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Plant communities of the maquis on ultramafic rocks of New Caledonia

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ABSTRACT

The soils derived from ultramafic rocks in New Caledonia support a rich and unique sclerophyllous shrubby vegetation: the maquis. A phytosociolgical analysis was carried out to identify the different plant communities of this maquis. We surveyed areas of Plaine des Lacs, Mont Dore, Montagne des Sources, Mount Dzumac and Mount Humboldt (Great South region), and along a broad elevation gradient on Mount Boulinda (central-west region). Multivariate analyses revealed 17 plant associations grouped in 5 alliances and 3 orders. The distribution of these associations appears determined by several parameters, including elevation, precipitation, topography, and the local edaphic, physicochemical and hydric conditions. The diversity of plant associations observed in New Caledonia is one of the most remarkable among vegetations on ultramafic rocks globally.

This article is a translation of the chapter « Les groupements végétaux des maquis »(pp 69–120) of Jaffré (1980), with minor updates.

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KEYWORDS
Edaphic condition; open ecosystems; phytosociology; plant associations; serpentine; shrub

Introduction

A detailed study of plant communities on ultramafic substrates was conducted to characterise the diversity of the maquis of New Caledonia (Jaffré 202Xa) and establish a preliminary classification of these communities. The survey was carried out in the Southern Massif, in the sectors known as the Plaine des Lacs, Plum and Mont Dore for low-altitude maquis, in the Humboldt, Dzumac and Montagne des Sources massifs for high-altitude maquis, and in the Boulinda Massif located in the central-western part of the territory (Figure 1).

Material and methods

The floristic composition of plant communities was defined by comparing field surveys conducted according to the principles of the sigmatist method.

Data collection

Each floristic inventory was carried out on a homogeneous surface, usually square, with a surface area larger than the minimum area, that is, about 100 m^2 for low maquis and about 150 m^2 for taller maquis. Each species was assigned a coefficient of abundance-dominance according to the Braun-Blanquet scale. Mosses, lichens, low ferns and lycophytes were not surveyed. The names of the plant taxonomic units were updated according to the nomenclature maintained in the FLORICAL database (Morat et al. 2012; Munzinger et al. 2022).

In several surveys considered representative of associations, soil samples were taken for analysis. The results are presented in Table 1 (Appendix). The soil typology was also updated using the WRB terminology (IUSS Working Group WRB. 2015). Thus, soils previously classified as Brown Hypermagnesic soils are now assigned to Magnesic Cambisols in the WRB classification and to Leptosols when highly eroded. Ferralitic soils are now found in the Ferralsol group. Here, however, we classify them in the Ferritic Ferralsol subgroup, whose characteristics ("Ferritic") specific to Ferralsols on ultramafic rocks were described in New Caledonia by Latham (1975).

Data interpretation

The processing of floristic data was carried out according to the factorial correspondence analysis method (Cordier 1965; Benzecri 1973). The mathematical aspects of this method and their phytosociological applications are indicated in several books and articles (Dagnelie 1960; Roux and Roux 1967; Gounod 1969; Benzécri 1973; Guinochet 1973; Briane et al. 1974). The principle of the method, as emphasised by Guinochet (1973), "*consists in representing all the R surveys and the E species on the same plane or spatial map in such a way that each survey is surrounded by its*

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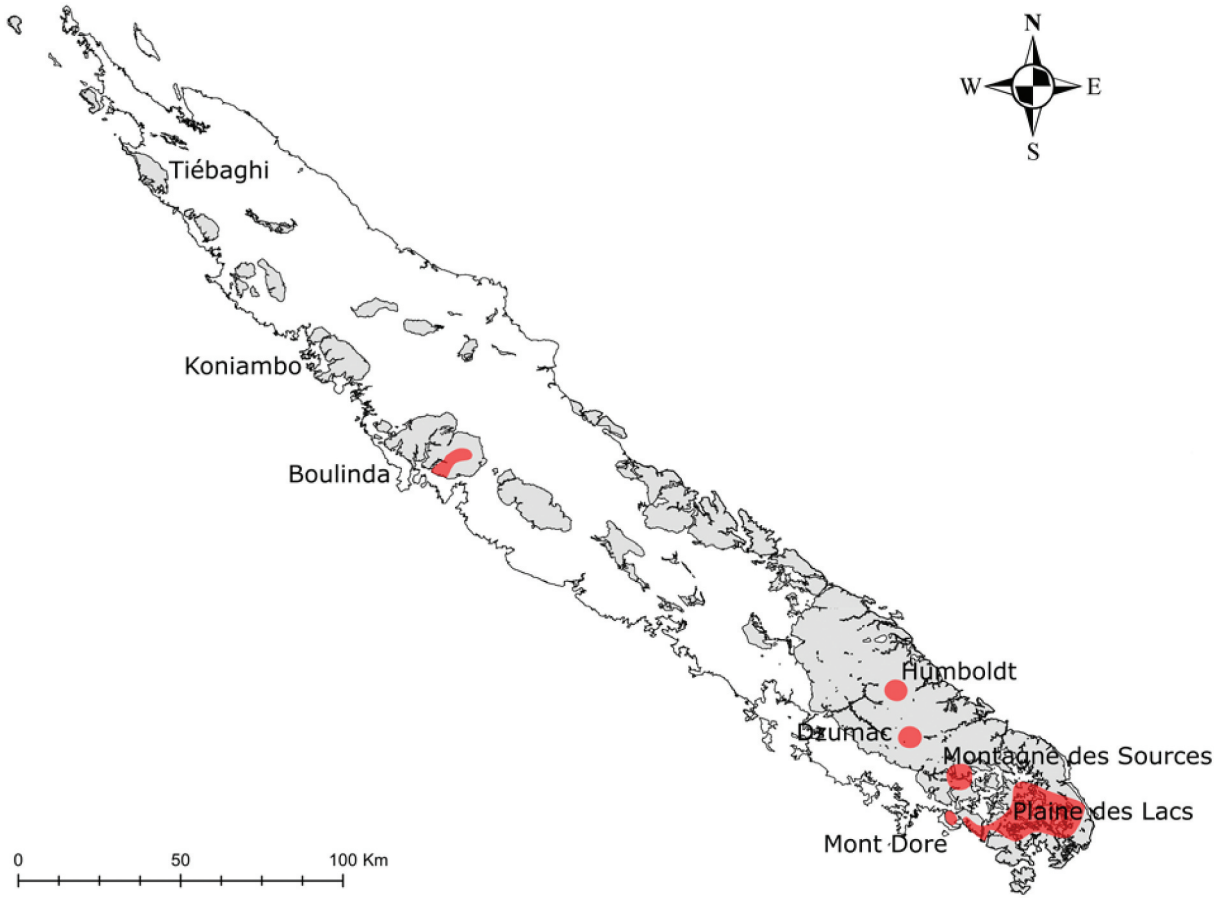

Figure 1. Location of areas where phytosociological surveys were carried out (in red). Areas covered with ultramafic rocks are shown in grey.

species and each species by the surveys in which it appears. As a result, similar surveys and associated species are grouped together".

The interpretation of the mathematical images obtained from the projection of the survey constellation allowed us to distinguish sets of related surveys corresponding to various phytosociological units. During the preliminary analysis, certain data groups, generally, well distinct floristically, led to the clustering of all the other data near the origin. To eliminate this influence, we proceeded to a partial treatment (Lacoste and Roux 1971, 1972) by deleting the initially well-discriminated data groups. The mathematical calculations only take into account the presence or absence of species in the surveys.

The analysis covered 295 surveys and 318 species for the Southern Massif and 160 surveys and 272 species for the Boulinda Massif. The large number of surveys required a pooled data analysis for the Southern Massif (Briane et al. 1978). The data belonging to the different groups that were clearly identified by the analyses were used to compile the phytosociological tables. However, for some groups, not all data could be included in the tables because of their excessive number. In addition, the intermediate data, which proved to be heterogeneous on examination, were not included. Characteristic species were determined by examining the resulting factorial maps and phytosociological tables. Overlaying the species factorial map with the survey factorial map generally found characteristic species within or near the areas circumscribed by the surveys belonging to the same phytosociological unit. We also considered our field observations on the distribution of species in different massifs, and abundance in different biotopes. In light of the results obtained for the Southern Massif and the Boulinda Massif, and referring to observations made on the Koniambo (Jaffré 1974) and Tiébaghi massifs, we propose a general classification of plant communities in maquis.

Results

Analyses of the Southern Massif surveys

The factorial map formed by axes 1 and 3 of the correspondence analysis (Figure 2(a)), shows the clear separation of two groups of surveys: the orophilous maquis surveys on Mount Humboldt (group I) and the shrubby maquis surveys on serpentinite at the base of Mont-Dore (group II). On Figure 2(b), the factorial map constituted by axes 2 and 3 after removing the two distinct groups from

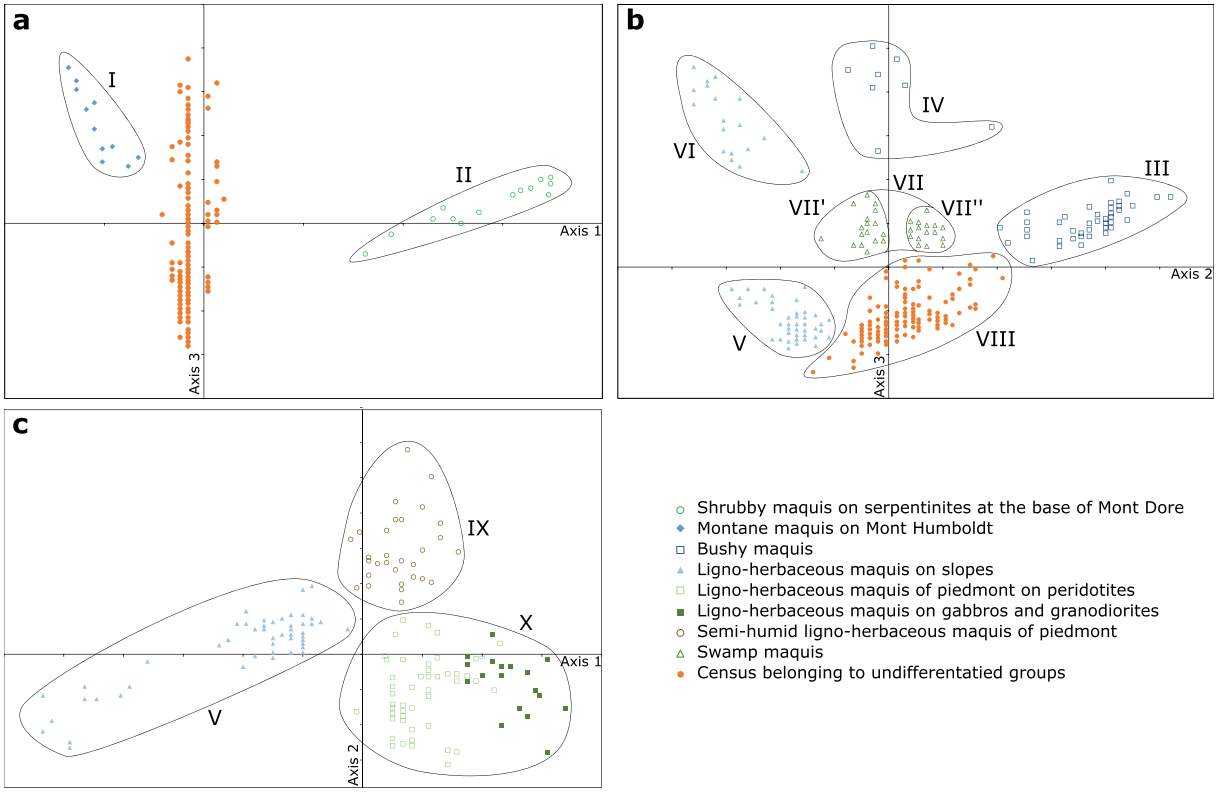

Figure 2. Factorial correspondence analyses of the floristic surveys of the Southern Massif maquis. **A**: All the surveys projected on axes 1 and 3; **B**: All the surveys after excluding the surveys of Mount Humboldt (group I) and Mont Dore (group II), projected on axes 2 and 3; **C**: Surveys of groups V and VIII projected on axes 1 and 2.

Figure 1(a), the surveys fall into six clear groups. Groups III and IV correspond to surveys in the bushy maquis and groups V and VI to surveys in the ligno-herbaceous maquis.

Group III and V surveys were conducted at low elevations, while Group IV and VI surveys were conducted above 650 m in altitude. Group VII corresponds to surveys carried out in the swamp maquis. It can be divided into two subgroups: subgroup VII' consisting of surveys of the central swampy area of the Plaine des Lacs and subgroup VII" consisting of surveys of rocky areas. Group VIII corresponds to all the surveys of the ligno-herbaceous maquis in the piedmont area and to the surveys of the ligno-herbaceous maquis on gabbros and granodiorites. Figure 2(c), constituted by axes 1 and 2 of the correspondence analyses of the surveys of groups V and VIII, divides group VIII into two groups. Along the positive section of the vertical axis is a set of surveys carried out in the semi-wet ligno-herbaceous maquis (group IX); in contrast, group X stands out, consisting of surveys carried out in the ligno-herbaceous maquis of piedmont and the surveys of the ligno-herbaceous maquis on gabbros and granodiorites. Along the negative section of the horizontal axis, group V, which already appears on Figure 2(b), stands out again, consisting of surveys of ligno-herbaceous maquis on slopes.

Analyses of the Boulinda Massif surveys

The factorial map constituted by axes 1 and 2 of the correspondence analysis (Figure 3(a)) is based on the totality of the 160 surveys. Its shows that all the floristic surveys carried out in the shrubby maquis at the base of the massif occupy the negative section of the horizontal axis. In contrast, the surveys carried out in the ligno-herbaceous maquis and in the bushy maquis occupy the positive section of this axis. The floristic surveys made in the shrubby maquis, more or less bushy, are grouped at the intersection of the two axes. The surveys located on the negative section of the horizontal axis are divided along the vertical axis into three distinct groups: near the origin are the surveys of shrubby maquis on serpentinite at the base of the massif (Group I), slightly above them are the surveys of tall maquis with *Acacia spirorbis* dominating the flat areas at the base of the massif (Group II), and along the negative section of the axis are the surveys of shrubby to tall maquis on steep slopes (Group III). The surveys located on the positive section of the horizontal axis are divided into four groups along the vertical axis: along the negative section of the axis and near the origin are the surveys of ligno-herbaceous maquis on slopes (Group IV), and then the surveys of ligno-herbaceous maquis of piedmont (Group V), along the positive section of the axis, moving away from the origin are the surveys carried out in the bushy maquis of low altitude

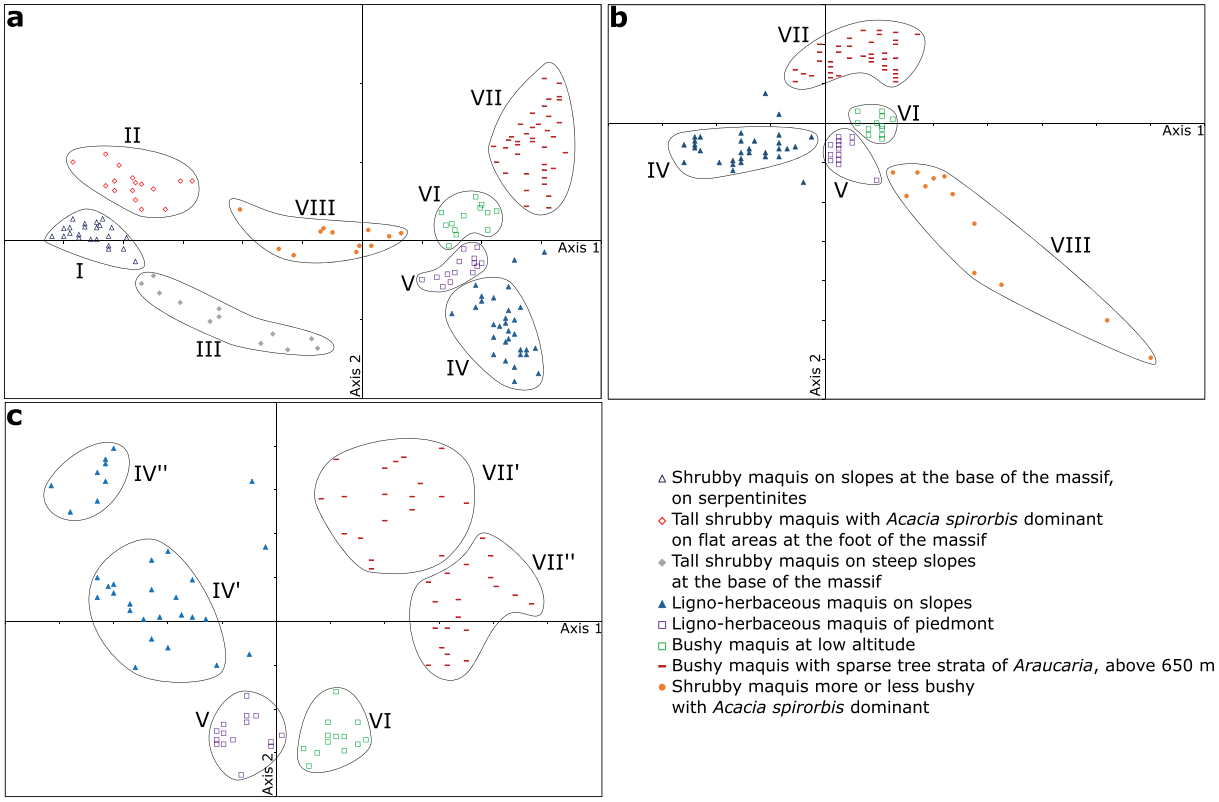

Figure 3. Factorial correspondence analyses of the floristic surveys of the Boulinda Massif maquis. **A**: All surveys projected on axes 1 and 2; **B**: All surveys after exclusion of groups I, II and III, projected on axes 1 and 2; **C**: All surveys after exclusion of groups I, II, III and VIII, projected on axes 1 and 2.

