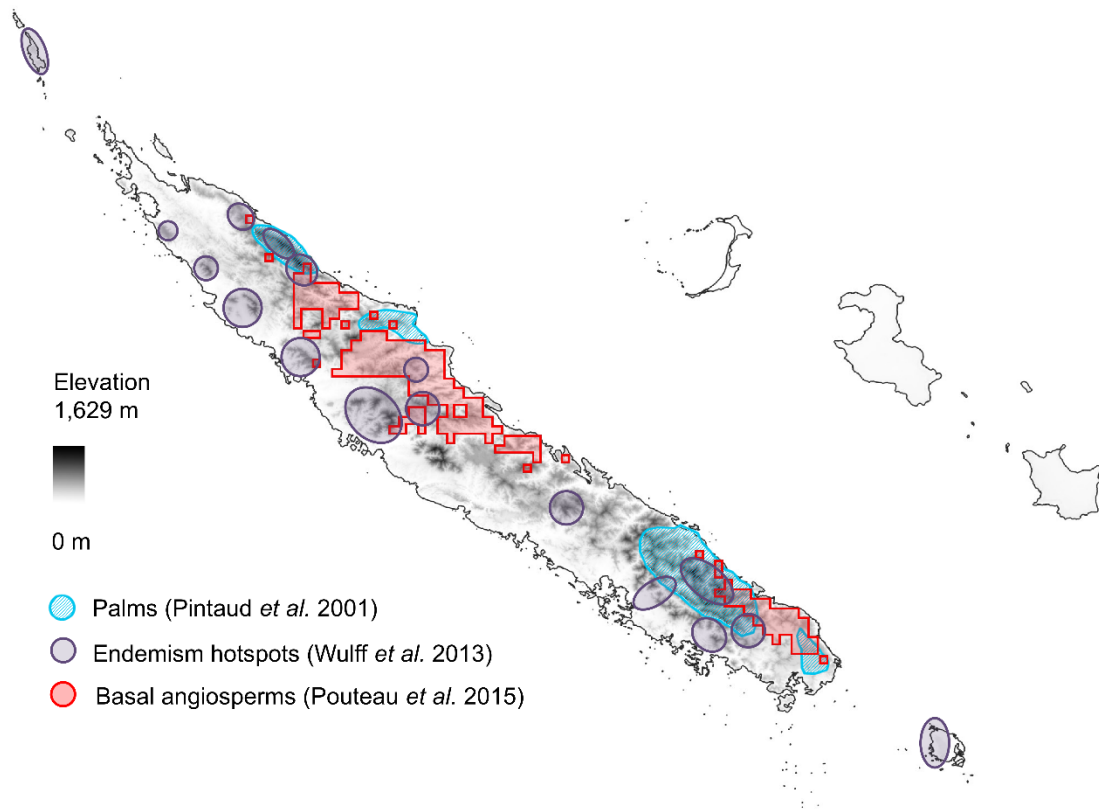
**Figure 2.** Simplified pedological map of New Caledonia.



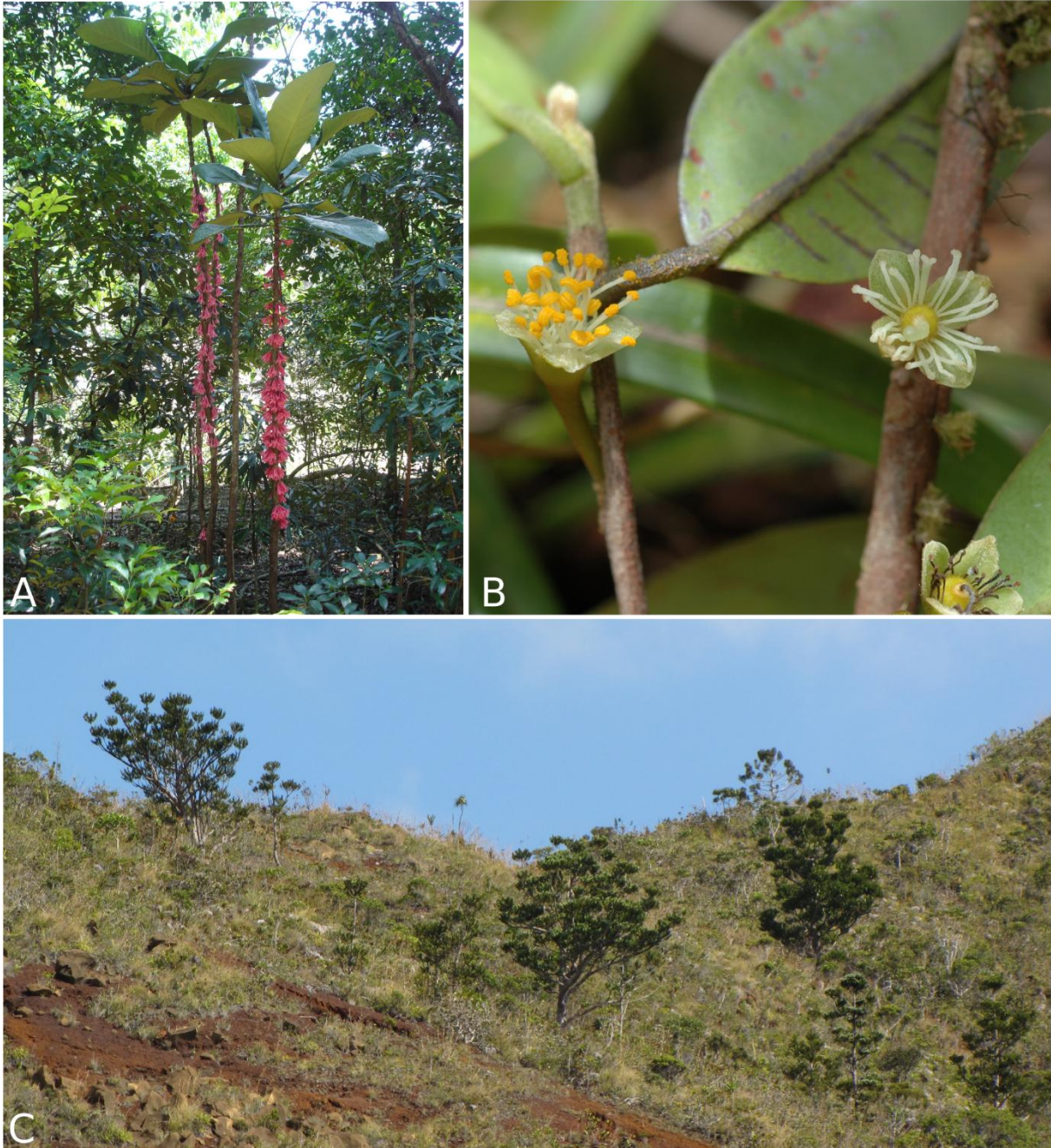
**Figure 3.** Past climate change velocity since the Last Glacial Maximum in the southeastern Pacific Ocean (data from Sandel *et al.*, 2011).



