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EDITORIAL

The vegetation on ultramafic rocks in New Caledonia

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New Caledonia, an archipelago in the South West Pacific, is a biodiversity hotspot (Myers 1988; Myers et al. 2000) which rich and unique flora has generally been associated with the diversity of geological substrates. New Caledonia has one of the largest extent of ultramafic rocks in the world (Garnica-Díaz et al. 2023). Ultramafic rocks are igneous rocks that are poor in silicon and rich in iron and magnesium. When weathered, they produce soils that impose difficult conditions for plant growth (Kazakou et al. 2008), and they have often been referred to as “ultrabasic rocks” or “serpentine” in the literature.

The peculiarity of New Caledonia was noted by its earliest European visitors. In his journal, James Cook wrote that “our botanists did not complain for want of employment at this place ; every day bringing something new in botany or other branches of natural history” (Cook 1777 p. 124). Although they did not visit ultramafic outcrops, the naturalists accompanying James Cook were also struck by the geological distinctiveness of New Caledonia. For instance, Georg Forster (1777 p. 576) anticipated that “there was some probability of meeting with rich and useful minerals upon this island, which, as far as we saw, distinguished itself from all those we had hitherto examined in the South Seas, in being entirely destitute of volcanic productions”. Georges’ father, Johann Forster (1778 p. 34), similarly wrote that “the mountains of New Caledonia are the most likely to contain the richest metallic veins”. Later, the geologist Jules Garnier explored more extensively the main island of New Caledonia noting the large areas of “*terrains serpentineux*” (serpentine terrains) and revealing the abundance of nickel ores (Garnier 1885). This dramatically changed the future of the island where the mining industry now plays a major role.

The earliest European naturalists exploring New Caledonia focused on inventorying the diverse flora of the archipelago, and had limited interest or time to study its ecology, including plant-soil relationships. Robert Virost made the first substantial contribution to the ecology of the New Caledonian flora with his thesis “*La végétation canaque*” (1956). After spending several years on the

island, he was able to give an overview of the biological forms, plant formations, and phytosociology of the flora. His work prefigures that of Tanguy Jaffré.

In 1980, Tanguy Jaffré published his Ph.D thesis entitled « Etude écologique du peuplement végétal des sols dérivés de roches ultrabasiqes en Nouvelle-Calédonie » (« *Ecological study of the plant population of soils derived from ultrabasic rocks in New Caledonia* »). Although it was published in French by ORSTOM (now IRD) with limited dissemination, this work has attracted a large and steady number of citations over the years (figure 1). With this in mind, we thought it would be useful to make this work more accessible to the scientific community as a whole. Thanks to the support of the Société Botanique de France, an English translation is published in this special issue. The three thesis chapters, « les formations végétales des terrains ultrabasiqes » (“*Plant formations on ultramafic rocks*”), « les groupements végétaux des maquis » (“*Plant communities of the maquis*”), and « phytogéochimie » (“*Plant mineral nutrition*”) representing about 73 % of the pages of the original text, are published as three articles in this special issue. The figures were reformatted and are published in colour for greater clarity. The plant taxonomy was updated following the FLORICAL database (Morat et al. 2012; Munzinger al. 2023b) and the soil classification follows the World Reference Base (IUSS Working Group WRB 2015). Minor alterations to the text were made to avoid anachronisms with the current state of the art on the ecology of ultramafic vegetation and the New Caledonian flora.

