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What Makes New Caledonia's Flora So Outstanding?

3

Sandrine Isnard and Tanguy Jaffré

Abstract

This chapter explores the main characteristics of New Caledonian plant biodiversity, and provides a condensed picture of the major unique elements of its flora. We present the results of recent research conducted in a territory that has much to contribute to science and society. We explore the original and unique representation of some plant lineages and functional groups, as well as the rich and diversified vegetation.

Keywords

Biodiversity hotspot · Endemism · Island flora · New Caledonia · Ultramafic vegetation

3.1 Introduction

New Caledonia is undoubtedly one of the most fascinating regions for many botanists. The territory harbours a highly diverse and endemic flora with approximately 3400 autochthonous vascular species, of which 75.5% are endemics (i.e. species that occur nowhere else) (Morat et al. 2012; Munzinger et al. 2022). Ultramafic substrates, that is, metal-rich and nutrient-poor soils with chemical and physical properties that constrain plant growth, have strongly influenced the exceptional endemism and richness found in New Caledonia (Isnard et al. 2016). When global endemism is compared to other regional flora, New Caledonia is ranked third after Hawaii (89%) and New Zealand (82–89%). The distinctiveness of New Caledonia rests on the concentration of endemism and richness (Schmid 1982) found in a relatively small surface area (ca. 19,000 km^2). The archipelago is also remarkable for harbouring three endemic families (Amborellaceae, Phellinaceae and Oncothecaceae) (Fig. 3.1) and a high number of endemic genera, currently estimated between 62 and 91 (Munzinger et al. 2022; Pillon et al. 2017). New Caledonia is also rich in relict lineages, that is, remnant plant species from a large group where most taxa are now extinct, leading several authors to recognize New Caledonia as a phytogeographic unit ("region" (Guillaumin 1934) or "sub-kingdom" (Takhtajan 1969)). Despite geographic proximity, floristic affinities with Vanuatu are relatively low (Schmid 1990), possibly because of their recent proximity and their edaphic divergence (Mueller-Dombois and Fosberg 1998; Schmid 1990). Analyses of floristic affinities (Morat et al. 1994; Mueller-Dombois and Fosberg 1998), supported by phylogenies (Barrabé et al. 2014; Swenson et al. 2014; Thomas et al. 2014; Turner et al. 2013), have identified Australia and then New Guinea and the geographic area of *Flora Malesiana* as the most likely origin for a substantial proportion of the New Caledonian flora.

New Caledonia is also recognized as a major hotspot of terrestrial biodiversity, because of its high endemism but also because of the threats to habitats, as more than 70% of the original vegetation has been lost (Myers et al. 2000). This recognition of a unique biological heritage should drive greater protection of natural habitats, as highlighted by Ibanez et al. (2019), to reduce the impact of anthropogenic activities on natural resources.

Some of the most threatened formations unique worldwide are maquis (a non-forest vegetation on ultramafic substrates), areas of dry forest and the relics of rainforest on ultramafic substrates (which are also sources of nickel, chromium and cobalt from peridotite and serpentinite rocks) (Bouchet et al. 1995; Ibanez et al. 2019; Jaffré et al. 2010).

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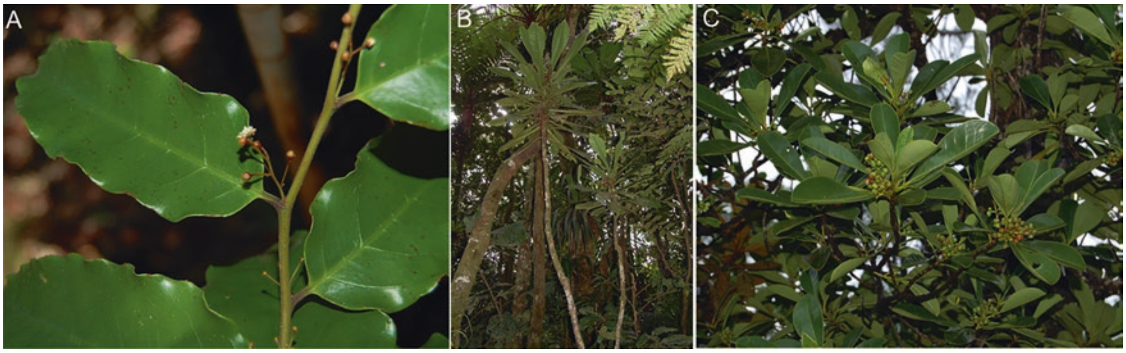

Fig. 3.1 The three endemic families of New Caledonia. (**a**) *Amborella trichopoda* (Amborellaceae); (**b**) *Phelline macrophylla* (Phellinaceae); (**c**) *Oncotheca humboldtiana* (Oncothecaceae)

Climate change could affect species richness in New Caledonia as indicated by a recent study estimated that 87–96% of species could decline by 2070 and up to 15% could become extinct (Pouteau and Birnbaum 2016).