(group VI), then the surveys carried out in the bushy maquis with loose *Araucaria* tree stratum (group VII). The surveys of the shrubby maquis more or less bushy, dominated by *Acacia spirorbis* (group VIII) are found at the intersection of the two axes.

Figure 3(b), constructed from axes 1 and 2 after elimination of groups I, II and III, distinguishes groups IV, V, VI and VII again and shows a very clearly group VIII, which was located at the intersection of the two axes in diagram 3A. Figure 3(c), constructed from axes 1 and 2 after eliminating surveys from groups I, II, III, and VIII, shows six distinct groups. Surveys conducted in ligno-herbaceous maquis (groups IV and V) are located along the negative section of axis 1. In contrast, surveys of the bushy maquis (groups VI and VII) are located along the positive section of this axis. The surveys of the ligno-herbaceous maquis on slopes (group IV) are divided into two subgroups, subgroup IV' corresponding to the surveys of the upper and middle slopes, and subgroup IV", the furthest from the origin, corresponding to the surveys carried out on the most overgrown soils, generally on ridges. The surveys of the bushy maquis with loose *Araucaria* tree stratum, group VII, are divided into a sub-group VII' which includes the surveys carried out in the most degraded sectors, and a sub-group VII" including the surveys of the least disturbed sectors.

Plant associations of the Southern Massif

Group II – Association with *Soulamea pancheri* and *Hibbertia vieillardii* (Figure 4(d), Supplemental material: Table S1)

It is an open maquis with a very specialised flora. The herbaceous layer is very sparse and leaves the eroded soil largely bare. Its cover varies from 20 to 40% and is always lower than the cover of the shrub layer. From a floristic point of view, this herbaceous layer is composed of magnesicolous Cyperaceae: *Gahnia aspera, Fimbristylis neocaledonica, F. ovata*, with sometimes others Cyperaceae that have less strict ecological requirements: *Tetraria raynaliana, Schoenus juvenis*, (preferentially associated with eroded stony soils), *Schoenus neocaledonicus, Tetraria breviseta* and *Lepidosperma perteres*.

The shrub layer consists of nano- and microphanerophytes. It is discontinuous; its average height is about 1.50 m, but it is not uncommon for it to be dominated by isolated shrubs of *Grevillea gillivrayi* exceeding 3 m high. The majority of species in this layer have serpentinophilous and magnesicolous features: *Soulamea pancheri, Hibbertia vieillardii, Tarenna microcarpa, Xanthostemon multiflorus, Xanthostemon ruber, Sannantha virgata, Cleistanthus stipitatus, Stenocarpus milnei* and *Austrobuxus carunculatus*. Some species, which are constantly found in the area and do not deviate from it, can be considered

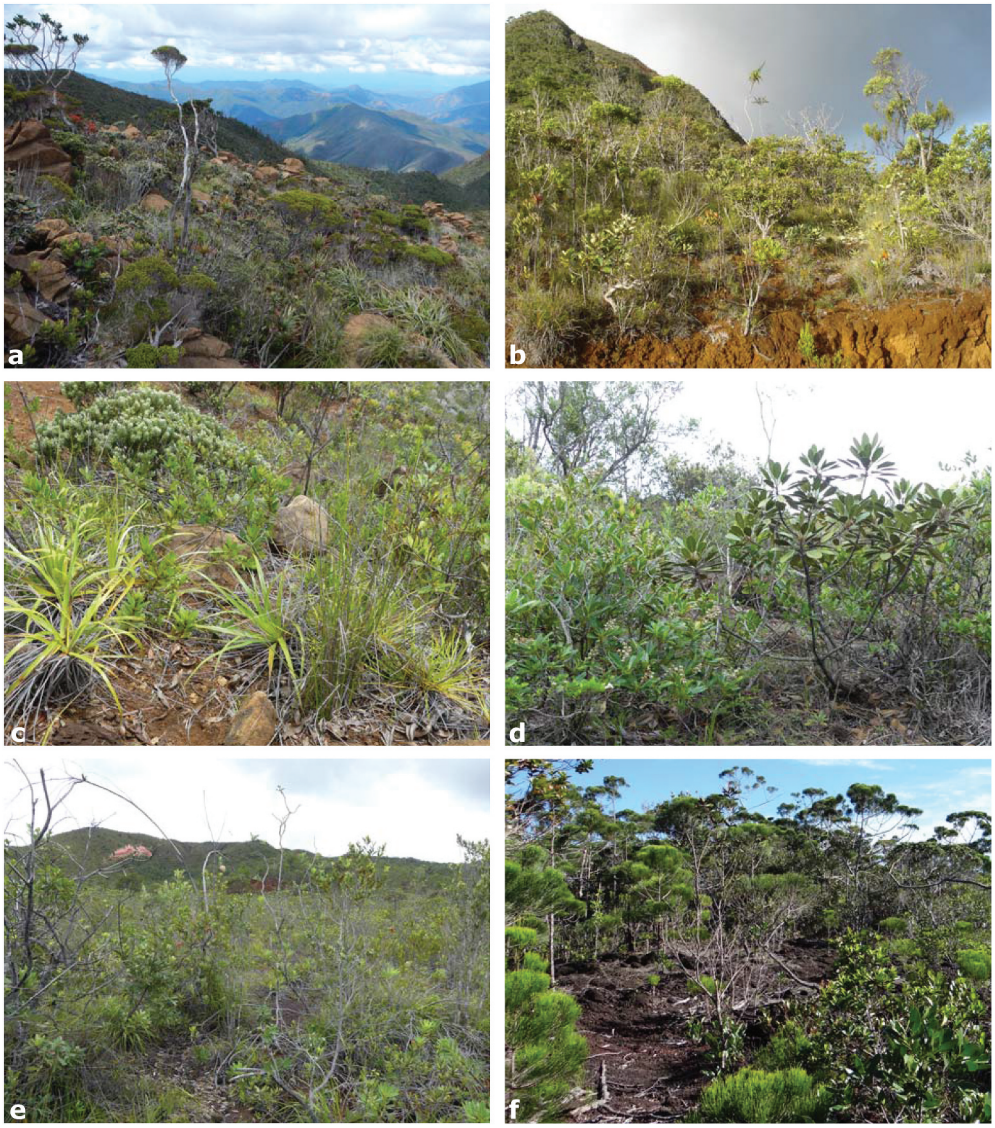

Figure 4. Examples of plant associations of southern New Caledonia. **A**: association with *Metrosideros tetrasticha* and *Quintinia oreophila*¸Mont Humboldt; **B**: association with *Codia discolor* and *Eugenia stricta*, La Coulée; **C**: association with *Tetraria raynaliana* and *Cyathopsis albicans*, col des deux Tétons; **D**: association with *Soulamea pancheri* and *Hibbertia vieillardii*, col de Plum; **E**: association with *Homalium kanaliense* and *Tetraria comosa*, lac de Yaté; **F**: association with *Tarenna hexamera* and *Gardenia aubryi*, Prony. Photos Credit: A: G. Gâteblé,B: Y. Pillon, C-E: T. Jaffré, F: B. Suprin.

characteristic of the group locally. However, they are also found elsewhere in different environmental conditions. This is the case of *Cloezia artensis*, which is found in dry forests on limestone islands of the West Coast, and of *Styphelia cymbulae* and *Scaevola montana*, which are among the main components of the maquis on non-ultramafic rocks in the north of the territory. However, these species can be represented by different ecotypes on the other substrates where they occur.

Besides the species linked to this very magnesicolous environment, some species have less strict ecological requirements. They are commonly found in various low altitude groups and include species not specific to ultramafic substrates: *Dodonaea viscosa, Geniostoma densiflorum* and *Wikstroemia indica*, widely distributed on different types of soils derived from ultramafic rocks. The latter can be divided into rupicolous species, *Cyathopsis albicans, Myrtastrum rufopunctatum, Normandia neocaledonica*, and species with poorly specified ecology but which do not deviate from ultramafic rocks: *Montrouziera sphaeroidea, Scaevola beckii, Solmsia calophylla, Notelaea autrocaledonica* and *Longetia buxoides*.

In the study area, where the vegetation has been largely affected by human activity and fire, transition forms to denser associations are rare. They are isolated in small talwegs and are marked by *Schoenus tendo* in the herbaceous layer and *Geissois pruinosa, Hibbertia lucens* and *Garcinia* sp. in the shrub layer. Very degraded stages cover large areas at the base of Mont-Dore, where only thin vegetation remains with a predominance of rupicolous species (*Schoenus juvenis, Tetraria raynaliana, Normandia neocaledonica*).

This very characteristic association occupies only small areas, at altitudes between sea level and 150 m, at the base of Mont Dore and in Plum area toward Prony. The floristic lists given by Virot (1956) for the low areas of the Tontouta Basin seems to indicate that the association is also found in this area.

The association is found at low elevations (<300 m) on Magnesic Cambisols on serpentinite. These soils are shallowly eroded, very stony, and have affinities with Magnesic Leptosols. They are often covered with fragments of highly eroded serpentinite. In places, due to increased colluvium, they may be deeper, changing to Magnesic Vertisols. The average chemical composition of the soil (Table 1) indicates a high exchange capacity (>20 me/100 g), a large excess in Mg and very low levels of all other major elements (Ca, K, and P). Their pH is neutral or weakly acidic. Nickel and Cr levels are low to moderately high (Ni < 0.5%, Cr < 1%). These soils have an unfavourable water balance (Jaffré et al. 1971). Indeed, the quantity of water "easily available" to plants, given by the difference between the maximum quantity of water retained in the soil at pF 3.0 (pressure of 1 kg per cm^2) and at pF 4.2 (pressure of 16 kg per cm^2), or wilting point, is low in these soils because of high moisture content at pF 4.2.

Group V – Association with *Tetraria raynaliana* and *Cyathopsis albicans* (Figure 4(c), Supplemental material: Table S2)

This association is a ligno-herbaceous maquis with a well-developped herbaceous layer and a cover of about 70 to 80%. This layer consists almost exclusively of Cyperaceae associated with ultramafic rocks, which are widely represented on all categories of Ferralsols, *Chamaedendron nervosa, Lepidosperma perteres, Schoenus neocaledonicus, and Tetraria breviseta*. Others are preferentially associated with eroded Ferralsols: *Tetraria pubescens* and *Schoenus juvenis*.

The discontinuous shrub layer consists of nanophanerophytes hardly exceeding 1.50 m. Its cover generally does not exceed 50%. The most abundant in this association are species that find their optimal development and their highest density there without being strictly restricted to this group. They shape the physiognomy of this formation: *Peripterygia marginata, Grevillea rubiginosa, Codia nitida, Hibbertia pulchella, Pancheria alaternoides*, and, to a lesser extent, *Cloezia artensis, Hibbertia trachyphylla* and *Garcinia amplexicaulis*.

The most characteristic shrubby species of the group are species with distinctive rupicolous affinities: *Normandia neocaledonica, Cyathopsis albicans, Myrtastrum rufopunctatum, Ficus asperula, Argophylum montanum*. Besides these species, we also find a whole range of heliophilous species widely distributed on ultramafic rocks. The most frequent are *Montrouziera sphaeroidea, Phyllanthus aeneus, Scaevola beckii, Uromyrtus emarginatus, Dracophyllum ramosum* and *Sannantha leratii*. In this assemblage, only *Pteridium esculentum*, abundant on burned surfaces, and *Sannantha leratii* are not species strictly related to ultramafic substrates.

The evolution of this association is hardly perceptible on a human scale. When the vegetation cover is destroyed by fire, it recovers very slowly, with many species growing back from the stump. Still, for many years *Pteridium esculentum* becomes dominant and creates particular facies. On chaotic rocky ridges where fire is rare, humus is partly prevented from being carried away by runoff. Due to its good water retention, it creates small wetter areas where mesophilous species become more abundant. The vegetation becomes taller and bushier, but without any evolution towards a forest stage.

The surveys carried out between 600 and 670 m of altitude on the summit of the Pic du Pin (highest point of the Plaine des Lacs) represent a specific phytosociological sub-unit. It differs from the typical association by the presence of orophilous species (*Montrouziera verticillata, Earina deplanchei*), several species growing in adjacent forests (*Styphelia coryphila, Agathis ovata, Thiollierea campanulata*) and a few species with an orophilous tendency and limited geographical distribution (*Soulamea trifoliolata, Melaleuca dawsonii, Araucaria muelleri*). The phytosociological status of this sub-unit, which occupies a restricted area on the only high point of the Plaine des Lacs, is unclear. It could be a mixed unit, intermediate between the low altitude association with *Tetraria raynaliana* and *Cyathopsis albicans* and a distinctly orophilous association (association with *Hibbertia altigena* and *Beaupreopsis paniculata*) which is not found in the Plaine des Lacs area.

The association with *Tetraria raynaliana* and *Cyathopsis albicans* occurs between 200 and 650 m of altitude on ridges and steep slopes, on the upper and middle peridotite hillsides of the narrow ranges surrounding the basins of the main rivers that drain the south of the island.

The association is found on eroded Ferralsols, locally slightly colluvial, which are shallow and scattered with more or less weathered boulders, and often covered with veneers of colluvium from more highly desaturated Ferralsols, which fill in the hollows and cover the small flats between the boulders. When vegetation does not colonise these earthy zones, they take a weathered and smooth aspect due to superficial encrustation.

The chemical composition of the soil varies a lot depending on the rate and nature of colluvium and stoniness. The soil chemical analysis (Table 1) shows low N, P, K and Ca levels and a predominance of Mg over Ca in the exchange complex. Ni and Co levels can be very high, with Ni and Co levels commonly reaching 1% and 0.1%, respectively. These soils most often have a pH of about 6.

In general, the colluvium is not sufficient to prevent the root systems from reaching the alteration cortex that surrounds the floating or anchored peridotite blocks in the profile. In this cortex, there is an enrichment in SiO_2, Mg and Ni, the latter reaching levels above 1.5% (Jaffré et al. 1971) compared to the desaturated colluvium that fills the rocky interstices. Here, Ni is probably in an assimilable form due to the significant exchange capacity of the clays.