The first article entitled “Plant formations on ultramafic rocks in New Caledonia” (Jaffré 2023a) starts with a description of three contact zones between ultramafic rocks and other substrates. These suture zones have received little attention since, although they are interesting systems to study. They are known as areas of micro-endemism (Pintaud and Hodel 1998; Pillon et al. 2008; Gâteblé and Munzinger 2018). There, species with distinct soil preferences can co-occur and hybridize, which may trigger speciation (Pillon et al. 2009). The second part of the article describes the main plant formations occurring on ultramafic rocks in New Caledonia. Contrary to many other

areas in the world (particularly temperate regions), ultramafic substrates of New Caledonia can harbour dense and diverse forests. The forests of New Caledonia have received significant attention (e.g. Jaffré and Veillon 1995; Ibanez et al. 2014; Birnbaum et al. 2015). The article also mentions several cases of monodominant formations, where one tree species represents a large proportion of the individuals reaching the canopy. A wide diversity of species can be dominant in New Caledonia (Pillon et al. 2021), and some monodominant formations have also received much attention (e.g. Read and Jaffré 2013). The first article also describes the “maquis”, this unique sclerophyllous evergreen shrubby vegetation observed on ultramafic rocks (and occasionally on siliceous rocks), similar in appearance to the shrubby vegetation observed in the Mediterranean Basin (hence the name). An overview of biological forms in the maquis is given, and more studies on functional traits of the New Caledonian flora are still needed (but see, e.g. Read et al. 2006; Trueba et al. 2016; Bruy et al. 2018).

The second article “Plant communities of the maquis on ultramafic rocks of New Caledonia” (Jaffré 2023b) is a phytosociological study of the New Caledonian maquis. By using a large number of field censuses and a statistical approach (an improvement to Virot 1956), it describes the diversity of plant associations in this shrubby formation. The distribution of these associations is likely to be determined by factors such as elevation, topography, pedology, and climate. There have been few ecological studies on New Caledonian maquis since. This type of vegetation is often neglected and regarded as secondary vegetation, as many other open ecosystems (Bond 2019; Bond 2021).

Although their surface area has increased since the arrival of humans and the modification of fire regimes, several lines of evidence suggest that they had a long history before the Anthropocene. They are composed of diverse and unique species, including 840 (96.9 % endemic) restricted to these formations (Isnard et al. 2016). Some genera, that are mostly found in maquis, started diversifying several millions years ago such as *Dracophyllum* (5.2 Mya, Wagstaff et al. 2010) and *Grevillea* (*exul* group: 10.2 Mya, *gillivrayi* group 9.2 Ma; Pillon et al. 2023b). Compared to other open areas, the presence of open ecosystems in New Caledonia cannot be explained by the presence of large

herbivores (Pillon et al. 2021). An important question is therefore the original extent, distribution and dynamics of the maquis, particularly in regard to the forest before human settlement.

The third article “Plant mineral nutrition on ultramafic rocks of New Caledonia” (Jaffré 2023c) corresponds to the most impactful part of Tanguy Jaffré’s original work. In New Caledonia, the environmental heterogeneity on ultramafic rocks is a major driver of plant diversity. This chapter explores one of the most fascinating aspects of the New Caledonian flora, which is how plants cope with soil nutrient deficiency and toxicity, and how the soil mineral composition translates into the diversity of plant mineral nutrition and plant distribution. The first part of this article compares the plant mineral composition on ultramafic substrates and other substrates, and in different environments on ultramafic rocks. Several common and ubiquitous species were investigated such as *Acacia spiroides* Labill. (Fabaceae) and *Myodocarpus fraxinifolius* Brongn. & Gris (Myodocarpaceae). The mineral composition of the leaf tissue of species growing on ultramafic rocks reflects, to some extent, the mineral imbalance of the soils. It is particularly marked by abnormal high foliar concentration in trace elements (Ni, Mn, Cr, Co). The second part of this article deals with the nutritional strategy of species strictly growing on ultramafic rocks. The study relied heavily on the collection of the herbarium of New Caledonia (NOU, Bruy 2023). The results of this work have paved the way to a vast field of research in New Caledonia and abroad. One of the major discovery was the extraordinary accumulation of nickel in *Pycnanandra acuminata* (Pierre ex Baill.) Munzinger & Swenson (Sapotaceae), an endemic tree of New Caledonian rainforests. This work introduced the term “hyperaccumulator” in the scientific literature (published for the first time a few years before in an article, Jaffré et al. 1976) to characterise species with the capacity to concentrate high quantities of metals in their aerial tissues. Several now famous Ni and Mn hyperaccumulator species were identified, that have been the subject of recent publications (Gei et al. 2020; Bihanic et al. 2021; van der Ent et al. 2022). The foliar mineral element concentration reflects the strong specificity of the mineral nutrition, and adaptation to metal toxicity on ultramafic rocks. The results of this section confirm the very low nutrient availability for plants in all ultramafic environments. The low stocks in