3.2 A Complex Geological and Biota History

The floristic richness and particularly the supposed archaism of the New Caledonian biota have long been interpreted as a Gondwanan heritage (Holloway 1979; Morat 1993; Mueller-Dombois and Fosberg 1998). However, newer geological evidence demonstrates a complete marine submersion of New Caledonia for a long period of time, after the fragmentation and rifting of Zealandia from Gondwana (Maurizot and Campbell 2020; Pelletier 2006). The main island of New Caledonia (Grande Terre) was completely submerged between 75 and 60 Ma. The landmass is older than 25 Ma, as attested by geological evidence. Emergent land areas probably existed in the Southwest Pacific from 60 to 34 Ma, possibly including some locations on Grande Terre, suggesting a plausible scenario of re-colonization from short- and/or long-distance plant dispersal (Maurizot and Campbell 2020). Overthrusting of oceanic mantle (obduction) occurred at 34 Ma and gave rise to the ultramafic bedrock that, after erosion and fragmentation, covers today about one-third of the surface area (including the Belep Islands and the Isle of Pines). This geological scenario is congruent with recent molecular dating of the crown age of several lineages (Barrabé et al. 2014; Grandcolas et al. 2008; Maurizot and Campbell 2020; Murienne et al. 2005; Nattier et al. 2017; Pillon 2012; Swenson et al. 2014). The geological and biotic history of Grande Terre is certainly more complex than previously thought, and future research on past events will hopefully shed light on the remaining grey areas. The Loyalty Islands are much younger and lower islands, composed of recent uplifted carbonate platform deposits, whose first emergence date back to the Pliocene (Maurizot and Campbell 2020). The flora of Loyalty Islands is relatively poor (ca. 400 species) compared to the main island, with a small number of endemic species (25–30 species) (Schmid 1969).

3.3 Phylogenetic Originalities of the Flora

3.3.1 The Emblematic Conifers

The archipelago hosts 47 conifer species (for a total of ca. 650 worldwide), in 13 genera and 4 families (Munzinger et al. 2022), representing 7% of conifers species worldwide. An astonishingly high proportion of conifer species are, however, threatened with extinction (Farjon and Page 1999; Jaffré et al. 2010). Conifers are clearly among the most emblematic trees of New Caledonia, especially the genus *Agathis* ("kaori") (5 species) and *Araucaria* (14 species out of 20 worldwide) with *Araucaria columnaris* ("Pin colonnaire"), a symbolic tree for the Kanak, producing famous picture-postcard landscapes. The tallest harvested trees reached 60 m on Lifou Island (Schmid 1981). All conifer species are endemics, often narrow endemics (Jaffré 1995) (i.e. occurring in one or widely separated small populations; Drury (1980)). By 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. Most species are indeed distributed on ultramafic rocks (Jaffré et al. 2010). Although they constitute only one-third of the surface of the Grande Terre, these soils are home to 42 conifer species, that is, more than 93% of the species, of which 28 species (62% of the total) are strictly soil endemics.

Among the remarkable examples of conifers found in the island are the unique parasitic species of gymnosperm: *Parasitaxus usta* (Farjon and Page 1999; Feild and Brodribb 2005). The oldest tree so far dated in New Caledonia is an *Agathis ovata* ("mountain kaori") whose age has been estimated at over 1500 years for a 97-cm-diameter tree

(Enright et al. 2003). Some New Caledonian conifers are also notable for their slow growth. Plant height and diameter (at breath height) growth rate for *Araucaria goroensis* (previously confused with *A. muelleri*) are among the slowest recorded for any tree species (Enright et al. 2014). Some Araucariaceae species are long-lived, slow-growing trees and show long-term persistence in environments ranging from maquis to forest, where they emerge above the canopy (Rigg et al. 2010).

The ascription of the "relictual" or "Gondwanian" attribute to the New Caledonia flora is based, at least in part, on the high concentration of conifers (Jaffré 1995), this group being sister to the more recently derived angiosperms. Conifers indeed dominated the world before the emergence of angiosperms in the Cretaceous. Recent studies, however, indicate that some groups, like *Araucaria*, diversified recently in New Caledonia (Gaudeul et al. 2012; Pillon 2012; Setoguchi et al. 1998).

The rapid diversification of Araucariaceae species may be the result of adaptive radiation of forest conifers on ultramafic substrates in open conditions (Enright et al. 2014; Setoguchi et al. 1998). Conifers succeed and dominate in many habitats, not only where their competitors, angiosperms, have low tolerance and reduced competitive ability (Brodribb et al. 2012). In New Caledonia, with the exception of a few shade-tolerant Podocarp species, most of the species belonging to *Araucaria*, *Agathis*, *Podocarpus*, *Dacrydium* and *Callitris* genera grow in conditions exposed to wind and light, often on the steep slopes of the ultramafic massifs (Jaffré 1995). In some forests on ultramafic soils, conifer species (e.g. *Araucaria* and *Agathis*) may form part of the canopy or are present as emergent. Some species also form emergent layers in the maquis, producing an unusual structural association. Because of their growth dynamics in their ability to develop in full sun, *Araucaria* species are good candidates for the recovery of areas that have been destroyed by fires (Rigg et al. 2010).

3.3.2 Basal Angiosperm and Relictual Lineages

Relicts, or the so-called left behind, are species or groups of species remaining from larger and/or more widespread group of organisms in which most taxa are now extinct (Grandcolas et al. 2008). A quirky characteristic of the New Caledonian flora is the diversity of relictual lineages and the presence of numerous early branching lineages, due to their phylogenetic positions (hereafter called "basal angiosperms"). Even if they are not primitive per se, the study of basal angiosperms can provide insightful information for understanding the early stages of flowering plant evolution. Together with relictual lineages, they also constitute good models to understand the biogeography and history of the regional flora.

The most famous lineage of basal angiosperms is represented by *Amborella trichopoda* belonging to the endemic and monospecific family of Amborellaceae. Molecular phylogenetic studies indicated that this species is the only extant member of the sister group to all other living flowering plants (APG 2016), and its lineage has been estimated to be at least 160 Ma, in the Early Cretaceous (140–180 My ago) (AmborellaGenomeProject 2013). Considered a "witness of the past" (Poncet et al. 2019), *Amborella* has been the subject of intense studies from a wide range of disciplines (Pillon and Munzinger 2005), since the origin of angiosperms, famously characterized by Charles Darwin as "an abominable mystery", continue to fuel debates.