This assemblage develops in highly ventilated areas with intense insolation. Given the lack of depth of the soil, the steepness of the slope, which leads to rapid drainage of rainwater and the low water retention capacity of the soil, it is likely that in periods of drought, the vegetation must cope with a significant water deficit.

Group VI – Association with *Hibbertia altigena* and *Beaupreopsis paniculata* (Supplemental material: Table S2)

This ligno-herbaceous assemblage is physiognomically very similar to the previous (group V) but floristically quite distinct. The herbaceous layer differs little from that of the association with *Tetraria raynaliana* and *Cyathopsis albicans*. It is dominated by *Chamaedendron nervosa* and *Schoenus juvenis*, the latter being rupicolous. The low altitude species, *Tetraria raynaliana*, a rupicolous species, and *Lepidosperma perteres*, a species always found in the ligno-herbaceous maquis, become rare.

The shrub layer is composed of orophilous species characteristic of the association: *Hibbertia altigena, Beaupreopsis paniculata, Eucarpha deplanchei, Pancheria engleriana*, rupicolous species: *Myrtastrum rufopunctatum, Ficus asperula, Normandia neocaledonica*, a group of species associated with ligno-herbaceous maquis on well-drained soils: *Peripterygia marginata, Hibbertia trachyphylla, Grevillea rubiginosa*, species with broader distribution on ultramafic rocks: *Scaevola beckii, Pancheria alaternoides, Dracophyllum ramosum, Geniostoma densiflorum*, and two ubiquitous species not restricted to ultramafic rocks: *Tetraria arundinacea* and *Sannantha leratii* which become more important here because of the desaturation of the soil in exchangeable cations.

The signs of an evolution towards a taller maquis are hardly visible. A few stands of *Melaleuca sphaerodendra*, 4 to 5 m high, generally very open and only located on certain ridges and valleys, could indicate an evolution towards low forest [maquis préforestier]. Still, the significance of their occurrence is uncertain.

The association occurs at elevations between 600 and 1200 m on steep slopes or ridges on eroded soils, similar in many ways to those of the previous association with *Tetraria raynaliana* and *Cyathopsis albicans*. They are shallow, very rocky, and their chemical composition (Table 1) is not very different from the soils of the previous association. They differ, however, by a lower pH linked to a higher rate of desaturation.

Group X – Association with *Codia discolor* and *Eugenia stricta* (Figure 4(b), Supplemental material: Table S3)

It is a more or less bushy and more or less dense ligno-herbaceous maquis whose height often exceeds 2 m. The structure is variable, but generally, the shrub cover allows enough light for a herbaceous layer to develop. The herbaceous layer can be dense or relatively sparse. There are primarily three Cyperaceae, *Chamaedendron nervosa*, predominant on loose soils, *Schoenus neocaledonicus* predominant on soils superficially indurated, *Lepidosperma perteres*, abundant in hemisciaphilous situations, and a fern, *Pteridium esculentum*. Other Cyperaceae occur sporadically, *Tetraria arundinacea, T. breviseta* and *T. raynaliana*, the latter sometimes developing significantly near boulders resulting from rockslides and creating micro-settlement conditions similar to those found on eroded Ferralsols.

The shrub layer is more or less open, sometimes continuous, but most often consisting of isolated shrubs. It is generally dominated by *Codia discolor*, whose presence and abundance are characteristic of the association. Among the most frequent species that find their maximum presence and abundance here are: *Eugenia stricta, Myodocarpus fraxinifolius, Guioa glauca, Styphelia pancheri, Hybanthus austrocaledonicus* forma *serratifolia, Casearia silvana, Hibbertia pancheri, Ixora francii, Gmelina neocaledonica, Alstonia coriacea, Pancheria billardierei, P. hirsuta* and *Styphelia cymbulae*. In addition to these characteristic species of the association, there are species common to all ligno-herbaceous maquis in non-hydromorphic environments (*Hibbertia trachyphylla, Grevillea rubiginosa, Myodocarpus involucratus, Codia nitida*) or associated with a large number of groups on ultramafic rocks, but largely contributing to the association's physiognomy (*Pancheria alaternoides, Montrouziera sphaeroidea, Scaevola beckii, Dracophyllum ramosum, Geniostoma densiflorum*).

This assemblage sometimes takes on the appearance of a tall maquis, mainly where humus accumulates at slope breaks, with floristic differences compared to the typical association. The woody layer is then enriched with shrubby species exceeding 3 metres in height, *Hibbertia lucens, Garcinia hennecartii, Alphitonia neocaledonica, Tabernaemontana cerifera, Eugenia veillonii* and in hemisciaphilous species, *Guioa villosa, Archirhodomyrtus turbinata, Litsea triflora, Scaevola balansae*. The herbaceous layer is

also modified. The importance of certain heliophilous species, *Chamaedendron nervosa* and *Schoenus juvenis*, decreases and *Lepidosperma perteres* becomes dominant, while *Schoenus tendo*, a hemisciophilous to sciaphilous species, appears. Because of its slow progressive evolution, hardly perceptible on a human scale, this plant association has often been described as "maquis paraforestier".

In addition, this lower slope association is one of the most exposed to fire. Its evolution towards a tall maquis or even a forest formation, which would not be impossible in the most favourable situations, is constantly challenged by fires. Most often, the vegetation cover regresses and, in extreme cases, almost completely disappears. The result is bare, superficially encrusted areas with deep gullies and only a few clumps of *Schoenus neocaledonicus* and bushes of *Tristaniopsis glauca, Xanthostemon aurantiacus* and *Pancheria billardierei* or *Pancheria alaternoides*. This is a considerably impoverished facies of the association with *Codia discolor* and *Eugenia stricta*. Experiments have shown that only loosening the soil allows the vegetation to return to the original association. This particular facies thus appears to be linked to physical changes in the soil, following the destruction of the plant cover.

The association with *Codia discolor* and *Eugenia stricta* is found in piedmont areas of lower slopes. It develops on deep colluvial Ferralsols, on low to medium slopes generally not exceeding 10%. These are clay-loam Ferralsols, sometimes moderately gravelly and with good water reserves. Their topographic position also ensures a good water supply. Their chemical composition (Table 1) indicates a less unbalanced Ca/Mg ratio than the eroded Ferralsols and more moderate soil poverty (especially true for the humus-rich soils). However, a slight excess of Mg over Ca is often observed. The Ni level is moderately high, and the Mn, Co and Cr levels are sometimes excessive.

Group IX – Association with *Homalium kanaliense* and *Tetraria comosa* (Figure 4(e), Supplemental material: Table S3)

It is a sparse ligno-herbaceous maquis that can be considered as semi-wet maquis. Most often, the Cyperaceae layer is discontinuous and leaves patches of gravelly or indurated soil. This layer includes two hygrophilous Cyperaceae fairly characteristic of the association: *Tetraria stagnalis* and *T. comosa*. They are associated with Cyperaceae of broad ecological distribution, *Tetraria breviseta, Lepidosperma perteres* and *Chamaedendron nervosa*, and with *Anthelepis guillauminii* and *Schoenus brevifolius*, which are very characteristic of wetlands.

The shrub layer is generally sparse, with a cover of around 50%. It reaches an average height of 1.50 m and is often dominated by isolated individuals of *Grevillea gillivrayi* whose tops rise to several metres in height. Among the most characteristic shrubby species of the assemblage are *Homalium kanaliense* and *Stenocarpus umbelliferus* var. *umbelliferus*. They are associated with hygrophilous species whose presence and abundance are maximum here: *Grevillea gillivrayi* and *Xanthostemon aurantiacus*. To these different species of humid environments are constantly attached a small number of common species of ligno-herbaceous maquis on peridotites: *Cloezia artensis, Hibbertia pulchella, Phyllanthus aeneus, Pancheria alaternoides* and *Dracophyllum ramosum*. The latter's abundance is sometimes such that its duster-like foliage and naked stems give the assemblage a distinctive appearance.

This association has a very homogeneous floristic composition; it appears relatively specialised and shows no sign of any evolution towards a higher and denser stage. The hydromorphy of the soil probably plays a significant role in the stability of this association.

The association with *Homalium kanaliense* and *Tetraria comosa* is located in the semi-wet zones formed by the lower parts of the low-slope glacis, between the association with *Codia discolor* and *Eugenia stricta* and the association that occupies the swampy area of the Plaine des Lacs. It develops on hydromorphic colluvial Ferralsols with temporary waterlogging. These soils have uneven textures but are rich in gravel. In the profile, we note the frequent presence of indurated Ferralsol beds and the constant presence of Mn concretions. The levels of major elements are low, except for Mg (Table 1). Without being very abundant, Mg dominates over Ca. Levels of Ni, Co and Mn are moderately high; Cr levels are very variable but can reach high levels. The most important distinctive feature of these soils is undoubtedly their high degree of hydromorphy.

Group VII – Association with *Pancheria communis* and *Cloezia buxifolia* (Supplemental material: Table S4)

This is a generally low (about 1.50 m) and very homogeneous assemblage. The herbaceous layer is based on Cyperaceae and Xyridaceae that are hygrophilous or even hydrophilous. Among the species that make the physiognomy of the association are Cyperaceae with cylindrical leaves: *Schoenus brevifolius, Chorizandra cymbaria, Anthelepis guillauminii* and *Lepidosperma perteres*, ubiquitous species of ultramafic rocks, here especially abundant, and other flat-leaved Cyperaceae: *Chamaedendron xyridioides, Schoenus rivularis*, and one Xyridaceae: *Xyris neocaledonica*. The dominance of one or other of these components contributes to the different aspects of the assemblage without any apparent link to edaphic variation. The herbaceous layer, which often exceeds 1 m in height, and whose flowering stems reach 2 m and more for certain Cyperaceae (*Gahnia, Tetraria* et *Chamaedendron*), dominates the sparse constituents of the shrub layer. The most common species in the

shrub layer is a sparsely branched Cunoniaceae, *Pancheria communis*. A shrubby Myrtaceae, also characteristic of the association, *Cloezia buxifolia*, is found sporadically. Finally, we regularly observed some species widely distributed on ultramafic substrates: *Scaevola beckii, Eriaxis rigida, Sannantha leratii, Tetraria brevista, Machaerina deplanchei, Drosera neocaledonica* and *Gleichenia dicarpa*.

This association occupies the low, swampy plains of the central area of the Plaine des lacs. It develops on alluvial and colluvial Ferralsols that are hydromorphic, more or less peaty, sometimes indurated at depth or, more rarely, at the surface. These are soils that are permanently waterlogged and temporarily flooded during the rainiest periods, very poor in all the major elements (Table 1) except for Mg, which can be found in slight excess, and with moderate levels of Ni, Co, Mn and Cr.

This association is a highly specialised assemblage very dependent on the hydromorphy of the soil. Only a decrease in the level of hydromorphy is likely to lead to a change in the plant cover. On the banks of watercourses, the association with *Pancheria communis* and *Cloezia buxifolia* differentiates into a particular assemblage that can be considered as a sub-association: the sub-association with *Melaleuca gnidioides* and *Dracophyllum cosmelioides*.

There are many variants in terms of physiognomy. The herbaceous layer can be a very dense mat with *Chamaedendron xyridoides* or, on the contrary, a sparse mat where several Cyperaceae live side by side: *Anthelepis guillauminii, Chamaedendron xyridioides, Lepidosperma perteres, Tetraria breviseta*, and *T. stagnalis*. The shrub layer can vary in height and density. It is often between 50 cm and 2 m high and not very dense (50% cover). It includes a large number of characteristic riparian species: *Melaleuca gnidioides, M. brongniartii, Dracophyllum cosmelioides, Myodocarpus tourreteorum, Styphelia longistylis, Scagea oligostemon* and *Xanthostemon myrtifolium*, with various species from swampy areas: *Xyris pancheri, Cloezia buxifolia, Pancheria communis*, or from semi-wet zones: *Grevillea gillivrayi, Homalium kanaliense, Stenocarpus umbelliferus* var. *umbelliferus* and *Xanthostemon aurantiacus*. On the fringes of this sub-association, near the watercourse, are large stands of two rare Gymnosperms: *Retrophyllum minus* and *Dacrydium guillauminii*.

Group III – Association with *Tarenna hexamera* and *Gardenia aubryi* (Figure 4(f), Supplemental material: Table S5)

It is a bushy maquis. From a physiognomic point of view, apart from the virtual absence of a herbaceous layer, it displays multiple variations corresponding to various stages from pioneer maquis, through thickets of varying height and density, to tall maquis. However, the most frequent type of vegetation, and therefore the most representative, is an open vegetation made of isolated groves.

The herbaceous layer is minimal, generally not exceeding 5% cover. A single species, *Gahnia sieberiana*, although not very abundant, is regularly found. Very sporadically, it occurs with *Tetraria arundinacea*, characteristic of non-ultramafic rocks, *T. comosa* and *Gahnia novocaledonensis*, species with a hygrophilous tendency, and *T. raynaliana*, a rupicolous species. The low cover of the herbaceous layer leaves the soil largely bare; but at the base of the bushes, where organic matter accumulates, a few ferns can occur (*Stromatopteris monoliformis, Schizaea dichotoma, Adiantum fournieri, Lindsaea nervosa*) as well as terrestrial fruticose lichens (*Pulchrocladia retipora* and *Cladonia* cf. *rangiferina*).

This association is relatively rich floristically, with a total of 90 species. The woody population generally comprises two layers: a high layer, which can reach 5 to 6 m, consisting of small trees (*Gymnostoma deplancheanum, Dacrydium araucarioides*), and a low shrub layer, from 30 cm to 1.50 m. The latter includes, in addition to individuals of the two species mentioned above, a range of species characteristic of the association: *Tarenna hexamera, Gardenia aubryi, Stenocarpus comptonii, Tristaniopsis guillainii, Styphelia veillonii, Pycnandra lissophylla* and *Eugenia veillonii*, associated with low altitude gravelly or indurated Ferrasols, and other species occurring on the same type of soil at various altitudes: *Dacrydium araucarioides, Gymnostoma deplancheanum, Pancheria confusa, Myrtopsis sellingii, Myrsine asymmetrica, Dracophyllum involucratum, Pleioluma baueri* and *Polyscias pancheri*. It also includes a large number of less specialised species widely distributed on ultramafic substrates: *Dracophyllum ramosum, Solmsia calophylla, Scaevola beckii, Styphelia cymbulae, Guioa glauca, Stenocarpus umbelliferus* var. *billardieri, Uromyrtus emarginatus, Tristaniopsis calobuxus* . . .

This association is sometimes dominated by dead trees of *Arillastrum gummiferum* ("chêne gomme"), indicating the existence of a forest before the establishment of the maquis. Nowadays, this type of forest is only weakly represented, and young *Arillastrum* are not very common in the current maquis. Therefore, the association with *Tarenna hexamera* and *Gardenia aubryi* does not seem to be evolving into an *Arillastrum* forest. In many cases, it is clear that we are witnessing an evolution towards a slowly changing tall maquis dominated by *Gymnostoma deplancheanum*.

The floristic composition of some of the records indicates a *Callitris pancheri* subgroup. However, the small size of the known populations makes it difficult to characterise their phytosociological status. The flora of the *Callitris pancheri* assemblages includes, in

addition to the usual number of species associated with indurated or gravelly Ferralsols: *Dacrydium araucarioides, Gymnostoma deplancheanum* (scarce), *Lomandra insularis, Gahnia novocaledonensis* and *Dracophyllum involucratum*, several species with variable hygrophilous tendencies: *Melaleuca brongniartii, M. gnidioides, Styphelia longistylis*, and a set of species from colluvial Ferralsols: *Tristaniopsis glauca, Myodocarpus fraxinifolius, Pancheria hirsuta*, and *Chamaedendron nervosa*. Apart from *Callitris pancheri*, only one species appears to be restricted to this particular facies, a Cyperaceae, *Chamaedendron fragilis*.

Callitris pancheri is a gregarious gymnosperm, which is not exclusively associated with indurated soils. In the Madeleine area (Plaine des Lacs), it extends onto colluvial soils scattered with ironcrust; on the Montagne des Sources plateau, at higher altitude, it occupies soils derived from gabbros. Because *Callitris pancheri* is a species with a disjunct and relictual distribution, one could hypothesise that this plant association, impoverished in characteristic species, could have had, as shown by the presence of hygrophilous species, a wider distribution during a more humid period.