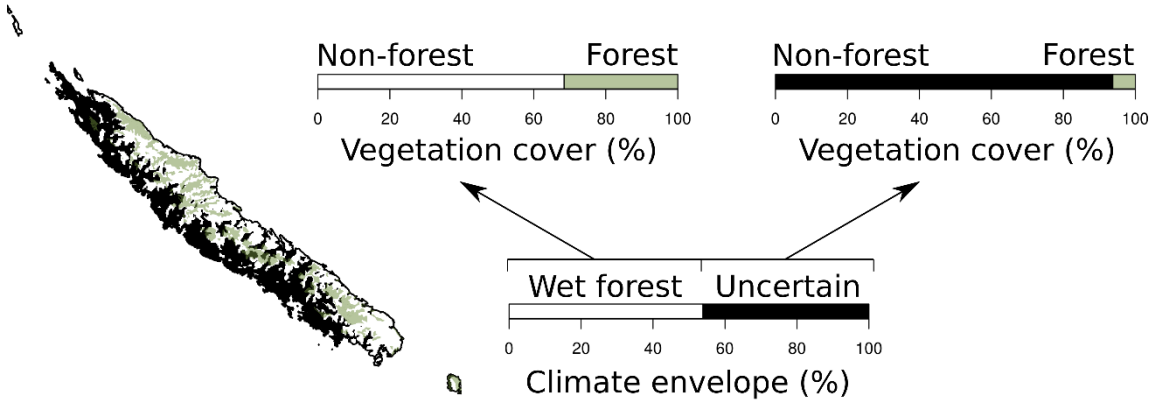
**Figure 4.** Major climate refugia and centres of endemism in New Caledonia. Blue areas display 3,000 mm isohyets with high species richness and endemism of palms interpreted as boundaries of possible Pleistocene refugia (Pintaud, Jaffré, & Puig, 2001). Purple areas are hotspots of plant micro-endemism (Wulff *et al.*, 2013). Red areas have been projected to be suitable for at least one species of “basal” angiosperms (ANA grade + Magnoliids) during the last glacial maximum (Pouteau *et al.*, 2015).



**Figure 5. A.** *Ixora margaretiae* (Rubiaceae), one of 182 monocaulous plant species endemic to New Caledonia. **B.** *Lethedon leratii* (Thymelaeaceae), a dioecious species, like 21% of the New Caledonian native flora (the highest percentage in the world). **C.** An example of “maquis minier”, the typical shrubby vegetation on ultramafic substrate, here with some centuries-old trees (*Agathis ovata*, Araucariaceae). Pictures: A,C by Y. Pillon, B by J. Munzinger.



**Figure 6.** Distribution and coverage of areas of New Caledonia falling into the ‘ecosystems uncertain’ (in black) climate envelope of Whittaker’s (1975) global biome (see Bond, 2005) based on CHELSA climatology at ~1 km spatial resolution (Karger *et al.*, 2017). Climate into ‘ecosystems uncertain’ areas can equally support maquis, savannas, or forests. White areas correspond to wet forest climate envelope and green areas to the current wet forests (main forest massif in 2010, Jaffré, Rigault, & Munzinger, 2012).





**Figure 7.** Horticultural terraces (left) and small enclosed gardens on slope (right), Isle of Pines  
(Pictures & Drawing by L. Lagarde).