In New Caledonia, basal angiosperms are represented by 109 species (90% are endemics) distributed in 22 genera and 10 families (Trueba 2016). Relictual lineages can also be found in other parts of the angiosperm phylogeny. The fact that many endemic genera (26–35, Pillon et al. 2017) are monospecific and most of them have few species is suggestive of declining lineages and extinction events inside formerly diverse clades. This relictual diversity is illustrated by several lineages, such as the mono-generic *Strasburgeria* which is thought to have been widely distributed in the Antarctic region in the early Eocene (Contreras et al. 2013). Other potential examples include the endemic monospecific genera *Paracryphia* (Paracryphiaceae), *Nemuaron* (Atherospermataceae), *Platyspermation* (Alseuosmiaceae) and *Phelline* (Phellinaceae).

3.4 Major Radiations and Diversification

A conspicuous feature of many islands is the phenomenon of "adaptive radiation" that implies the diversification of ecological roles, and attendant array of morphological and physiological attributes, from a single colonizer (Givnish et al. 2014). New Caledonia has few examples of dramatic adaptive radiation (Pillon et al. 2017). The largest genera of New Caledonia, in terms of species numbers, are *Phyllanthus* with 108 species, *Psychotria* with 83 species and *Syzygium* with 68 species (Morat et al. 2012; Munzinger et al. 2022). The monophyly (a common ancestor) of these genera is however doubtful (Barrabé et al. 2014; Biffin et al. 2006; Kathriarachchi et al. 2006). To our knowledge, very few examples of adaptive radiation have been highlighted in New Caledonia, and these concern the genus *Geissois* (Cunoniaceae) related to diversification of biochemical strategies on different soils (Pillon et al. 2014) and in the genus *Oxera* (Lamiaceae), where niche shift has been associated with pollination, dispersal and life form traits (Barrabé et al. 2018).

The paucity of large adaptive radiation in New Caledonia is attributed to the fact that the flora is essentially woody. In addition, the age of the main island increases the probability of extinction and colonization within the same groups, along with competition with new migrant species.

3.5 Functional and Taxonomic Disharmony

Disharmony is a key concept in island biology that describes the biased representation of higher taxa on islands compared to their mainland source regions. Generally, the disharmony results from taxa having differential colonization success (i.e. selective dispersal) and environmental and/or biotic filtering. As in many island systems, the flora of New Caledonia is strongly disharmonic, with some groups being predominant. In New Caledonia, the disharmony of the flora is often attributed to ultramafic soil conditions, which would have favoured the settlement and diversification of some pre-adapted plant groups (Jaffré et al. 1987; Pillon et al. 2010), while dispersal limitation would have played a less important role (Pillon et al. 2010). Adaptation to ultramafic soils is associated with drought stress, nutrient limitation and high levels of potentially phytotoxic metal, all major sources of stress in ultramafic environments (Isnard et al. 2016; Kazakou et al. 2008). The archipelago is recognized as a hotspot for plants growing on metal-rich soils, as more than 70% of the endemic flora and 63% of species occur on these ultramafic soils (Isnard et al. 2016). The chemical and physical adversity of ultramafic soils has driven some plants into spectacular transformations, remarkably illustrated by the evolution of trace element hyperaccumulation (Jaffré et al. 2018; Paul et al. 2020). The word “hyperaccumulator” was introduced in a publication reporting the extraordinary accumulation of nickel in *Pycnandra accuminata* (formerly *Sebertia*), a New Caledonian endemic tree (Jaffré et al. 1976). The famous “blue sap” species accumulates an astonishing 20–25% nickel in its latex, which is coloured blue-green from nickel complexes. The extremely high level of Ni tolerance is posited to derive from the unique properties and large volume of laticifers (Isnard et al. 2020). The over-representation of groups associated with ultramafic soils might also have been accentuated by the evolution of metal accumulation syndrome in many lineages. A recent study, carried out on herbarium specimens (Herbarium of New Caledonia, NOU), confirmed that New Caledonia is a global hotspot for hyperaccumulator plants, as 3–4% of the dicotyledonous flora are Ni hyperaccumulators (Gei et al. 2020). This represents a strong functional disharmony, compared to other regional or worldwide flora.

Ultramafic substrates are not the only driver of the disharmony in the New Caledonian flora, however. The prevalence of several relictual rainforest lineages has been attributed to a preference for this habitat, and their persistence in climatic refugia, protected from recent major climate-driven extinction events, which have otherwise affected Australia and some nearby South Pacific islands more strongly (Byrne et al. 2011; Pouteau et al. 2015). Several regions of the Pacific where relict angiosperms are also abundant are also recognized as having rainforests that persisted during the late Quaternary through glacial refugia such as in Southeast Asia, New Guinea and Queensland (Byrne et al. 2011; Wurster et al. 2010). The rainforest refugia at the last glacial maximum (LGM, around 23,000–18,000 years BP) of relict angiosperms (Pouteau et al. 2015), including *Amborella* (Poncet et al. 2013), coincide with refugia proposed for palms (Pintaud et al. 2001). The last glacial maximum has been shown to shape the population dynamics of *Amborella trichopoda* and to impact their present intra-specific genetic structure. In New Caledonia, the almost exclusive rainforest distribution of basal angiosperms is explained by wood (xylem) vulnerability to drought-induced embolism (Trueba et al. 2017). Another recently discovered example of functional disharmony concerns the unbranched woody plants (i.e. monocaulous plants or “palm-like”) (Bruy et al. 2018). This growth habit, which has been previously described by botanists studying the New Caledonian flora (Schmid 1990; Veillon 1976), represents ca. 9% of woody flora, belonging to 41 genera, 30 families thus representing an important phylogenetic diversity and a new case of convergent evolution on islands (Bruy et al., unp.data).