The association with *Tarenna hexamera* and *Gardenia aubryi* occupies plateaus at an altitude of about 250 m. It develops on very deep Ferralsols, with an upper horizon of gravel and ironcrust resulting from the dismantling of an ancient Ferricrete. This horizon contains very few fine elements. When the vegetation is sufficiently dense, the entanglement of roots and the accumulation of plant debris lead to the formation of a characteristic spongy horizon on the surface. This soil analysis (Table 1) indicates an acidic pH, a low exchange capacity (due mainly to the organic matter), and high cations desaturation. Calcium is often predominant over Mg in the exchange complex, which is very poor in all elements. Chromium reaches excessive levels, while Ni, Mn and Co levels generally remain relatively low.

Group IV – Association with *Codia albifrons* and *Exocarpos pseudocasuarina* (Supplemental material: Table S5)

This association is physiognomically similar to the association with *Tarenna hexamera* and *Gardenia aubryi*, to which it is floristically related. It is characterised by the presence of species associated with gravelly or indurated Ferralsols: *Gymnostoma deplancheanum* (less abundant here, however), *Dacrydium araucarioides* (more abundant than at lower altitudes), *Myrtopsis sellingii, Myrsine asymmetrica, Gahnia novocaledonensis, Pleioluma baueri, Lomandra insularis*, and by the presence of several widely distributed species on ultramafic substrates: *Montrouziera sphaeroidea, Dracophyllum ramosum, Eriaxis rigida, Uromyrtus emarginatus, Solmsia calophylla* . . . This association is nevertheless perfectly distinguishable by the presence of orophilous species, among which are the following species, characteristic of the association: *Codia albifrons, Styphelia macrocarpa, Exocarpos pseudocasuarina*, and several orophilous species with a wider ecological distribution: *Baloghia buchholzii, Metrosideros engleriana, Myodocarpus crassifolius, Earina deplanchei, Neoschmidia pallida*, and *Montrouziera verticillata*. In protected areas, this association is replaced by a dense thicket or even a forest dominated by *Agathis ovata*, which could be the corresponding forest association.

The association with *Codia albifrons* and *Exocarpos pseudocasuarina* is located on plateaus above 600 to 700 m in altitude, on gravelly or indurated Ferralsols. It occupies only small areas. We observed it on the Montagne des Sources and the Dzumac. The nature of the soil is identical to that of the association with *Tarenna hexamera* and *Gardenia aubryi*. From a chemical point of view (Table 1), this soil shows few differences from that of the previous association, except for a higher desaturation rate.

Group I – Association with *Metrosideros tetrasticha* and *Quintinia oreophila* (Figure 4(a) Supplemental material: Table S6)

It is a ligno-herbaceous assemblage with a dominant bushy shrub layer. The umbellate habit of several shrub layer species is characteristic of this association, which Virot (1956) described as "orophilous maquis of the summits with umbelliform nano- and micro-phanerophytes". The herbaceous layer is usually discontinuous. It includes a few Cyperaceae that are widespread on ultramafic substrates: *Chamaedendron nervosa, Schoenus neocaledonicus*, a rupicolous Cyperaceae: *Schoenus juvenis*, a Cyperaceae with a hygrophilic tendency: *Tetraria comosa*, several distinctly hygrophilic species: *Chamaedendron xyrioides, Tetraria stagnalis* (Cyperaceae), *Xyris neocaledonica* (Xyridaceae), and several orophilous species that are characteristic of the association: *Earina deplanchei, Megastylis montana* (Orchidaceae), *Greslania circinata* (Poaceae Bambusoideae), and *Xeronema moorei* (Xeronemataceae). In places, ferns (*Pteridium esculentum, Dicranopteris linearis, Gleichenia dicarpa*) and Lycophytes are abundant. Their frequent presence at the edge of the forest indicates a relatively recent regression of the latter.

The height of the shrub layer varies from 50 cm on exposed ridges to 2.5 m in areas sheltered from the wind. Its cover is very variable. It is composed of branchy shrubs with leathery or hairy leaves, often small and overlapping. Its floristic composition is characterised by the predominance of orophilous species, several of which are strictly restricted to this assemblage. There are several Cunoniaceae: *Cunonia bullata,*

C. rotundifolia, Pancheria engleriana, P. multijuga, P. robusta, some Myrtaceae: *Metrosideros humboldtiana, M. tetrasticha*, gymnosperms: *Podocarpus gnidioides, Libocedrus chevalieri*, and several other species belonging to various families: *Argophylum ellipticum* (Argophyllaceae), *Geniostoma imbricatum* (Loganiaceae), *Dracophyllum alticola* (Ericaceae), *Dubouzetia guillauminii* (Elaeocarpaceae), and *Quintinia oreophila* (Paracryphiaceae). This association, which includes a large number of characteristic species, appears to be highly specialised. Besides the orophilous, the usual ubiquitous species of ultramafic substrates (*Sannantha leratii, Scaevola beckii, Chamaedendron nervosa, Dracophyllum ramosum*, etc.) have a secondary role, as do the rupiculous species: *Normandia neocaledonica, Schoenus juvenis*, and *Myrtastrum rufopunctatum*. Here, however, they find favourable edaphic conditions for their establishment.

On ridges and steep slopes, the very rocky substratum favours the development of the shrub layer. In contrast, on flat areas, with deeper but poorly drained soil, the herbaceous layer, mainly made up of hygrophilous species (*Chamaedendron xyrioides* dominating), becomes more prevalent to the detriment of the shrub layer. The montane maquis then takes on the appearance of a montane wet meadow. This association can be locally dominated by a loose tree layer of *Araucaria humboldtensis*. In some sheltered places but never on exposed ridges, the maquis gradually changes to a low forest. The low forest still includes many maquis species, reaching 6–10 m in height, while two more characteristic forest gymnosperms appear: the abundant *Callitris neocaledonica* and *Acmopyle pancheri*.

The association with *Metrosideros tetrasticha* and *Quintinia oreophila* was studied on the Humboldt Massif, where it is found above 1200 m in altitude. This montane association is found under similar conditions on the second summit of the Southern Massif: the Kouakoué Massif. It occupies areas subject to contrasting climatic conditions, often swept by clouds, sometimes above the cloud cover and subject to high insolation. During the cool season, relatively low temperatures, with minima close to 0°C, were recorded at these altitudes.

This association develops on Leptosols often scattered with boulders or on deeper Ferralsols with indurated levels in the profile. From a chemical point of view (Table 1), these soils are moderately to highly desaturated, lacking the main major elements and moderately rich in Ni, Mn and Cr.

Nine different plant associations were described in the Southern Massif. Their distribution according to topology, altitude and soil type was represented on three schematic toposequences: the Plaine des Lacs toposequence (Figure 5), the Humboldt toposequence (Figure 6) and the Montagne des Sources toposequence (Figure 7). The detailed studies have focused on only a few well-defined zones. Additional studies may reveal the existence of other plant associations, particularly in the Tontouta and Dumbéa basins and in the Thio region.

Plant associations of the Boulinda Massif

Group I – Association with *Atractocarpus deplanchei* and *Grevillea meisneri* (Figure 8(d), Supplemental material: Table S7)

It is a very sclerophyllous shrubby maquis. The irregular and discontinuous herbaceous layer leaves the soil largely exposed. It is composed of magnesicolous Cyperaceae characteristic of assemblages on magnesic soils: low Cyperaceae, *Fimbristylis neocaledonica, F. ovata, Scleria brownii* and scattered tufts of a taller Cyperaceae, *Gahnia aspera*.

The shrub layer, 50 cm to 3 m high, is generally sparse but can also take the form of a dense thicket or a low forest, 2 to over 6 m high. The flora includes a very large number of species characteristic of magnesic soils, which are often at their most abundant levels here: *Grevillea meisneri, Atractocarpus deplanchei, Bocquillonia* sp., *Eugenia gacognei, Erythroxylum novocaledonicum, Hybanthus caledonicus, Storckiella pancheri* subsp. *pancheri, Pittosporum poumense, Alstonia deplanchei, Austrobuxus carunculatus, Gymnostoma chamaecyparis, Tarenna microcarpa, Phyllanthus montrouzieri, Cloezia artensis, Polyscias sp., Stenocarpus milnei, Denhamia fournieri* . . . There are also some ubiquitous thermophilous species of low altitude shrub assemblages: *Alphitonia neocaledonica, Acacia spirorbis, Dodonaea viscosa, Homalium deplanchei, Ixora collina, Styphelia cymbulae*. Serpentinophyte ecotypes were identified among these species.

The dense stands of *Gymnostoma chamaecyparis*, a gregarious Casuarinaceae with a umbelliform top, exclusive of magnesic soils, constitute a particular facies of this assemblage classified as "maquis paraforestier" (Jaffré 1974; Jaffré and Latham 1974) because of the absence of progressive evolution perceptible on a human scale. Their flora is not very different from that of the typical association. The association with *Atractocarpus deplanchei* and *Grevillea meisneri* thus appears relatively stable and in balance with the environmental conditions. It is also not very prone to fire due to its sparse herbaceous layer that does not facilitate its progression. Locally, closer to talwegs, where conditions are more favourable in terms of the water supply to the plants, the vegetation becomes higher and changes to a formation that could be described as a dry forest, but in which there are still many maquis species reaching their maximum development.

The association is found on serpentinite slopes at the base of the massif, below 500 m in altitude. It occurs on Magnesic Cambisols formed from

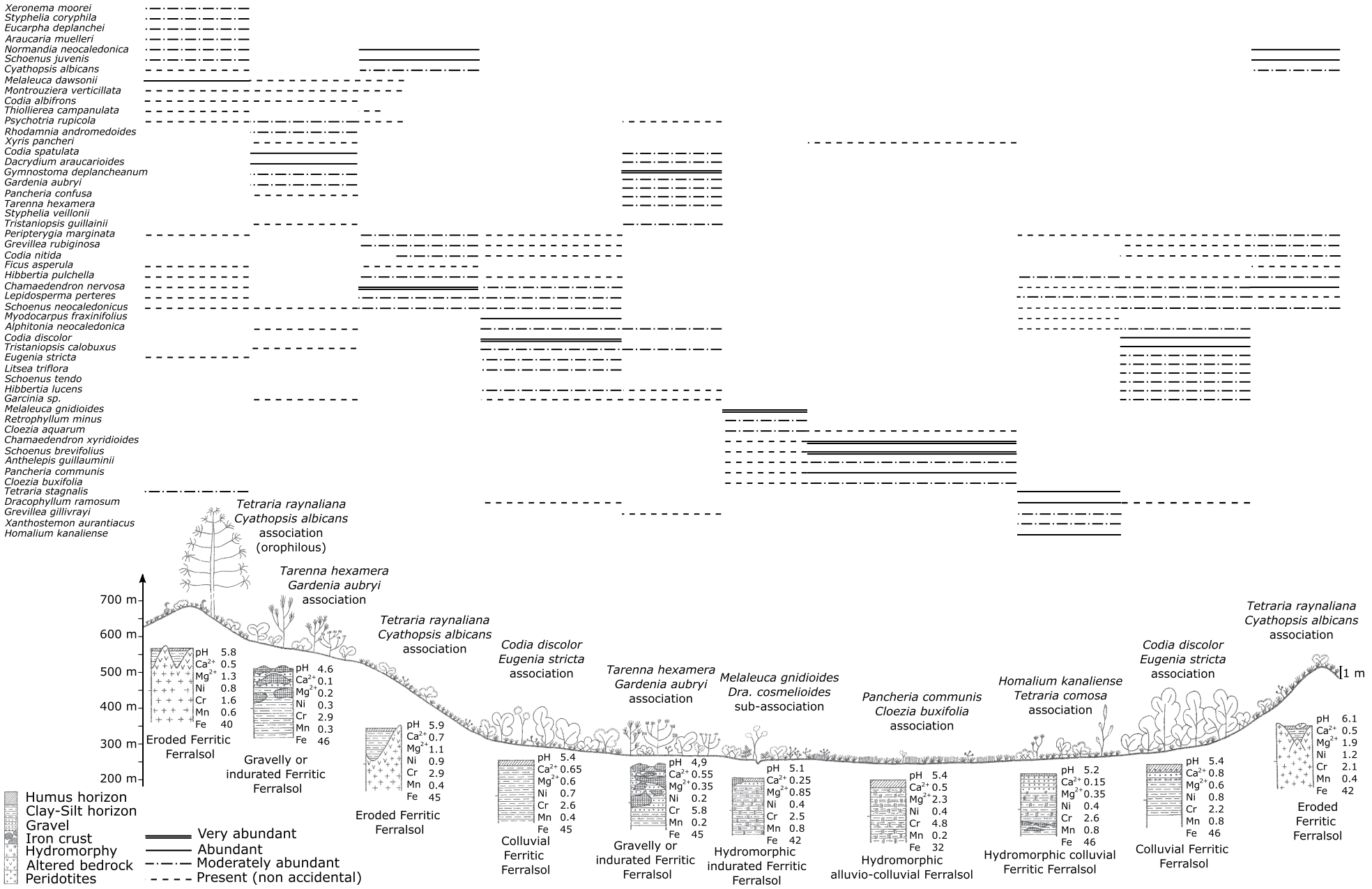

Figure 5. Toposequence of the Plaine des Lacs: distribution of selected species, vegetation profile, soil profiles and soil chemical characteristics. Exchangeable cation concentrations in me/100 g are given for Ca^{2+} and Mg^{2+}. The total levels of Cr, Fe, Mn and Ni are in percent. *Dra. cosmelioides* = *Dracophyllum cosmelioides*.

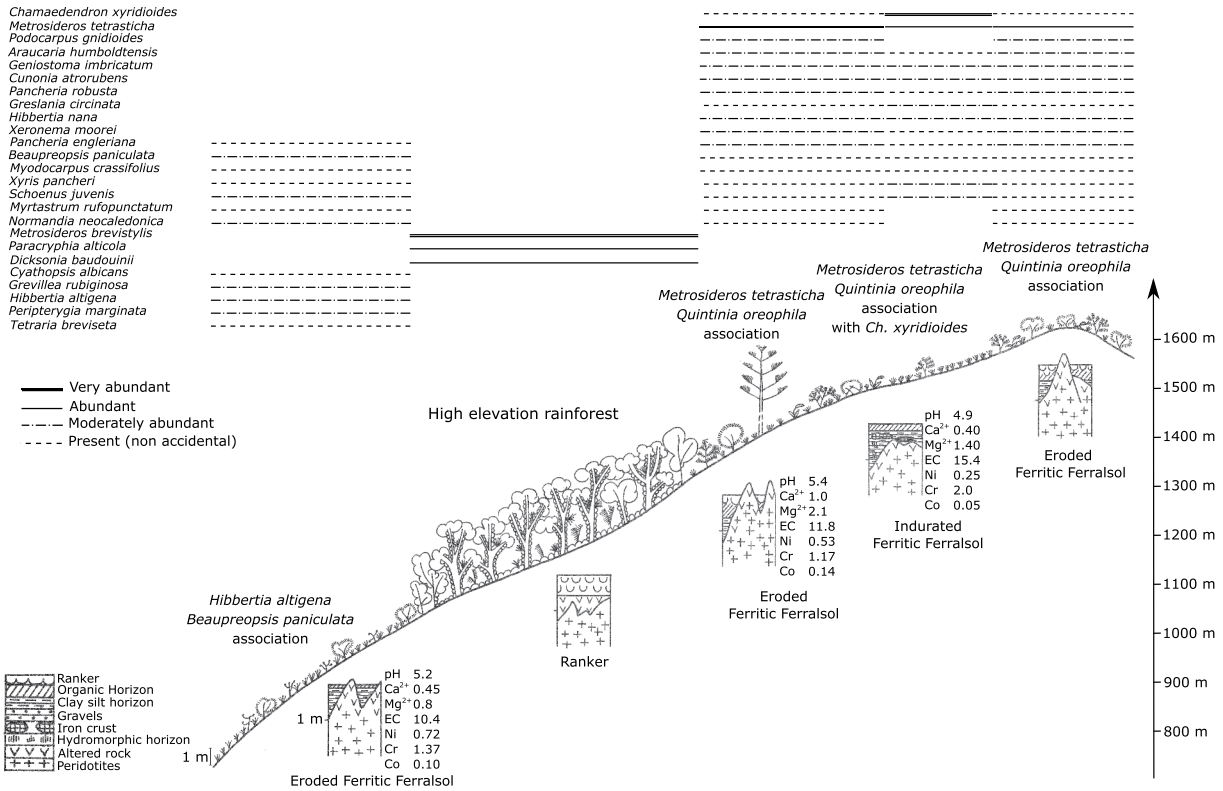

Figure 6. Toposequence of Mount Humboldt: distribution of selected species, vegetation profile, soil profiles and soil chemical characteristics. The concentrations of total exchangeable cations (EC) and for Ca^{2+} and Mg^{2+} are given in me/100 g. Total Cr, Co and Ni levels are in percent. *Ch. xyridioides* = *Chamaedendron xyridioides*.

serpentinites and serpentinised peridotites. These are eroded soils, sometimes close to Magnesic Leptosols, and are shallow, containing numerous pebbles and blocks of serpentinites more or less weathered in the profile. These soils have a reasonably large water reserve (moisture content at pF3 around 50%), but the amount of water retained at the wilting point is also high (moisture content at pF4.2 of around 40%), which limits the amount of water readily available to plants (Jaffré and Latham 1974). The results of the chemical analysis (Table 1) show a high exchange capacity (>30 me/100 g), almost entirely saturated by Mg, very low levels of N, P, K, Ca, low to medium levels of Ni, Co, Cr and Mn.