major elements, except for Mg, is proposed as one of the main causes of the general poor fertility of soils on ultramafic rocks in New Caledonia.

Ultramafic rocks of New Caledonia host a disproportionate number of endemic plant species (Isnard et al. 2016), but also of genera and families (Pillon et al. 2017). While the number of endemic genera is likely to decrease with advances in molecular phylogenetics (Munzinger et al. 2023a; Pillon et al. 2023a), some may still be identified by phylogenetic studies (e.g. Larridon et al. 2018) or field discoveries (e.g. McPherson and Lowry 2004). It is likely that New Caledonia will remain the Pacific island with the largest number of endemic genera and families. With 89 endemic genera and three endemic families currently accepted taxonomically (Munzinger et al. 2023b), it even surpasses the much larger (but less isolated) New Guinea (c. 61 endemic genera, Cámara-Leret et al. 2020), Borneo (65, Neo et al. 2020), and Cuba (63, Berazaín Iturralde 2008). Madagascar seems to be the only island (Australia excluded) with more endemic genera (321) and families (5) (Callmander et al. 2011).

Some areas of New Caledonia are still under-surveyed (Birnbaum et al. 2023) and dozens of plant species remain to be described (Lannuzel et al. 2022). However, as more data is collected and collated (Lannuzel et al. 2022), it is becoming easier to assess species correctly according to IUCN criteria (Meyer et al. 2022), and to decide where new protected areas should be established to best complement New Caledonia's currently insufficient and imbalanced protected areas (Ibanez et al. 2019). Designing an appropriate network of nature reserves to adequately conserve the naturally fragmented ultramafic substrates characterized by pronounced micro-endemism (Wulff et al. 2013; Caesar et al. 2017; Lannuzel et al. 2022), is challenging. The compilation of metadata can help to set priorities and the ultramafic areas in the Northern Province of New Caledonia clearly emerge as a priority target for future conservation efforts (Birnbaum et al. 2023).

Ultramafic substrates may have an important filtering effect on floras (Pillon et al. 2019), and they may have favoured the diversification of plants that are frugal in nutrient such as Proteaceae (Pillon et al. 2023b), to the detriment of climbing plants (Isnard and Bruy 2023). To cope with the low

levels of essential elements and high metal concentrations in ultramafic substrates, plants may be involved in an important diversity of root symbioses (Pillon et al. 2021). Arbuscular mycorrhiza play an important role in the nutrition of plants on ultramafic substrates, even in plants that are often considered as non-mycorrhizal such as Cyperaceae (Amir et al. 2023). The filtering effect of ultramafic substrates may not only affect plants, but also bees, and their interaction through pollination (Zakardjian et al. 2023).

By republishing Tanguy Jaffré's pioneer work online and in English, in conjunction with recent studies on the biota of New Caledonia's most emblematic landscapes, we hope to make this knowledge more accessible to the community working on ultramafic ecosystems (Echevarria et al. 2018), open ecosystems (Bond 2019), and Old Climatically Buffered Infertile Landscapes (OCBIL, Hopper 2009), in order to improve their understanding and conservation.

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YP, SI and LM contributed to this editorial.

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Figure 1. Number of citations through times of the Tanguy Jaffré's ph.D thesis, cited either as « Étude écologique du peuplement végétal des sols dérivés de roches ultrabasiqes en Nouvelle Calédonie » or « Végétation des roches ultrabasiqes en Nouvelle-Calédonie », according to Google Scholar.