3.6 Principal Vegetation Types

The vegetation of New Caledonia has been described by numerous authors (Jaffré 2022a; Jaffré et al. 2012; Morat et al. 1981; Mueller-Dombois and Fosberg 1998; Virot 1956). The following treatment is based on the last synthesis of these works, published in the Atlas of New Caledonia (Jaffré et al. 2012) (Fig. 3.2).

The landscape is a mosaic of secondary vegetation (c. 50%); low- to mid-elevation shrublands or “maquis” found on ultramafic substrates (c. 25%), including ca. 50 km^2 of wetland and marshes of the Plaine des Lacs; and another quarter of low- to mid-elevation rainforests growing on various substrates. There is also ca. 1% of montane rainforests and shrublands found above 800 m. This mosaic also includes few relictual patches of dry sclerophyllous forests scattered along the west coast on volcano-sedimentary rocks.

The floristic diversity of New Caledonia is unevenly distributed over less than two-thirds of the archipelago, mainly in forests and maquis on ultramafic rocks. On the basis of their very contrasting floristic compositions, two main types of vegetation can be distinguished. Vegetation is dominated by introduced species with very few endemics, referred to as “modified vegetation” and vegetation termed “autochthonous

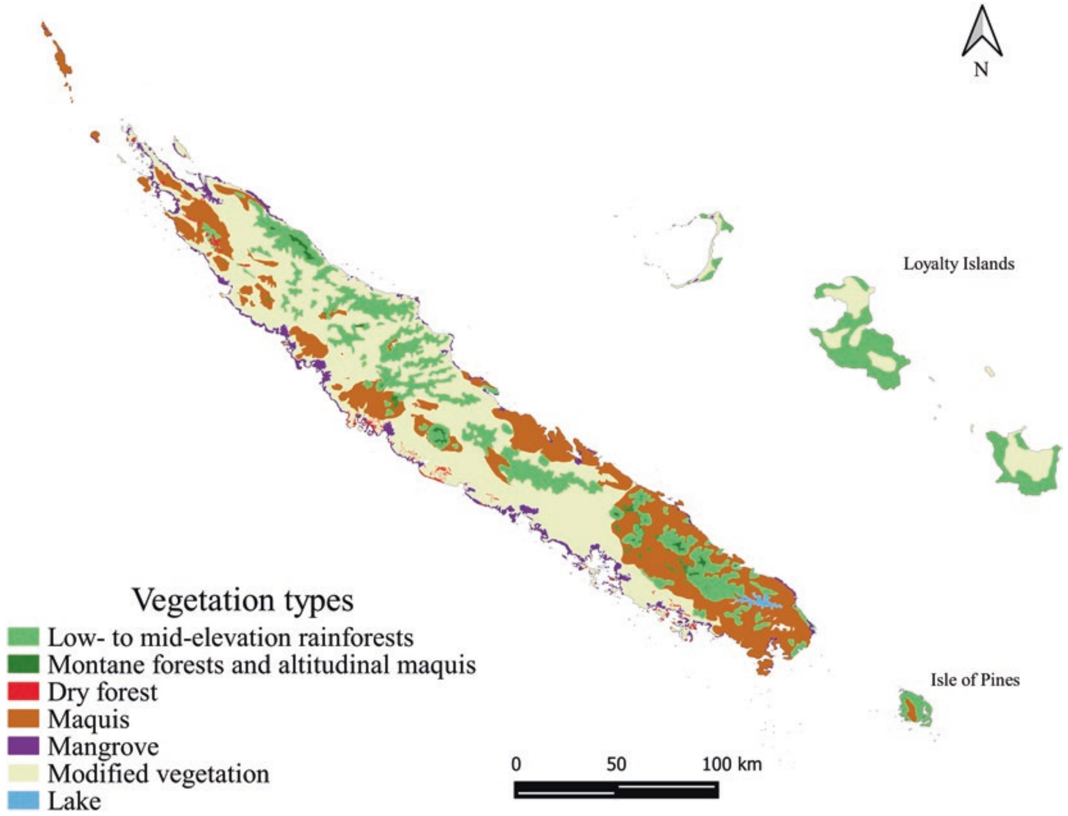

Fig. 3.2 Simplified vegetation map illustrating the main vegetation types. (Modified from Jaffré et al. 2012)

vegetation", whose flora is mostly composed of native species with a high proportion of endemic species. The frequency and distribution of vegetation result from a dynamic process particularly influenced by human activities (Ibanez et al. 2013; Morat et al. 1981; Stevenson et al. 2001).

3.6.1 The Modified Vegetation

The modified vegetation contributes poorly to the diversity and originality of the flora but comprises species traditionally used by local populations for various practices related to traditional medicine as well as domestic purposes (Lormée et al. 2011; Rageau and Schmid 1973). The modified vegetation covers about 7000 km^2, more than one-third of the Archipelago, and mostly includes savannas and secondary thickets, with a total of ca. 400 native species of vascular plants and an endemic rate of only 11% (Jaffré et al. 2009). Less than five endemic species are found exclusively in this vegetation type. A significant proportion of the 2000 inventoried introduced species occurs in the modified vegetation (Hequet et al. 2009), including about 360 naturalized species. Some species that frequently dominate the secondary thickets, "Lantana" (*Lantana camara*), "Goyavier" (*Psidium guajava*) and "False mimosa" (*Leucaena leucocephala*), are very prolific and competitive in degraded habitats and described as invasive because of their wide coverage and ecological and/or socio-economic impacts (Meyer et al. 2006).