Group III – Association with *Maxwellia lepidota* and *Stenocarpus trinervis* (Figure 8(c), Supplemental material: Table S8)

It is a dense shrubby maquis ressembling a thicket that sometimes (slope break, areas with more abundant scree) becomes a tall maquis of 6 to 8 m high. The discontinuous herbaceous layer, arranged in patches, has a very variable cover. It is mainly formed of Cyperaceae with broad ecological requirement: *Lepidosperma perteres, Machaerina deplanchei, Tetraria arundinacea*. Some magnesicolous Cyperaceae, *Fimbristylis neocaledonica* and *Gahnia aspera*, appear where erosion has removed colluvium from Ferralsols. Where the vegetation becomes taller, an endemic Poaceae, *Setaria jaffrei*, is found under light shade, always growing in such conditions and restricted to the Northwest region of the Grande Terre.

The shrub layer is 1 to 4 m high and does not show any clear stratification. The flora includes, on the one hand, species most often associated with Ferralsols: *Tristaniopsis calobuxus, Grevillea exul, Didymochiton rufescens, Acridocarpus austrocaledonicus, Peripterygia marginata*, and, on the other hand, magnesicolous species: *Gymnostoma chamaecyparis, Tarenna microcarpa, Stenocarpus milnei, Cleistanthus stipitatus, Alstonia deplanchei, Deplanchea sessilifolia*, the latter acting as a pioneer species in forest formations. A few species with broad ecological distribution are also present: *Acacia spirorbis, Hibbertia pancheri, Dodonaea viscosa, Scaevola montana, Styphelia cymbulae*.

This association is relatively heterogeneous, and the most characteristic species are difficult to identify. We note the following: *Maxwellia lepidota, Stenocarpus trinervis, Podonephelium plicatum, Oxalis novaecaledoniae* and *Deplanchea sessilifolia*, which find their maximum presence and abundance in this association. Near talwegs, where the slopes are covered with scree, the water conditions are more favourable, and the vegetation becomes taller. Some of the above-mentioned species reach 8 to 10 m in height

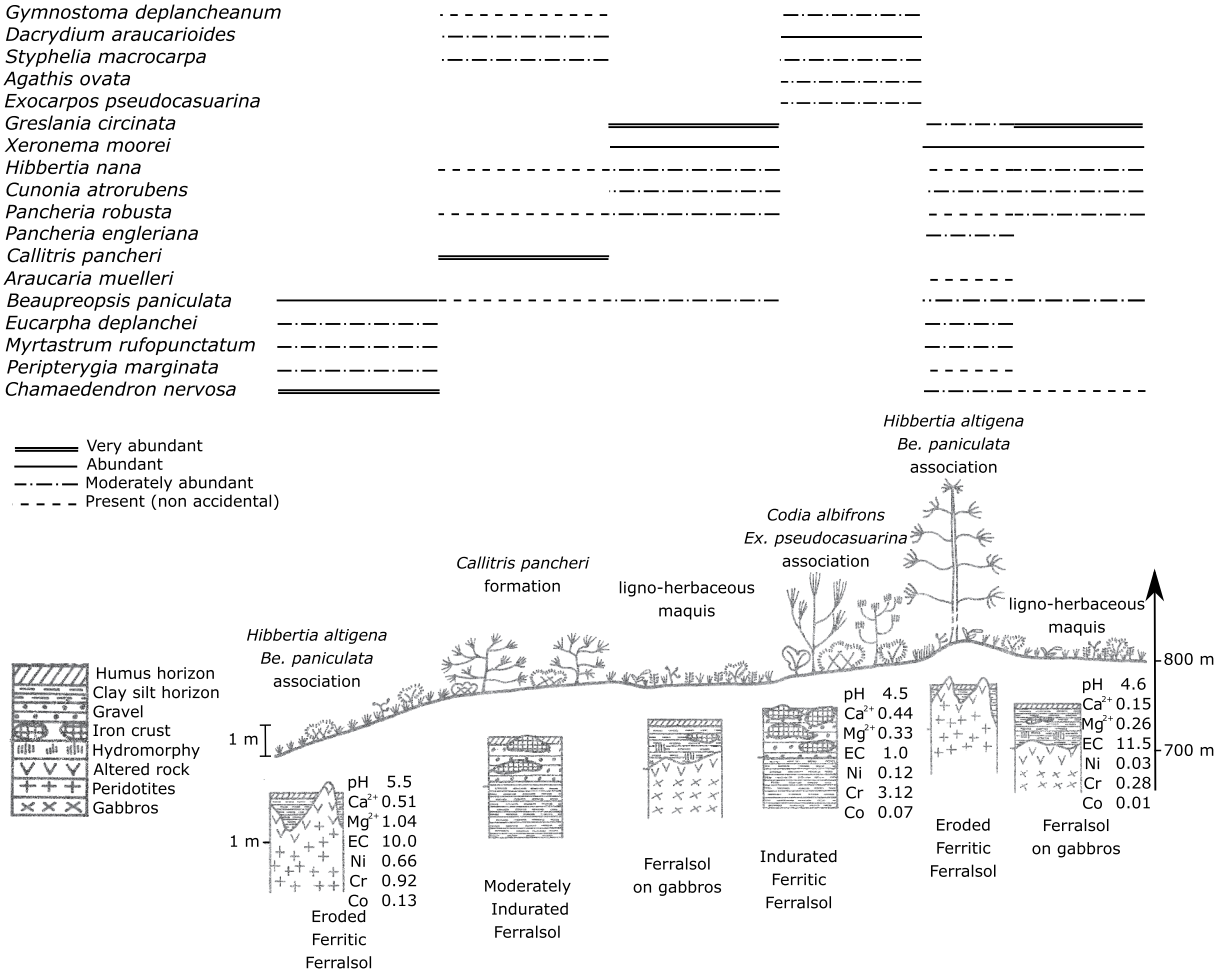

Figure 7. Toposequence of the Montagne des sources plateau: distribution of selected species, vegetation profile, soil profiles and soil chemical characteristics. The concentrations of total exchangeable cations (EC) and for Ca^{2+} and Mg^{2+} are given in me/100 g. The total levels of Cr, Co and Ni are in percent. *Be. paniculata* = *Beaupreopsis paniculata*. *Ex. pseudocasuarina* = *Exocarpos pseudocasuarina*.

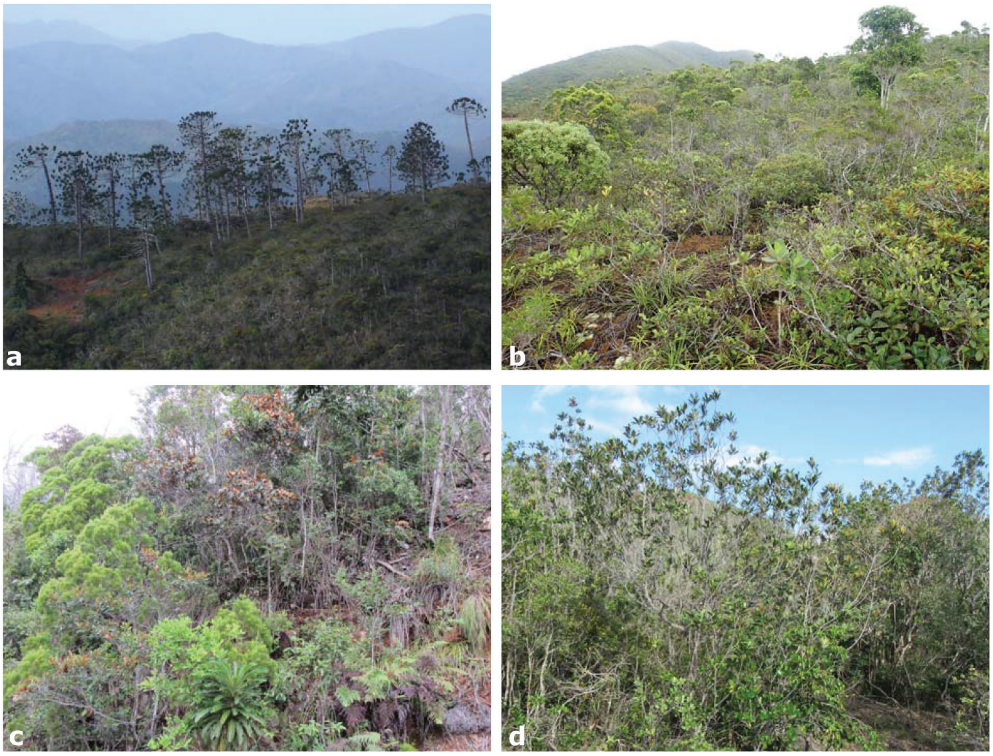

Figure 8. Examples of plant associations of northwest New Caledonia. **A**: Association with *Myrsine asymmetrica* subsp. *parviflora* and *Araucaria rulei*, Mont Paéoua; **B**: Association with *Myodocarpus vieillardii* and *Medicosma verticillata*, Pic Poya; **C**: Association with *Maxwellia lepidota* and *Stenocarpus trinervis*, Pic Poya; **D**: Association with *Atractocarpus deplanchei* and *Grevillea meisneri*, Koniambo. Photo credits: A: Y. Pillon, B-D: D. Fleurot.

(*Tristaniopsis calobuxus, Deplanchea sessilifolia, Gymnostoma chamaecyparis*). Some heliophilous species disappear while pioneer species of forest formation appear (*Garcinia neglecta, Schoenus tendo*). In some cases, we noted the presence of some typical forest species of the genera *Tapeinosperma, Psychotria* and *Myrsine*.

The association with *Maxwellia lepidota* and *Stenocarpus trinervis* is found on steep slopes difficult to access, at altitudes generally below 500 m. It occurs on complex soils resembling low desaturated Ferralsols that have been rejuvenated. They are shallow and covered with serpentinite scree and colluvium, often with gravel from Ferralsols. These soils are very heterogeneous. The study of a typical profile (Jaffré and Latham 1974) indicates that the upper horizon has a low water retention capacity, increasing in the deeper horizon. The pH is weakly acidic at the surface and neutral at depth. Cations are not very abundant and relatively balanced in Ca and Mg in the upper part of the profile; at depth, however, the very abundant Mg is practically the only exchangeable cation. Nickel levels are very high, possibly exceeding 1.5%.

Group II – Association with *Psydrax odorata* and *Gardenia urvillei* (Supplemental material: Table S8).

The vegetation is a regressing maquis, which in some cases is very close to the degraded dry forest on non-ultramafic substrates. *Acacia spirorbis*, the dominant species, creates an original physiognomy with its rounded tops. The herbaceous layer, whose cover does not exceed 10%, comprises magnesicolous Cyperaceae: *Fimbristylis neocaledonica, Scleria brownii, Gahnia aspera*, and some Poaceae with magnesicolous tendencies: *Aristida pilosa, Themeda gigantea, Eragrostis elongata, Sporobolus creber*.

The upper shrub layer is continuous but not very dense, reaching 3 to 4.5 m in height. Like the rest of the shrub population, it is mainly composed of thermophilous species of the lower zones (*Acacia spirorbis, Psydrax odorata*). Here and there, we note the presence of a few *Melaleuca quinquenervia* (niaoulis) and a few *Casuarina collina*, the latter being, here, typically magnesicolous. The dominant shrub layer (50 cm to 2 m high) includes magnesicolous species common to all groups on magnesic soils: *Alstonia deplanchei, Austrobuxus carunculatus, Casearia deplanchei, Cloezia artensis, Rauvolfia semperflorens*, and several species with a poorly defined edaphic status: *Acacia spirorbis, Codia montana, Gardenia urvillei, Acronychia laevis*.

The plant association is relatively constant, but the importance of the role played by the different species varies considerably according to edaphic conditions. When the thickness of the upper horizon of colluvial Ferralsol origin exceeds 15 to 20 cm, *Codia montana* and *Acronychia laevis* become more abundant. However, as soon as this horizon thins out, revealing the serpentinite alluvium, *Acacia spirorbis* becomes dominant. Like the previous assemblage, and no doubt due to the mixed nature of the soil, this association does not include any well-defined characteristic species. We will only note that *Psydrax odorata* and *Gardenia urvillei* are at their most abundant level on an ultramafic substrate.

This association, which has 70 species but is dominated by a gregarious species, *Acacia spirorbis*, can be considered thermophilic and magnesicolous. It occupies flat areas at the base of the massif where it develops on complex soils, comprising a more or less gravelly or sandy-clay upper horizon derived from Ferralsols, resting on magnesic and clayey alluvium derived from serpentinites. These soils are slightly hydromorphic and show traces of Mn segregation in the profile. Chemically (Table 1), they are characterised by a neutral or slightly acidic pH, an excess of Mg in the exchange complex, moderately high Ni levels, high Cr levels (5 to 10%) and very high Mn levels (1 to 3%).

Group VI – Association with *Syzygium kriegeri* (Supplemental material: Table S9).

It is a bushy maquis of 1 to 2 m in height. The herbaceous layer, most often non-existent, does not exceed 10%. It consists of a few scattered clumps of Cyperaceae common on ultramafic rocks, *Tetraria comosa, Lepidosperma perteres, Chamaedendron nervosa*.

The very discontinuous shrub layer is formed by isolated bushes at the foot of which poorly decomposed organic matter accumulates. In this layer, a Myrtaceae, *Tristaniopsis guillainii*, is largely dominant. The relatively poor flora does not include species that are specific to the association. It mainly contains species associated with gravelly or indurated Ferralsols: *Syzygium kriegeri, Gynochthodes sp., Alyxia poyaensis, Pittosporum gracile, P. kaalense, Styphelia macrocarpa, S. veillonii*, with low altitude thermophilic species: *Acacia spirorbis, Acridocarpus austrocaledonicus*, and some ubiquitous species: *Hibbertia pancheri, Codia montana*, and *Wikstroemia indica*. We counted a total of about 50 species. Therefore, the association is characterised more by its structure and the strong dominance of *Tristaniopsis guillainii* than by exclusive species. The association with *Syzygium kriegeri* is a very stable assemblage with no signs of evolution towards denser and higher formations.