Widely represented from sea level to 600–700 m, except on ultramafic substrate, savannas are characterized by a continuous grass layer with a discontinuous shrub or tree cover, most often the autochthonous "niaouli" (*Melaleuca quinquenervia*). The expansion of the modified vegetation results from the destruction of an initial vegetation cover, since human arrivals from about 3000 year BP, under the effect of repeated fires as well as clearing for crops and livestock (Ibanez 2012; Schroers and Tron 2013; Virot 1956). The process of expansion and contraction of forests and savannas is principally driven by bush fires, locally depending on climate, humidity, wind strength and direction, and the quantity of combustible plant matter (fuel) (Ibanez et al. 2013). *Pinus caribaea*, introduced in the 1960s in New Caledonia for timber exploitation, has now a distribution that exceeds areas used for forestry. This species frequently invades modified vegetation (savanna and maquis) and is considered as one of the most threatening non-native species (Hequet et al. 2009; Kohler 1984).

3.6.2 Natural Vegetation

3.6.2.1 Low- to Mid-Elevation Rainforests on Various Substrates

Rainforests on ultramafic substrates are a unique ecosystem and under severe threat with more than 75% of the original cover already destroyed (Jaffré et al. 1998). Forests survive as scarce remnant fragments scattered in a matrix of maquis (Mc Coy et al. 1999) (Fig. 3.3c). Most forest fragments are under direct threat from mining activity (Ibanez et al. 2017b, 2019). Forests on volcano-sedimentary rocks on the east coast are principally threatened by fire, clearing and introduced species (deer, pig and *Pinus caribaea*) (Schroers and Tron 2013).

Rainforests cover about 3900 km^2 in areas with mean annual rainfall between 1300 and 3500 mm (Jaffré et al. 2012). They occur at low altitude in the Loyalty Islands and the Isle of Pines and from 300 m up to 900–1000 m on the main island, where they extend discontinuously along the central mountain range. On isolated massifs, rainforests are usually confined to steep slopes and high valleys. In the southern massif, rainforests occur below 300 m where annual rainfall exceeds 1600 mm, for example, along the rivers. The dense humid forests of New Caledonia are found on acidic rock types (volcano-sedimentary and metamorphic) covering 1800 km^2, on ultramafic rocks covering 1200 km^2 and on limestone rocks covering 900 km^2 principally in the Loyalty Islands and Isle of Pines (Jaffré et al. 1997).

The rainforest is the richest native flora, at all taxonomic levels with ca. 2100 species of vascular plants (endemicity of 83.2%), belonging to 474 genera and 135 families (Morat et al. 2012; Munzinger et al. 2022. [continuously updated]).

Rainforests on volcano-sedimentary and ultramafic substrates, with about 1360 species and endemic rates of, respectively, 76% and 82%, are more diversified than the limestone forest that principally occurs on the Loyalty Islands and Isle of Pines and harbours only 225 species with an endemic rate of 48% (Jaffré et al. 1997). A Permanent Plot Network (NC-PIPPN) was set up in 2005 and currently consists of 220 plots of 0.04 ha) (20 × 20 m) and 21 1-ha plots, located on the main island (Birnbaum et al. 2015; Ibanez et al. 2014). The network is intensively used in ecological studies and provide a comparative framework with other regional or worldwide flora. High species richness and floristic dissimilarity recorded from the plots confirm that New Caledonian mixed rainforest is exceptionally rich (Ibanez et al. 2014; Jaffré 1993). Rainforest species exhibit a strong spatial aggregation, thought to express limited dispersal ability (Birnbaum et al. 2015). The flora on ultramafic versus volcano-sedimentary soils are dissimilar from species to