The association is found on terraces or plateaus between 200 and 550 m in altitude. It occupies deep Ferralsols with a thick and coarse gravel horizon on the surface, devoid of any structure (about 80% gravel in the first 30 cm). The very low content of fine elements in the upper horizon limits its water reserve. However, in the same way as a mulch, it minimises losses due to evaporation from the underlying horizons, which have a good water retention capacity

(Jaffré and Latham 1974). Chemical analyses (Table 1) indicate a weakly acidic pH, a low exchange capacity, very low exchangeable cation levels, with a slight excess of Mg over Ca. Ni levels are relatively low, and Cr, Co and Mn levels are moderately high.

Group VIII – Association with *Helichrysum neocaledonicum* and *Guioa pectinata* (Supplemental material: Table S9)

The vegetation is a shrubby maquis, slighty bushy (2.5 to 3 m high), generally dense and dominated by *Acacia spirorbis*. The herbaceous layer has a low cover (5 to 15%) and consists of isolated clumps of *Lepidosperma perteres*.

The shrub layer consists of only a few species. In addition to the dominant *Acacia spirorbis*, there are various species already recorded as components of other assemblages: *Codia montana*, which is very abundant here, *Guioa pectinata* and *Acridocarpus austrocaledonicus*, which are most abundant here, *Deplanchea sessilifolia* and *Rauvolfia semperflorens*, both of which are magnesicolous species, and finally *Tristaniopsis guillainii*, which does not play such an important role here as on gravelly Ferralsols. Only *Helichrysum neocaledonicum* is relatively characteristic of the association, which appears to be intermediate between the association with *Psydrax odorata* and *Gardenia aubryi* and the association with *Syzygium kriegeri*.

The presence, in places, of pioneer forest species (*Geissois lanceolata, Garcinia* sp., *Deplanchea sessilifolia, Hibbertia lucens*) indicates the possibility of an evolution towards higher and denser vegetation.

The association is very limited in area and can be found in patches in flat areas at around 200 m altitude. It grows on deep Ferralsols with little gravel on the surface, very rich in silty elements throughout the profile, which are resting on serpentinites and are distinguished from other Ferralsols by their light red colour. From a chemical point of view, these soils are characterised by average acidity (pH 5.4 to 5.7), low levels of exchangeable bases, no excess of Mg over Ca, moderately high levels of Ni and Co, and medium to high levels of Mn and Cr (Mn 0.35% to 1.70%, Cr 1.95% to 6.2%) (Table 1).

Group IV – Association with *Eucarpha deplanchei* and *Argophyllum grunowii* (Supplemental material: Table S10)

It is a low ligno-herbaceous maquis that hardly exceeds 1.50 m in height. The herbaceous layer is very developed, only interrupted by rocky outcrops. It includes a rupicolous Cyperaceae, *Schoenus juvenis*, several Cyperaceae species with a wide ecological distribution, which find their optimal development here: *Chamaedendron nervosa*, the dominant species, *Lepidosperma perteres, Schoenus neocaledonicus*, two Cyperaceae with a hygrophilic tendency, *Tetraria comosa* and *T. breviseta*, and a ubiquitous fern, *Pteridium esculentum*.

The shrub layer is discontinuous, with a cover ranging from 30 to 60%. It is composed of more or less rupicolous species that are strongly associated to and can be considered as characteristic of the association: *Eucarpha deplanchei, Argophyllum grunowii, Hibbertia altigena, Geniostoma* sp., *Normandia neocaledonica, Phyllanthus serpentinus, Codia triverticillata*, to which some species are more loosely associated, but which find their optimal development there: *Peripterygia marginata, Homalium kanaliense* var. *boulindae*, broadly distributed orophilous species: *Metrosideros punctata, Earina deplanchei*, and several ubiquitous species of ultramafic substrates: *Codia montana, Scaevola* sp., *Polyscias* sp., *Tristaniopsis calobuxus, Hibbertia pancheri*, etc.

Floristic variations lead to the distinction of a sub-association characterised by the presence of *Pancheria engleriana, Myrtastrum rufopunctatum, Thiollierea macrophylla* and *Pichonia* sp. These species are associated with very eroded soils that are more or less rocky, by the presence of a few orophilous species with a wide distribution at high altitude: *Earina deplanchei, Cunonia lenormandii, Boronia pancheri*, and by a larger abundance of *Schoenus juvenis*. It is also characterised by the disappearance of certain ubiquitous species such as *Codia montana* and *Lepidosperma perteres*. The orophilous and rocky tendency, already well represented in the most widespread typical association, is emphasised in this sub-association. It is mainly found above 900 m, where it occupies very exposed areas on ridges where the ground is very rocky. In favourable locations, both within the typical association and within the sub-association, it evolves towards a higher and denser formation reflected in the flora by the appearance of *Geissois lanceolata* and *Rhodomyrtus locellata*.

The association with *Eucarpha deplanchei* and *Argophyllum grunowii* occurs on steep slopes and narrow summits, between 500 and 950 m in altitude. It is found on eroded Ferralsols. These are shallow soils, generally, very rocky and with low water reserves due to the small volume of soil available. From a chemical point of view (Table 1), these soils differ from deep Ferralsols by a less acidic pH (around 6), a higher exchange capacity (3 to 6 me/100 g), significantly higher Mg levels (1.90 to 4.40 me/100g) and relatively high Ni and Co levels, which can reach 1% and 0.1% respectively.

Group V – Association with *Myodocarpus vieillardii* and *Medicosma verticillata* (Figure 8(b), Supplemental material: Table S10)

The vegetation is a ligno-herbaceous maquis, changing locally to a higher and denser maquis. The herbaceous layer is well developed, with a cover of around 70%. It consists of Cyperaceae with a wide ecological distribution: *Lepidosperma perteres, Chamaedendron*

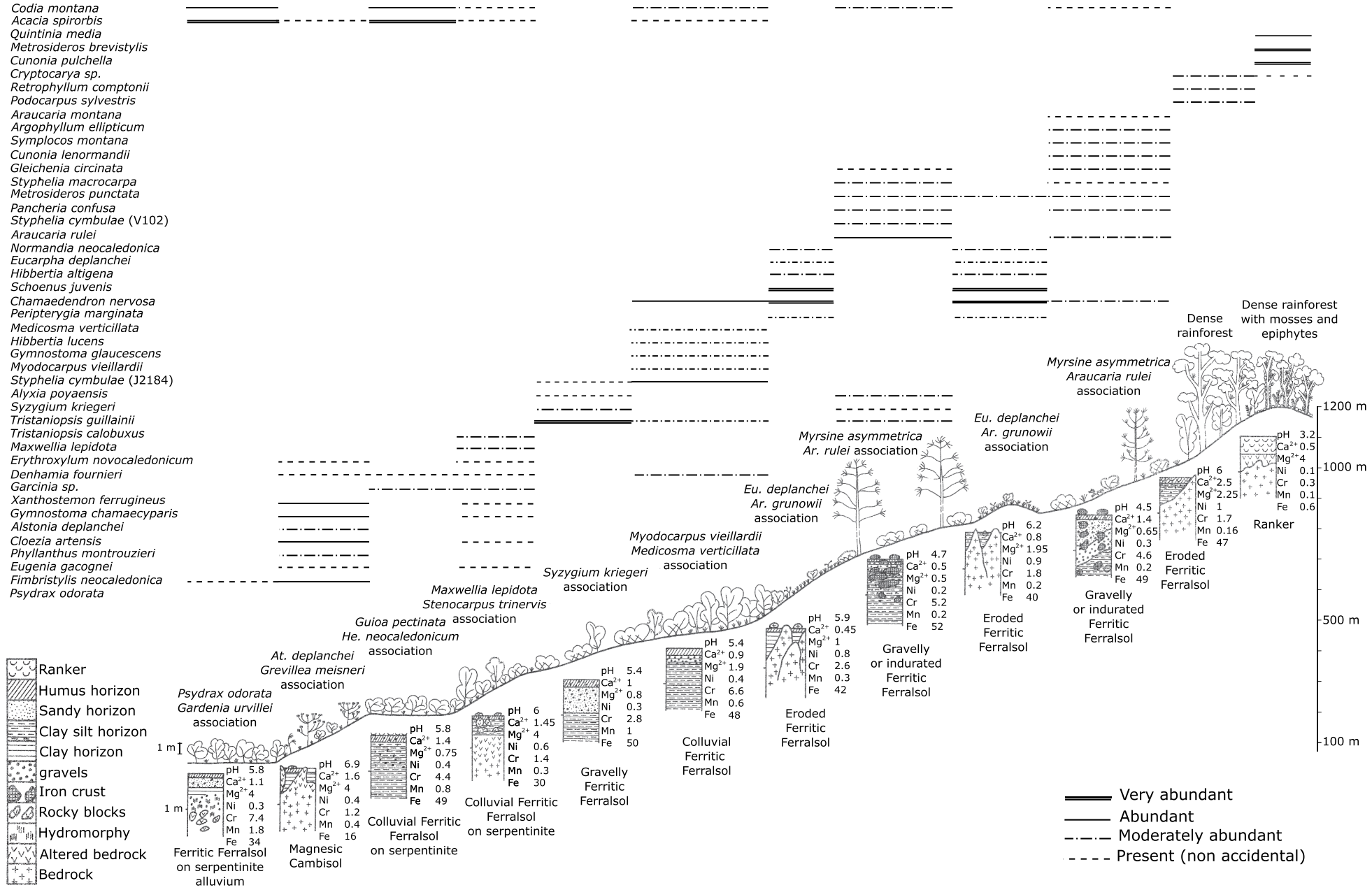

Figure 9. Toposequence of the western slope of the Boulinda Massif: distribution of selected species, vegetation profile, soil profiles and soil chemical characteristics. Exchangeable cation concentrations in me/100 g are given for Ca^{2+} and Mg^{2+}. The total levels of Cr, Fe, Mn and Ni are in percent. *Ar. rulei* = *Araucaria rulei*. *Ar. grunowii* = *Argophyllum grunowii*. *At. deplanchei* = *Atractocarpus deplanchei*. *Eu. deplanchei* = *Eucarpha deplanchei*. *He.* = *Helichrysum neocaledonicum*.

nervosa, Tetraria breviseta and *T. raynaliana*, the latter being relatively characteristic of the association on the Boulinda Massif.

The shrub layer has a variable cover. Its height varies from 1.50 m to 5 m and more. Among the species most closely related to the assemblage are: *Medicosma verticillata, Styphelia cymbulae, Myodocarpus vieillardii* and *Ixora francii*. The ubiquitous thermophilous species predominately associated with low altitudes are well represented: *Codia montana, Acacia spirorbis, Dodonaea viscosa, Montrouziera sphaeroidea*. Several species are linked to gravelly Ferralsols on plateaus: *Tristaniopsis guillainii, Styphelia veillonii, Pancheria billardierei*, and eroded Ferralsols: *Peripterygia marginata, Phyllanthus* sp., *Dracophyllum ramosum, Homalium kanaliense* var. *boulindae, Stenocarpus milnei* and *Notelaea austrocaledonica*. Finally, several pioneer species of forest formations are pretty characteristic of the association: *Garcinia neglecta, Gymnostoma glaucescens*, and *Hedycarya parvifolia*. These species' frequent and relatively constant presence indicates the possibility of a progressive evolution towards a forest. However, this evolution remains very slow.

The association occupies a small area in the piedmont zone, at around 500 m altitude, where it is associated with colluvial Ferralsols with varying degrees of gravel. These are deep soils with a good water capacity, characterised from a chemical point of view by a weakly acidic pH and low levels of

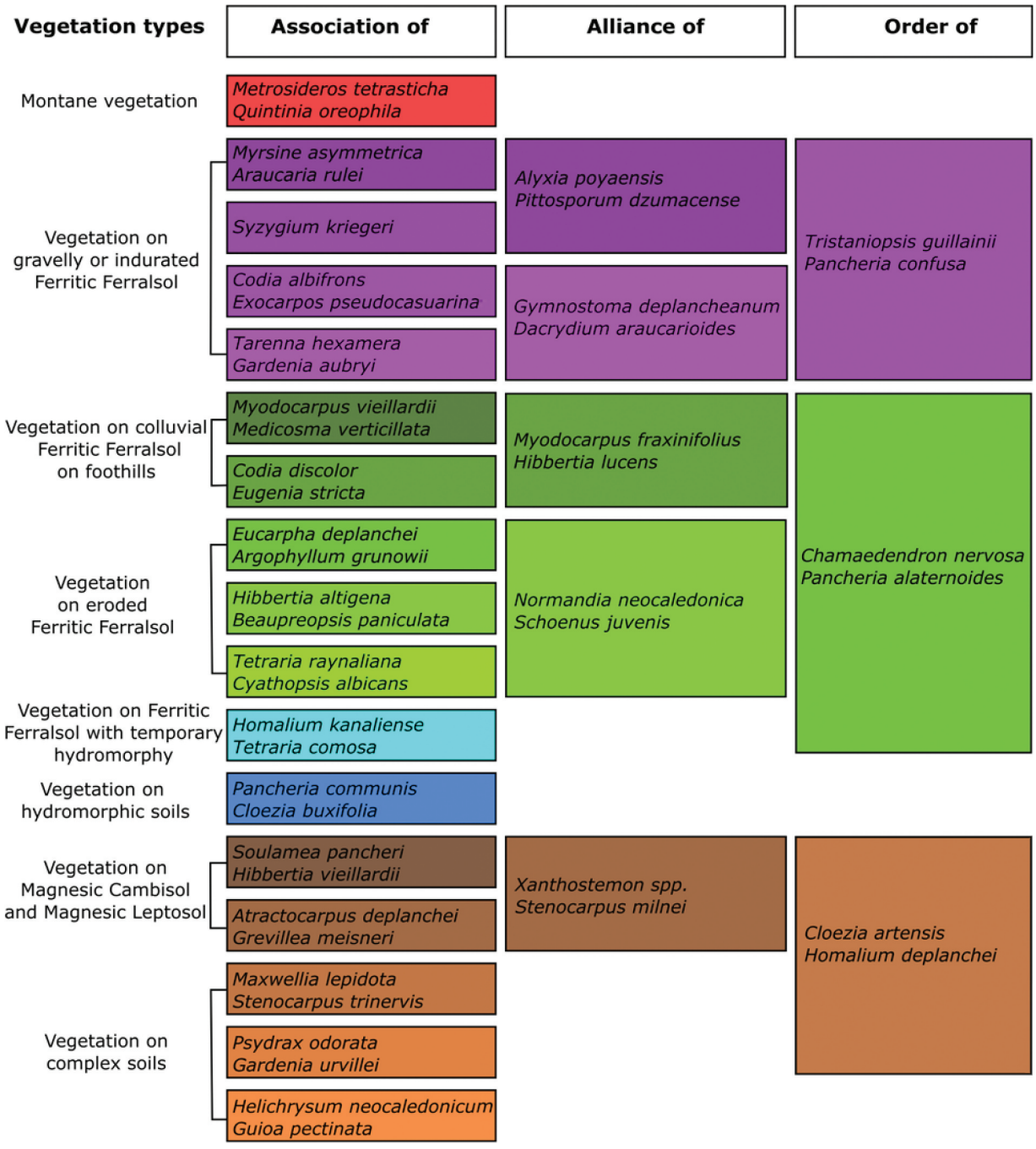

Figure 10. Phytosociological classification of maquis plant groups on ultramafic rocks in New Caledonia.

exchangeable elements, with Mg predominating in the exchange complex. Ni, Cr, Mn and Co levels are moderately high (Table 1).

Groupe VII Association with *Myrsine asymmetrica* subsp. *parviflora* and *Araucaria rulei* (Figure 8(a), Supplemental material: Table S9).

The vegetation is a very open shrubby maquis, bushy or prostrate, often dominated by a few scattered *Araucaria rulei*, the largest of which reach 15 to 20 m. The herbaceous layer is generally not very important (<10% cover). It consists of common species: *Lepidosperma perteres, Chamaedendron nervosa* (Cyperaceae), *Pteridium esculentum* (fern) and species more characteristic of the association: *Gahnia novocaledonensis* (hygrophilous Cyperaceae) and *Earina deplanchei* (orophilous Orchidaceae).