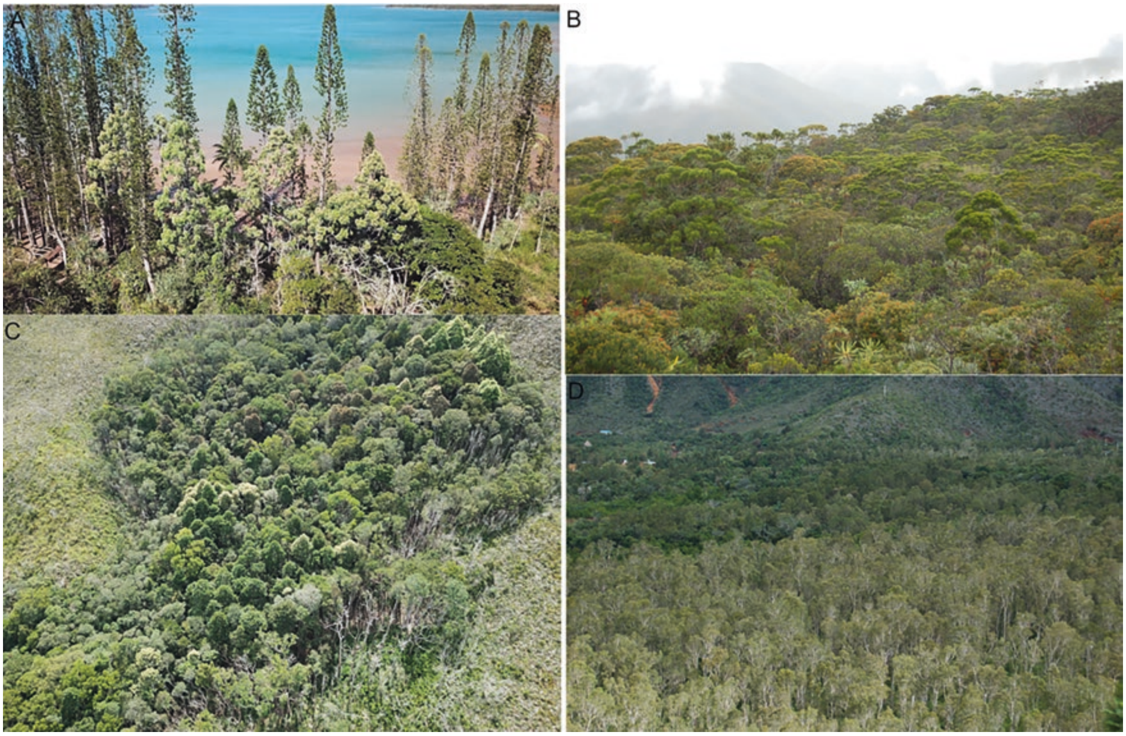

Fig. 3.3 Illustrations of New Caledonian landscapes. (**a**) *Araucaria columnaris* ("Pin colonnaire") growing at the edge of the sea, Prony, South of Grande-Terre; (**b**) Tall maquis containing abundant *Gymnostoma deplancheanum* trees, col. de Yaté; (**c**) Remnant fragment of rain forest on ultramafic substrate scattered in a matrix of maquis and burned vegetation; (**d**) Rainforest-Savana interface, with savanna composed of *Melaleuca quinquenervia* (in the foreground), South of Grande-Terre (Thio). (Photo credit: A & C, Jean-Michel Boré, IRD)

family level (Ibanez et al. 2014), while the number of species on both substrates (ca. 1300 species) and endemicity (76–82%) is fairly similar (Jaffré et al. 1997). The presence of highly heterogeneous soils combined with altitudinal and rainfall gradients is the main driver of the floristic dissimilarity (Ibanez et al. 2014).

Large-scale disturbances (cyclone and fire) have a strong influence on the composition and structure of the forests. By producing large canopy openings, large-scale disturbances play a crucial role in regeneration dynamics. They favour some monodominant and gregarious species including *Nothofagus* spp. (*Nothofagaceae*), *Arillastrum gummiferum* (*Myrtaceae*), *Cerberiopsis candelabra* (*Apocynaceae*), *Gymnostoma deplancheanum* (*Casuarinaceae*) and *Codia mackeeana* (*Cunoniaceae*) (Demenois et al. 2017; Ibanez and Birnbaum 2014; Mc Coy et al. 1999; Read and Jaffré 2013; Read et al. 2008). These long-lived, shade-intolerant trees are commonly secondary species but appear unable to maintain dominance in the absence of disturbance at low to mid-altitudes. Progression to mixed canopy forest is predicted in the absence of disturbance (Demenois et al. 2017; Mc Coy et al. 1999; Read and Jaffré 2013), for which there is some evidence in the Quaternary pollen record (Hope and Pask 1998).

In comparison with other rainforests in the Southwest Pacific, New Caledonian rainforests exhibit high average density (1253 stems ha^{-1}) including abundant palms and tree ferns, with the abundance of the latter being unparalleled outside New Caledonia (Ibanez et al. 2014, 2017a). New Caledonia rainforests are also distinctive for their low mean canopy height (ca. 16 m) (Blanchard et al. 2016). The frequent tropical cyclones affecting New Caledonia explain much about the structure of its rainforest (Blanchard et al. 2016; Ibanez et al. 2017a). In these forests, lianas diversity is low, and they represent only ca. 8% of the woody autochthonous flora (Isnard and Bruy, submitted). Lianas could be disadvantaged in low canopy forests with large-scale disturbances, as their diversity is known to be maintained by small-scale disturbances (canopy gaps) and they grow preferentially in tall and heterogeneous forests.

3.6.2.2 Montane Forests and Altitudinal Maquis

Maximum elevation is rarely above 1600 m, but mountain forests are found above 900–1000 m and sometimes at only 700–800 m on the windward rainy coast, where areas more than 3500–4000 mm of rain can fall per year (Nasi et al. 2002). The mountain flora of New Caledonia is characterized by a very high endemicity and by a specific richness in some original groups. Mountain maquis and low forests often have emergent conifers. Among the 47 conifer species occurring in New Caledonia, 33 extend to mountain ranges (Nasi et al. 2002). The flora, although impoverished in comparison to lower altitudinal forest, host several species of the endemic families Phellinaceae as well as most basal angiosperm lineages (Pouteau et al. 2020). The palms and tree ferns (Cyatheaceae, Dicksoniaceae) are also well represented. Climbing secondary hemi-epiphytes (e.g. *Freycinetia*) are abundant in some forests at high altitude and can replace liana whose abundance decreases with altitude, probably as a result of climate niche differentiation (Bruy et al. 2017). Some cloud forests have additional original vegetation, because of their frequent cloud presence, low light transmission, cool temperatures and reduced vapor pressure deficit (Brunijnzeel et al. 2010). The low canopy forest (6–10 m) ("forêt à mousse") has a low diversity among the angiosperms and gymnosperm flora. It is however rich in lichens, bryophytes and ferns (Hymenophyllaceae).

3.6.2.3 Tropical Dry Forest

Tropical dry forests (TDF or "forêt sèche") around the world consist of various plant associations. They can be loosely defined as forest in frost-free regions with 500–2000 mm of annual rainfall and a pronounced dry season of 4–7 months (Holdridge 1971). In New Caledonia, dry forests extend across areas with average annual rainfall below 1200 mm, very commonly below 1000 mm and episodically less than 800 mm, essentially on the western side and in the northern part of the main island. Dry forest occurs on sedimentary rocks (phtanites, sandstone, various sedimentary rock layers, limestones) or more rarely on basalts (Jaffré et al. 1993). It does not occur on ultramafic rocks where the edaphic conditions exert the major influence over the floristic composition (Jaffré et al. 1993; Morat et al. 1981).