The shrub layer is discontinuous and hardly exceeds 1.50 m in height. Among the most characteristic species are *Myrsine asymmetrica* subsp. *parviflora, Araucaria rulei, Alyxia caletioides, Guioa glauca* var. *vulgaris, Grevillea nepwiensis* and *Pancheria confusa*. Several species common to gravelly Ferralsols are often present: *Tristaniopsis guillainii, Styphelia macrocarpa, S. veillonii, Alyxia poyaensis, Pittosporum dzumacense, Longetia buxoides, Dubouzetia elegans, Styphelia cymbulae*, and species with an orophilous tendency: *Metrosideros punctata, Alyxia sp., Comptonella sessilifolia*.

Floristic variations lead us to distinguish a sub-association. It is linked, on the one hand, to degraded soils that are more or less indurated on the surface and located above 800 m in altitude, and on the other hand, to soils with temporary hydromorphy, indurated at depth, occupying the bottom of small enclosed basins. This sub-association has a well-developed herbaceous layer, consisting of two gregarious ferns, *Dicranopteris linearis* and *Gleichenia dicarpa*. The shrub layer is characterised by the presence of acidophilic orophilous species: *Symplocos montana* var *ultramafica, Argophyllum ellipticum, Myodocarpus crassifolius*, and the abundance of *Sannantha leratii*, an ubiquitous species with a predilection for strongly acidic and periodically flooded soils.

We did not observe any forms of transition from this association to a higher and denser vegetation. However, an arborescent species, *Araucaria rulei*, which is also part of the floristic composition of some of the forest patches it dominates, indicates a possible evolution towards a forest stage. Given the low nutrient content of the soil, this evolution can only be excessively slow.

The association with *Myrsine asymmetrica* subsp. *parviflora* and *Araucaria rulei* is found on plateaus and gentle slopes, not exceeding 15%, between 680 and 1000 m in altitude. It occupies deep Ferralsols with an upper horizon formed of coarse gravels associated with iron crust. This horizon is devoid of any structure and has a low water capacity. Where there is a lot of vegetation, it is covered by a layer of poorly decomposed organic matter, which, together with the porous gravel and the roots, can retain a large quantity of water. In addition, the deep horizons, which are clayey, have a substantial water retention capacity. The chemical analysis of the soil (Table 1) indicates an acidic pH (4.8 on average). Exchangeable elements are very low, Ni levels are low, and Cr levels are high (3–5%).

We identified eight plant associations on the Boulinda Massif. Compared to the Southern Massif, we note the absence of areas with high hydromorphy but the presence of mixed biotopes. The eight associations were represented on a schematic toposequence (Figure 9).

Discussion

Phytosociological classification of maquis plant groups

The floristic and ecological affinities identified between the plant associations of the Southern Massif and those of the Boulinda Massif led us to group certain associations into higher-ranking units and to lay the foundations for a classification of the plant assemblages of ultramafic rocks. We also took into account our observations on the Koniambo (Jaffré 1974) and Tiébaghi massifs.

Based on the predominant influence of certain environmental factors, or their combination, on the differentiation of phytosociological units, we distinguish seven main types of vegetation: the montane vegetation, the vegetation of highly hydromorphic areas, the vegetation on hydromorphic Ferralsols, the vegetation on Magnesic Cambisols and Magnesic Leptosols, the vegetation on eroded Ferralsols, the vegetation on colluvial Ferralsols of piedmont, and the vegetation on gravelly or indurated Ferralsols of the plateaus. We also distinguish the vegetation of complex soils, which includes three less well-differentiated mixed types (Figure 10).

Montane vegetation – It includes a single, highly specialised, clearly orophilous association, which occupies small areas due to the limited extent of the zones on ultramafic rocks above 1200 m: the association with *Metrosideros tetrasticha* and *Quintinia oreophila* found on the Humboldt and Kouakoué massifs.

Vegetation on highly hydromorphic soils – It includes a low altitude association: the association with *Pancheria communis* and *Cloezia buxifolia*, found in the Plaine des Lacs.

Vegetation on soils with temporary hydromorphy – This type of vegetation is only found in the Plaine des Lacs, in the association with *Homalium kanaliense* and *Tetraria comosa*. This assemblage is well-differentiated floristically, but depending on the degree of

hydromorphy of the soil, it more or less resembles the vegetation found on highly hydromorphic soils or the vegetation of piedmonts with sufficient drainage. Geographically, it is located between these assemblages.

Vegetation on Magnesic Cambisols and Magnesic Leptosols – It occurs on serpentinites or serpentinised peridotites in the driest and warmest parts of the massifs, at altitudes of less than 500 m. It is represented in the Southern Massif by the association with *Soulamea pancheri* and *Hibbertia vieillardii* and at the base of the Boulinda Massif by the association with *Atractocarpus deplanchei* and *Grevillea meisneri*. The vegetation of the Magnesic Cambisols and Leptosols of the Koniambo and Tiébaghi massifs also belongs to the association with *Atractocarpus deplanchei* and *Grevillea meisneri* as indicated by the presence of these two species and some others (*Pittosporum poumense, Phyllanthus montrouzieri, Storckiella pancheri* subsp. *pancheri*). The distribution ranges of these taxa do not extend much further south than the Boulinda Massif.

Throughout the territory, the vegetation of the Magnesic Cambisols and Magnesic Leptosols is represented by a single alliance characterised by widely distributed magnesicolous species such as *Xanthostemon* spp., *Stenocarpus milnei, Tarenna microcarpa, Cleistanthus stipitatus, Fimbristylis neocaledonica, Gahnia aspera, Scleria brownii*, and by the remarkable representation of some genera: *Xanthostemon, Alyxia* and *Phyllanthus*.

Vegetation on eroded Ferritic Ferralsols – It includes several associations that are physiognomically very homogeneous. The Southern Massif consists of two associations that differ according to altitude: the association with *Tetraria raynaliana* and *Cyathopsis albicans*, below 500 to 600 m, and the association with *Hibbertia altigena* and *Beaupreopsis paniculata*, between 600 and 1200 m.

In the Boulinda Massif, where eroded Ferralsols are hardly found below 500 m, only one association was found: the association with *Eucarpha deplanchei* and *Argophyllum grunowii*. An association similar to, or even identical to the latter seems to occur on the Koniambo Massif. On the Tiébaghi Massif, which only rises to an altitude of 550 m, the limited space occupied by eroded Ferralsols prevented us from carrying out a sufficient floristic inventory to allow comparisons.

These different associations can be grouped in the same alliance characterised by *Normandia neocaledonica, Schoenus juvenis, Myrtastrum rufopunctatum* and *Ficus asperula*, all of which are species with a rupicolous behaviour.

Vegetation on colluvial Ferritic Ferralsols of piedmont – It is a ligno-herbaceous vegetation well represented only in the Southern Massif, particularly in the Plaine des Lacs area, by the association with *Codia discolor* and *Eugenia stricta*. In the Boulinda Massif, where it is represented by the association with *Myodocarpus vieillardii* and *Medicosma verticillata*, it occupies only small areas. The same applies to the Koniambo and Tiébaghi massifs, where the small size of the piedmonts did not allow to determine the floristic composition of the vegetation.

In the Plaine des Lacs, the association with *Codia discolor* and *Eugenia stricta* does not exclusively occupy ultramafic rocks, it extends to the low areas on gabbros and granodiorites, which are overhung by ultramafic outcrops. The association is then slightly modified due to the increased presence of hygrophilic species such as *Xanthostemon aurantiacus* and the relative abundance of *Rhodamnia andromedoides*.

The two associations described for the Southern Massif and the Boulinda Masif belong to the same alliance. The alliance is characterised by species with flexible requirements, which find their maximum presence and abundance in these conditions (*Myodocarpus fraxinifolius, Ixora collina, Styphelia cymbulae, Alphitonia neocaledonica*) and by the presence of pioneer forest species (*Garcinia* sp., *Hibbertia lucens, Styphelia pancheri*).

The piedmont assemblages show a clear floristic relationship with eroded soils assemblages. Many intermediate formations exist between them, and the distinctions are not always clear. The alliance with *Normandia neocaledonica* and *Schoenus juvenis*, which group associations on eroded Ferralsols, and the alliance with *Myodocarpus fraxinifolius* and *Hibbertia lucens*, which group associations on colluvial Ferralsols of piedmonts, can be included in the same order, characterised by *Chamaedendron nervosa, Pancheria alaternoides, Cloezia artensis* and *Peripterygia marginata*. The association with *Homalium kanaliense* and *Tetraria comosa* also belongs to this order.

Vegetation on gravelly or indurated Ferritic Ferralsols – In each of the massifs studied, this vegetation consists of two associations located according to altitude: in the Southern Massif, the association with *Tarenna hexamera* and *Gardenia aubryi*, below 550 m, and the association with *Codia albifrons* and *Exocarpus pseudocasuarina*, between 600 and 1200 m; in the Boulinda Massif, the association with *Syzygium kriegeri*, below 550 m, and the association with *Myrsine asymmetrica* subsp. *parviflora* and *Araucaria rulei* at higher altitudes.

The two associations of the Southern Massif are part of the same alliance characterised by *Gymnostoma deplancheanum, Dacrydium araucarioides, Myrtopsis sellingii, Dracophyllum involucratum* and *Pleioluma baueri*. The two associations of the Boulinda Massif are part of an alliance characterised by *Alyxia poyaensis* and *Pittosporum dzumacense*. These two alliances are

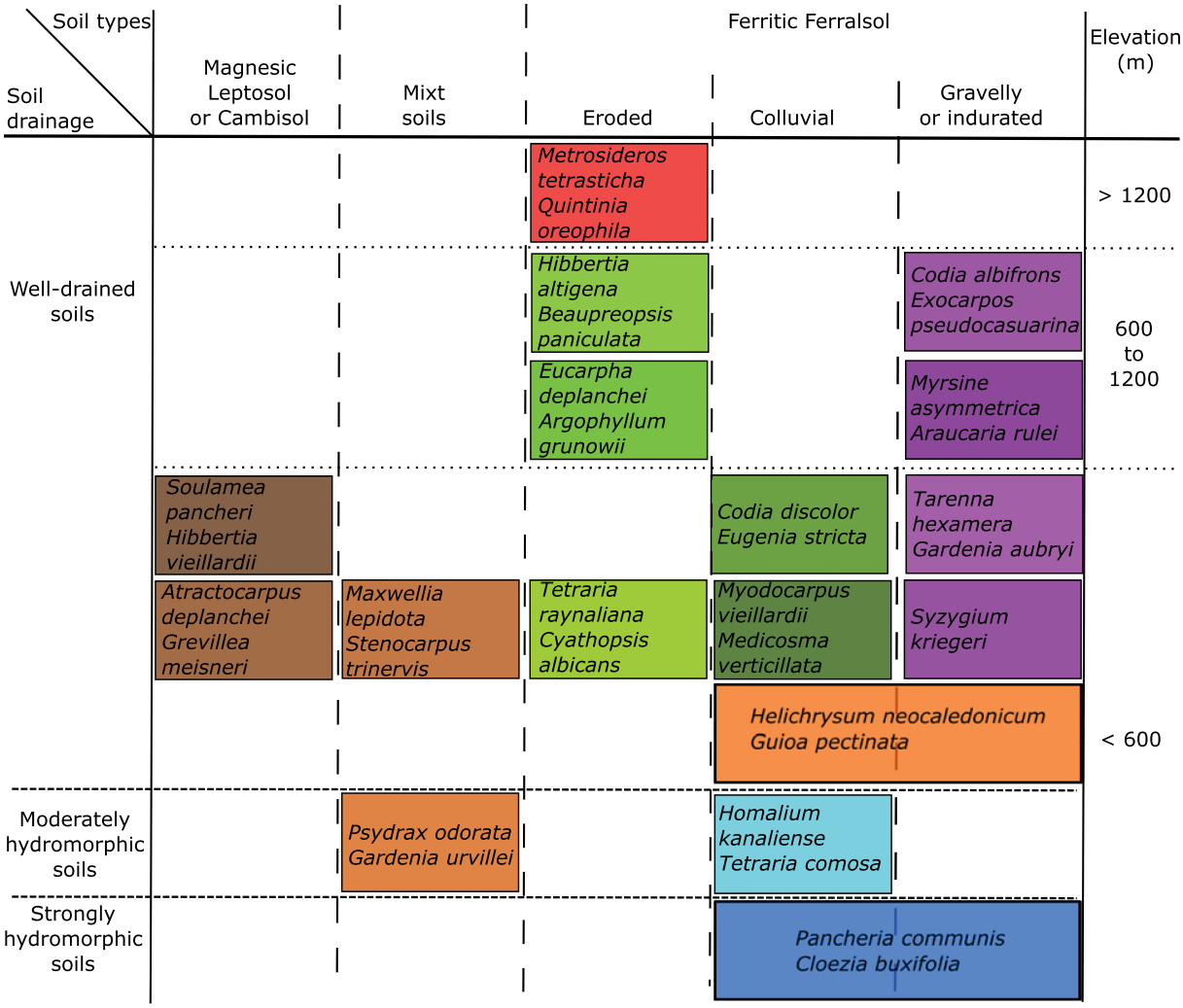

Figure 11. Links between maquis plant associations and the prevailing ecological factors of the environment.

part of an order characterised by *Tristaniopsis guillainii, Pancheria confusa* and *Styphelia veillonii*. The groups on gravelly or indurated Ferralsols of the Koniambo and Tiébaghi massifs belong to the same order.

Vegetation on complex soils – We have grouped three rather poorly differentiated associations under this heading, all three of which are found at low altitudes on the Boulinda Massif. Because of their structure and the presence of certain thermophilic species, the association with *Maxwellia lepidota* and *Stenocarpus trinervis* on steep slopes and the association with *Psydrax odorata* and *Gardenia urvillei*, on flat, more or less hydromorphic areas, are reminiscent of some of the degraded facies of the dry forest. However, considering their floristic compositions, they appear to be similar to the associations on Magnesic Cambisols, which we both include in an order characterised by *Cloezia artensis, Homalium deplanchei* and *Rauvolfia semperflorens*.

The third association on mixed soils (association with *Helichrysum neocaledonicum* and *Guioa pectinata*) of the Boulinda Massif appears to be very impoverished and occupies a small area. We compare it provisionally with the association with *Syzygium kriegeri* or the association with *Psydrax odorata* and *Gardenia urvillei*, with which it seems to have the most affinities.

Conclusions

This study of plant associations in the maquis revealed the distributions of plant communities and the role played by several ecological factors in this distribution: altitude, hydric conditions linked to soil drainage, and the physicochemical properties of the soil. These relationships are shown in Figure 11. Plant mineral nutrition is discussed in Jaffré (202Xb).

From an altitudinal point of view, three levels can be defined:

- from 0 to 600 m, a low and medium altitude zone characterised by more or less thermophilic lowland plant associations;

- from 600 to 1200 m, a medium and high altitude zone characterised by plant associations with orophilous affinities;

- above 1200 m, a montane zone, with a distinctly orophilous plant association.

Depending on the hydric conditions related to soil drainage, we have distinguished:

- Assemblages on well-drained soils. These are the most widespread and include a large number of plant associations with very different ecological requirements;

- Assemblages on soils with moderate or temporary hydromorphy;

- Assemblages on highly hydromorphic soils, well represented in the Southern Massif.

Depending on the physicochemical nature of the soil, we have distinguished:

- Assemblages on Magnesic Cambisols with a high exchange capacity saturated in Mg, including (i) plant associations on Magnesic Cambisols that are relatively poor in Fe; (ii) plant associations on complex magnesic oils that are better supplied with Fe, Cr and sometimes Mn;

- Assemblages on more or less desaturated Ferritic Ferralsols with very low exchange capacity, comprising three sets of plant associations: (i) associations on low to moderately desaturated eroded Ferralsols, all of which have a rupicolous affinity, occupying eroded ridges and slopes; (ii) associations on moderately to highly desaturated gravelly or indurated Ferralsols occupying low slope areas; (iii) associations on colluvial (or alluvial) Ferralsols occupying lower slopes and piedmonts.

Although far from exhaustive, this study shows the variety of plant associations in the maquis, reflecting the diversity of environmental conditions. The ecological sequences occur fairly consistently from one massif to another. Due to its higher rainfall and larger range of altitudes, the Southern Massif is the only region with true orophilous maquis and distinctly hydromorphic assemblages. Still, in the studied area the maquis does not have a wide range of magnesicolous vegetation as observed on the West Coast massifs.

No other region of the world, where ultramafic outcrops have been studied, exhibit such a variety of plant associations. From this point of view, New Caledonia offers undeniable originality that makes it particularly suitable for studying the various effects of ultramafic rocks on vegetation cover.

The floristic richness of the different plant associations, as revealed by our surveys, is very variable. With nearly 100 species, the associations on Magesic Cambisols and Magnesic Leptosols appear relatively rich. In contrast, the association on highly hydromorphic soils, with about 20 species, and the associations on certain Ferralsols, with about 50 species, appear relatively poor.

The specificity of the flora of the different plant associations decreases from magnesicolous associations on soils with a high exchange capacity, saturated in Mg, to associations on Ferritic Ferralsols with a low exchange capacity desaturated in cations. One is rich in species exclusive to substrates derived from ultramafic rocks, while the other is less specialised, apparently more closely related to the flora of groups on non-ultramafic rocks. This observation can be linked to the fact that the relationship between the soil and the parent rock loosens when one moves from Magnesic Cambisols and Magnesic Leptosols to desaturated Ferritic Ferralsols (Jaffré and Latham 1974).

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Disclosure statement

No potential conflict of interest was reported by the author.

References

Benzécri, JP. 1973. L'analyse des données. Dunod (Paris). Vol. 2.

Briane, JP, JJ Lazare, G Roux, C Sastre. 1974. L'analyse factorielle des correspondances et l'arbre de longueur minimum - exemples d'application. Adansonia. 2 (14):111–137.

Briane, JP, JJ Lazare, R Salanon. 1978. L'analyse en données groupées de très grands tableaux de correspondance. Cah Anal Données. 3(2):167–173.

Cordier, B. 1965. L'analyse factorielle des correspondances. *Thèse de 3ème cycle*, Rennes. 66.

Dagnelie, P. 1960. Contribution a l'étude des communautés végétales par l'analyse factorielle. Bull Serv de la Carte Phytogéographique. 5(1&2):7–71 & 93–195.

Gounod, M. 1969. Méthodes d'étude quantitative de la végétation. Masson et Cie., Paris. p. 314.

Guinochet, M. 1973. Phytosociologie. Masson et Cie. (Paris): 227.

IUSS Working Group. 2015. World reference base for soil resources 2015. Rome:FAO.IUSS.

Jaffré, T. 202Xa. Plant formations on ultramafic rocks in New Caledonia. Bot Lett. XXX:XXX–XXX.

Jaffré, T. 202Xb. Plant mineral nutrition on ultramafic rocks of New Caledonia. Bot Lett. XXX:XXX–XXX.

Jaffré, T, M Latham, P Quantin. 1971. Les sols des massifs miniers de Nouvelle Calédonie et leur relation avec la végétation. Rapp. Multigr. ORSTOM (Nouméa): 20.

Jaffré, T. 1974. La végétation et la flore d'un massif de roches ultrabasiques de Nouvelle Calédonie, le Koniambo. Candollea. 29:427–456.

Jaffré, T, M Latham. 1974. Contribution à l'étude des relations sol-végétation sur un massif de roches ultrabasiques de la côte Ouest de la Nouvelle-Calédonie: le Boulinda. Adansonia. 14(3):311–336.

Jaffré, T. 1980. Etude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle-Calédonie. In Travaux et documents de l'ORSTOM. Vol. 124. Paris: ORSTOM.

Lacoste, A, M Roux. 1971. L'analyse multidimentionnelle en physiologie et en écologie. Application à des données de l'étage subalpin des Alpes maritimes. I. L'analyse des données floristiques. Oecologia Plant. 6:353–369.

Lacoste, A, M Roux. 1972. L'analyse multidimentionnelle en physiologie et en écologie. Application à des données de l'étage subalpin des Alpes maritimes. II. L'analyse des données écolo giques et l'analyse globale. Oecologia Plant. 7:125–146.

Latham, M. 1975. Les sols d'un massif de roches ultrabasiques de la Côte ouest de Nouvelle-Calédonie. Le Boulinda Deuxième partie. Les sols à accumulation ferrugineuse relative. Cah ORSTOM série pédol. 13 (2):159–172.

Morat, P, T Jaffré, F Tronchet, J Munzinger, Y Pillon, J-M Veillon, M Chalopin. 2012. The taxonomic reference base florical and characteristics of the native vascular flora of New Caledonia. Adansonia. 34:179–221. doi:10.5252/a2012n2a1.

Munzinger, J, P Morat, T Jaffré, G Gâteblé, Y Pillon, G Rouhan, D Bruy, J-M Veillon, M Chalopin. 2022. FLORICAL: checklist of the vascular indigeneous flora of New Caledonia. Available at: http://publish.plantnet-project.org/project/florical

Roux, G, M Roux. 1967. A propos de quelques méthodes de classification en phytosociologie. Rev Stat Appl. 15 (2):59–72.

Virot, R. 1956. La végétation canaque. Paris: Editions du Muséum.

Appendix

Table 1. Soil chemical composition of the main maquis plant associations on ultramafic rocks.

			Echangeable elements							Total elements									
			CE	Ca	Mg	K	Na	Ni	Cr	P	Ca	Mg	K	Na	Fe	Mn	Ni	Cr	Co
Plant association (soil type)		pH	me/100 g					µg g^{-1}	µg g^{-1}	%									
Association with *Soulamea pancheri* and *Hibbertia vieillardii* (Magnesic Cambisol)	Mean (n = 10)	6.80	23.93	1.84	38.46	0.21	0.32	44.00	0.60	0.014	0.08	14.30	< 0.01	0.04	11.50	0.23	0.39	0.63	0.043
	Minimum and maximum	6.55	10.50	0.40	14.24	0.06	0.26	18.00	0.20	0.010	0.012	3.50	< 0.01	0.01	5.20	0.13	0.29	0.05	0.016
		7.25	29.13	4.34	54.72	0.46	0.50	58.00	1.00	0.019	0.20	16.00	0.018	0.015	24.00	0.50	0.55	1.65	0.10
Association with *Atractocarpus deplanchei* and *Grevillea meisneri* (Magnesic Cambisol)	Mean (n = 10)	6.90	33.60	1.45	32.65	0.21	0.31	66.00	0.22	0.023	0.04	7.94	0.013	0.01	15.30	0.40	0.47	1.27	0.057
	Minimum and maximum	6.40	25.70	0.14	23.00	0.11	0.16	25.00	0	0.014	0.01	2.05	< 0.01	< 0.01	8.60	0.19	0.36	0.50	0.02
		7.50	42.70	4.20	39.50	0.34	0.41	104.00	0.84	0.026	0.09	16.45	0.03	0.02	24.90	0.92	0.56	3.69	0.14
Association with *Psydrax odorata* and *Gardenia urvillei* (mixed soil consisting of Ferritic Ferralsol and magnesic alluvium)	Mean (n = 6)	6.02	13.37	1.81	8.30	0.20	0.43	0.36	8.06	0.020	0.02	1.20	0.015	0.01	33.46	1.92	0.35	8.06	0.093
	Minimum and maximum	5.60	0.80	0.25	1.48	0.08	0.15	0.14	5.56	(n = 1)	< 0.01	0.19	< 0.01	< 0.01	23.00	1.01	0.14	5.56	0.03
		6.40	22.70	4.70	16.80	0.45	0.85	0.61	10.33		0.05	2.07	0.02	0.01	41.50	2.98	0.61	10.33	0.26
Association with *Helichrysum neocaledonicum* and *Guioa pectinata* (colluvial Ferritic Ferralsol on serpentinite)0	Mean (n = 4)	5.60		1.29	1.14	0.09	0.10	0.40	5.00		0.01	0.34	< 0.01	0.03	50.63	0.70	0.37	3.49	0.07
	Minimum and maximum	5.40		0.90	0.34	0.05	0.04	0.39	4.37		0.01	0.17	< 0.01	0.01	41.50	0.35	0.28	1.95	0.04
		5.70		1.84	1.50	0.16	0.14	0.51	6.20		0.01	0.56	0.01	0.15	55.00	1.70	0.51	6.20	0.14
Association with *Tetraria raynaliana* and *Cyathopsis albicans* (eroded Ferritic Ferralsol)	Mean (n = 17)	6.07	6.20	0.66	1.53	0.04	0.06	8.70	1.43	0.015	< 0.01	0.58	< 0.01	0.01	44.18	0.38	1.04	2.55	0.08
	Minimum and maximum	5.40	2.96	0.15	0.63	0.02	0.03	1.70	0	(n = 1)	< 0.01	0.22	< 0.01	< 0.01	39.46	0.20	0.68	1.30	0.03
		6.50	10.60	1.23	2.80	0.09	0.09	34.00	11.40		0.05	1.32	0.02	0.04	48.40	0.67	1.31	3.60	0.19
Association with *Hibbertia altigena* and *Beaupreopsis paniculata* (eroded Ferritic Ferralsol)	n = 1	5.20	10.40	0.45	0.80	0.05	0.03				0.02	0.62	0.01	0.02	39.70	0.45	0.72	1.37	0.10
Association with *Eucarpha deplanchei* and *Argophyllum ellipticum* (eroded Ferritic Ferralsol)	Mean (n = 4)	5.87	4.08	0.86	1.94	0.04	0.07	27.40	1.61	0.020	0.01	0.54	0.01	0.01	37.90	0.29	0.65	2.87	0.075
	Minimum and maximum	5.50	2.80	< 0.01	0.54	0.02	0.05	10.80	1.29	(n = 1)	< 0.01	0.07	0.01	0.01	28.00	0.22	0.28	1.25	0.04
		6.30	6.24	1.59	4.41	0.07	0.11	43.90	1.93		0.02	1.51	0.01	0.01	46.80	0.33	1.02	4.96	0.10
Association with *Codia discolor* and *Eugenia stricta* (colluvial Ferritic Ferralsol colluvial of piedmont)	Mean (n = 25)	5.32	6.15	0.74	0.61	0.05	0.065	6.30	10.74	0.030	0.01	0.33	0.013	0.026	45.00	0.63	0.71	2.43	0.13
	Minimum and maximum	4.50	0.45	0.11	0.11	0.01	0.01	1.00	1.30	0.023	< 0.01	0.14	0.01	< 0.01	32.40	0.20	0.26	1.24	0.02
		6.00	12.80	2.20	1.69	0.06	0.22	16.00	56.20	0.043	0.06	1.30	0.09	0.25	58.70	1.50	1.05	5.40	0.43
Association with *Homalium kanaliense* and *Tetraria comosa* (slightly hydromorphic colluvial Ferritic Ferralsol)	Mean (n = 13)	5.24	2.77	0.15	0.35	0.03	0.03	8.47	2.76		< 0.01	0.22	< 0.01	0.02	46.43	0.70	0.52	2.59	0.07
	Minimum and maximum	4.80	1.00	0.01	0.07	0.01	0.01	1.00	0		< 0.01	0.10	< 0.01	< 0.01	44.00	0.36	0.40	1.90	0.05
		5.90	6.20	0.75	1.90	0.05	0.07	44.00	16.20		0.01	0.52	0.02	0.07	48.50	1.52	0.73	3.20	0.15
Association with *Pancheria communis* and *Cloezia buxifolia* (hydromorphic colluvial and alluvial Ferritic Ferralsol)	Mean (n = 13)	5.42	17.77	0.45	2.24	0.05	0.19	34.79	1.11		< 0.01	0.64	0.01	0.02	31.70	0.18	0.41	4.89	0.04
	Minimum and maximum	5.00	12.10	0.02	0.28	0.02	0.06	2.12	0		< 0.01	0.18	< 0.01	< 0.01	16.20	0.06	0.15	1.10	0.02
		6.10	26.90	0.88	5.34	0.08	0.87	110.50	3.39		0.02	1.50	0.06	0.14	43.34	0.41	0.90	12.4	0.07
Sub-association with *Melaleuca gnidioides* and *Dracophyllum cosmelioides* (hydromorphic alluvial Ferritic Ferralsol)	Sample 1	5.10	5.79	0.05	0.35	0.02	0.12				< 0.01	0.25	0.02	< 0.01	44.03	0.26	0.37	2.58	0.05
	Sample 2	5.20	5.20	0.45	1.33	0.08	0.21				< 0.01	0.20	< 0.01	< 0.01	40.00	1.15	0.50	2.24	0.05

(*Continued*)

Table 1. (Continued).

			Echangeable elements							Total elements									
			CE	Ca	Mg	K	Na	Ni	Cr	P	Ca	Mg	K	Na	Fe	Mn	Ni	Cr	Co
Plant association (soil type)		pH	me/100 g					$\mu g\ g^{-1}$	$\mu g\ g^{-1}$	%									
Association with *Myodocarpus vieillardii* and *Medicosma verticillata* (colluvial Ferritic Ferralsol on footslope)	n = 1	6.10	1.17	0.01	0.32	0.02	0.01				0.01	18.6	0.21	0.32	38.60	0.45	0.58	3.41	0.05
Association with *Tarenna hexamera* and *Gardenia aubryi* (gravelly or indurated Ferritic Ferralsol)	Mean (n = 12)	4.85	5.47	0.55	0.30	0.03	0.06	0.82	2.04	0.031	0.012	0.62	0.01	0.012	44.19	0.17	0.19	5.57	0.023
	Minimum and maximum	4.40	2.10	0.05	0.06	< 0.01	< 0.01	0	0.43	(n = 1)	< 0.01	0.10	< 0.01	< 0.01	37.05	0.11	0.10	1.50	0.020
		5.50	12.70	1.38	1.00	0.13	0.17	3.00	3.60		0.02	1.51	0.02	0.05	52.52	0.25	0.34	12.4	0.040
Association with *Codia albifrons* and *Exocarpos pseudo-casuarina* (gravelly or indurated Ferritic Ferralsol)	n = 1	4.40		0.15	0.16	0.02	0.02				0.15	0.16	0.02	0.02	47.50	0.20	0.19	3.00	0.02
Association with Syzygium *kriegeri* (gravelly Ferritic Ferralsol)	Mean (n = 5)	5.50	3.60	0.67	0.51	0.11	0.09	0.47	1.20		< 0.01	0.04	< 0.01	< 0.01	50.90	0.44	0.13	2.86	0.035
	Minimum and maximum	5.00	2.10	0.01	0.01	0.01	0.06	0.20	1.00		< 0.01	0.01	< 0.01	< 0.01	47.00	0.23	0.08	2.60	0.017
		5.90	6.60	1.12	1.20	0.13	0.15	0.78	1.40		< 0.01	0.10	< 0.01	< 0.01	51.90	0.64	0.25	3.29	0.06
Association with *Myrsine asymmetrica* and *Araucaria rulei* (gravelly or indurated Ferritic Ferralsol)	Mean (n = 12)	4.87	1.60	0.55	0.28	0.02	0.02	0.23	3.20		< 0.01	0.35	0.015	0.02	50.10	0.26	0.24	3.55	0.027
	Minimum and maximum	4.40	0.40	0.15	0.01	0.01	0.01	0.12	2.18		< 0.01	0.07	0.01	0.01	45.40	0.18	0.12	2.26	0.015
		5.40	5.40	1.50	0.91	0.10	0.06	0.36	5.64		0.01	0.96	0.16	0.15	54.30	0.47	0.36	5.64	0.12
Association with *Metrosideros tetrasticha* and *Quintinia oreophila* (eroded Ferritic Ferralsol)	Mean (n = 5)	5.28	18.78	0.85	6.08	0.10	0.10	20.60	0.27		0.05	0.91	0.01	0.02	29.58	0.96	0.29	1.39	0.03
	Minimum and maximum	4.90	11.80	0.40	1.40	0.05	0.05	12.20	0		0.01	0.42	< 0.01	0.01	14.20	0.19	0.16	0.74	0.05
		5.80	32.90	1.70	18.60	0.18	0.23	42.20	0.70		0.06	1.80	0.02	0.03	39.20	1.27	0.53	2.00	0.14