Tropical dry forest in New Caledonia is highly endangered (Gillespie et al. 2014). It has been reduced to <2% of its original extent in New Caledonia due to land clearance, cattle ranching and fire (Bouchet et al. 1995). Dry forest is also threatened by introduced species including *Leucaena leucocephala* ("faux mimosa"), *Acacia farnesiana* ("cassis"), several Poaceae and a few autochthonous species such as *Casuarina collina* ("bois de fer"), *Acacia spirorbis* ("gaïac") or *Trophis scandens* ("liane feu"), which prevent regeneration of native forest species (Bouchet et al. 1995; Jaffré et al. 2008). This critical situation led to studies of these forests, beginning in the late 1980s (Jaffré et al. 1993, 2008) and the inception in 2001 of an action programme dedicated to the preservation of dry forests ("dry forest programme") (Mansourian et al. 2018) today managed by the "Conservatoire d'Espaces Naturels".[1]

The dry forests are today restricted to small, more or less degraded, forest fragments totalling about 350 km^2. About 350 autochthonous vascular plants have been recorded, comprising 60% of endemic species (Jaffré et al. 2012; Morat et al. 2012). These forests are strongly marked by a physiog-

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[1] http://www.cen.nc/foret-seche

nomic and floristic heterogeneity, with species richness ranging between 10 and 70 species and endemicity rates ranging from 20% to 60% according to plant associations (Jaffré et al. 2008). Plant association varies with canopy openings created by the deer introduced in the 1800s, *Rusa timorensis* (De Garine-Wichatitsky et al. 2005), and the degradation or invasion by gregarious species (Gillespie et al. 2014; Jaffré et al. 2008).

Of relatively recent origin, the dry forests share major floristic affinities with Australia (Jaffré et al. 1993). Dry forests do not contain palms or conifers (Jaffré et al. 1993) and very few species belonging to basal angiosperm lineages.

New Caledonia's tropical dry forests contain significantly lower species richness than mainland tropical dry forests in biodiversity hotspots. Among Pacific islands, New Caledonia and Fiji harbour the highest native species richness followed by Hawaii, the Marianas and the Marquesas, while New Caledonia and Hawaii have the highest endemism (Gillespie and Jaffré 2003). Family composition is relatively similar to that of neotropical dry forests; however, there is no consistently dominant family of trees within Pacific dry forests. There is very little overlap at the species level among regions (Gillespie and Jaffré 2003).

3.6.2.4 Maquis

In New Caledonia, the maquis refers to all non-forest vegetation on ultramafic substrates (peridotites and serpentinites). The maquis flora harbours about 1140 species of vascular plants, of which more 90% are endemic to New Caledonia (Morat et al. 2012). At least 840 species are restricted to this vegetation type, whose 96.9% are endemic (Isnard et al. 2016). The richness of the maquis is particularly remarkable considering the relatively small area covered (4300–4400 km^2). The soil provides an ecological barrier against most introduced species (with the exception of the Caribbean pine), and invasive introduced species do not grow spontaneously in the maquis because of edaphic constrains. Most maquis species are poor competitors and do not establish in vegetation on more fertile substrates (Jaffré 1980; Jaffré et al. 1987).

The maquis of New Caledonia is strongly heterogeneous – floristically and physiognomically – and ranges from shrubby, evergreen, sclerophyllous to cyperoid vegetation depending on soil properties (Isnard et al. 2016; Jaffré 2022a). These soils are deficient in phosphorus, potassium and calcium and frequently abnormally rich in nickel, manganese, chromium and cobalt, as well as in magnesium for serpentinite soils (Isnard et al. 2016; Jaffré 2022b). The maquis develop in climatic conditions from sea level, in the driest areas of the west coast, to the highest mountain with annual rainfall exceeding 3000 mm. The vast majority of maquis results from the destruction of forest by repeated fires, as fire facilitates the propagation of maquis species. Palynological studies, carried out on the southern plateau of Grande Terre, revealed that natural fires have been widespread on the island over at least 130,000 years, thus before the arrival of humans (Stevenson and Hope 2005). The environmental instability during the Pleistocene played an important role in forest disturbance ecology and caused major vegetation changes in the Austral-Asian region (Hope et al. 2004). In New Caledonia, drier conditions probably increased fuel loads and the vegetation experienced recurrent cycles of destruction by fire favouring the expansion of open maquis followed by forest reconstitution (Stevenson et al. 2001). Some maquis, currently persisting in more or less degraded forms, originally occupied the ridges exposed above 800–1000 m, as well as the drier areas at the base of the massifs, in the form of stunted dry forests (Jaffré 2022a).

Mainly represented in the extreme south of Grande Terre, on about 250 km^2, the maquis on hydromorphic soils (flooding temporary to permanent) is relatively poor (ca. 40 species) but contains a very specialized association of species adapted to hydromorphic conditions and frequent periods of submersion (Jaffré 1980). The herbaceous layer is composed of Cyperaceae. The most characteristic species of the shrubby vegetation include several species of the genera *Pancheria* and *Cunonia* (Cunoniaceae), *Cloezia*, *Melaleuca*, *Xanthostemon* (Myrtaceae), *Styphelia* (Ericaceae), *Grevillea* and *Stenocarpus* (Proteaceae). The riverbanks are home to few shrubs, belonging to *Pandanus* (Pandanaceae), *Serianthes* (Fabaceae), *Gymnostoma* (Casuarinaceae) and two very rare conifers, *Retrophyllum minus* and *Dacrydium guillauminii*. Although fairly homogenous, wetland maquis contain several species with restricted distribution, listed on the IUCN Red List of Endangered Species. Their conservation in areas rich in lateritic minerals remains challenging but requires adequate conservatory actions considering the terrestrial plant originality and the specialized fauna and flora of the aquatic zones (L'Huillier et al. 2010).

Several features of New Caledonian maquis (high level of micro-endemism, nutritional specialization) suggest that this vegetation might qualify as an OCBIL (old climatically buffered and infertile landscape) (Pillon et al. 2021), suggesting that analogous conservation models could apply there.

3.6.2.5 Mangroves

The mangroves of New Caledonia occupy more than 35,000 ha, including ca. 9000 ha of salt flats and *Sarcocornia* salt marshes, and another ca. 26,000 ha of tree and shrub stands. Due to the coastal morphology, the great majority (88%) of mangroves are located on the west coast (Virly 2006). The flora of mangrove forests of New Caledonia includes 24 Indo-Pacific taxa, comprising 15 genera from 13 plant families (Duke 2007). Floristic composition and richness differ between the two coasts with highest richness on the east coast. The zonation is typical of semi-arid coastlines:

Rhizophora spp. are predominant in 50% of mangrove areas colonizing the seashore and *Avicennia marina* in >15% developing at the edge of salt flats (Virly 2006). Contrary to the rest of New Caledonian flora, the mangrove flora has stronger affinities with Asian mangrove.

Large amount of trace metals (Ni, Cr, Co) can be deposited in mangrove sediments (Marchand et al. 2012) as a result of natural erosion and sedimentation along the coastline that can be strongly amplified by open-cast mining activities (Fernandez et al. 2006). Studies assessing the impact of Ni mining on the downstream ecosystem showed that Ni concentrations are 10 to 100 times higher than in other New Caledonian mangroves. Mangroves might be a buffer between mining on land and the world's largest lagoon (> 20,000 km^2) (Marchand et al. 2016).

3.7 Conclusion

New Caledonia hosts a terrestrial plant biodiversity of undeniable importance, and this is widely and internationally recognized. The remarkable and idiosyncratic flora of the archipelago results from historical and environmental contingencies occurring on an old, large, isolated and heterogeneous island. Varying environmental conditions and recent climatic fluctuations have shaped the current original phylogenetic composition, after disharmonies resulting from plant colonization, and have promoted the endemism of the flora. In situ radiation and adaptation after colonization, often repeated within the same group, have led to the diversity of plant lineages. The adaptive and evolutionary responses of the flora to future global and local changes remain uncertain.

Recent advances in molecular and functional biology have showed that the originality of the flora is not only because of the large number of species or their endemicity. The idiosyncratic character of New Caledonia also comes from the phylogenetic diversity and originality of the flora and its functional and ecological diversity. These functional features related to plant morphology, anatomy and physiology are sometimes unique to New Caledonia or relatively well represented on the islands compared to flora worldwide.

Throughout its history, which might have begun 37,000,000 years ago, the vegetation of New Caledonia has experienced phases of stability, as well as successive phases of regression and expansion, accompanied by vegetation and floristic changes. The most recent change since the arrival of humankind 3000 years BP is undeniably anthropogenic: alteration of the vegetation cover and biodiversity loss. This decline has grown in pace with the expansion of agriculture, logging and industrial development, mostly from mining, which began in 1873 (see L'Huillier et al. (2010)). Human activity has resulted in land clearing, construction of access roads (to assess or to exploit resources) and an increase in the frequency of fire and the spread of invasive species. The increase in mining activity has certainly led to the irreversible destruction of plant cover and associated flora. Particularly important is the ultramafic substrate ("terrain minier") where nickel ores are found: it covers a third of the surface of Grande Terre but globally only 3–5% of the earth. Fire may destroy more vegetation than mining, but open-cast extraction is not followed by secondary or self-succession. In addition, surface mining or the storage of excavated material can wipe out relics of maquis and forests, currently saved from fires because of their topographical and microclimatic conditions. Mining activity can thus give the *coup de grace* to forest relics or small populations already endangered (Jaffré et al. 2010).

The originality and the complexity of New Caledonia's plant biodiversity require the implementation of specific conservation measures, including the rescue of rare and threatened species evaluated under IUCN criteria (Read List Authority, RLA-Flore NC, http://endemia.nc) and the protection of sites with micro-endemics (Narrow Endemic Species Hotspot, see Wulff et al. (2013)).

The risks of loss of terrestrial biodiversity cannot be evaluated based on species extinction risk alone. It is important, as advocated in other regions of the world and in a recent article by Ibanez et al. (2019), to set more ambitious objectives including the protection of habitats representative of the different environmental, soil and climate conditions and supporting populations (not just rare species) with genetic diversity. It is also important to identify and protect potential future refuge areas that would be less likely to be impacted by climate change. A better consideration of the preservation of the phylogenetic diversity should also be implemented with priority given to lineages that are only or preferentially represented in New Caledonia. In addition, the potential of innovative technologies and useful resources for societies remains understudied. Recent discoveries are encouraging, including in metal chemistry ("ecological catalysts" for chemistry) (Grison and Lock Toy Ki 2021; Losfeld et al. 2012), for new sources of natural dyes (Toussirot et al. 2012) or the medical value of plants (Coulerie et al. 2013; Hnawia et al. 2008; Lormée et al. 2011). New Caledonia has much to contribute to the understanding of plant evolution and island biogeography, but also for society, and should be at the centre of conservation concerns.

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