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Floristic and Ecological Diversity of the Vegetation on Ultramafic Rocks in New Caledonia

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Abstract

New Caledonia is well known for its unusual and rich flora and for its extensive outcrops of ultramafic rocks. The entire floristic diversity, as well as that of the two principal formations (the 'maquis miniers' and the dense humid forest), is analyzed. Despite several groups rich in species, the whole diversity of the flora of ultramafic rocks in New Caledonia is attributed above all to the plethora of environmental conditions that has permitted the establishment of species with varied requirements and degrees of tolerance. The richness and uniqueness of the present-day flora of New Caledonia, though certainly derived in part from its Gondwanian origin and ancient isolation, is also a result of the presence of important outcrops of ultramafic rocks. The latter have permitted post-Eocene differentiation of new species as well as the survival of relict species under conditions of unfavourable mineral nutrition, where they have benefitted from less severe interspecific competition. The collected data on the floristic diversity in New Caledonia could serve as a basis for comparative studies, still not numerous, on the floristic diversity of vegetation on ultramafic rocks in the tropical environment.

Introduction

It is generally considered that the richness and the uniqueness of the flora of New Caledonia result from its Gondwanian origin and its long isolation in comparatively constant climatic conditions. Some authors[1–4] have in addition, emphasized the part played by outcrops of ultramafic rocks in the phenomena of speciation, selection and post-Eocene preservation of taxonomic groups which today confer on the flora its singularity.

Outcrops of ultramafic rocks, known in New Caledonia as 'terrains miniers', cover 5500 km^2, a little less than a third of the archipelago. They extend from sea level to 1618 m altitude and offer a great variety of soils and of plant associations. The latter contribute in various degrees to the floristic diversity of the archipelago.

Various syntheses dealing with serpentine vegetation[5–7] show that floristic diversity based on number of species has been fairly widely studied on ultramafic

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rocks in the temperate, but little in the tropical zone. They show also that very few publications[8,9] take into consideration the number of species and their relative importance, and then only in the temperate zone. Development of such studies in the tropical zone would however allow a better understanding of the 'serpentine syndrome'[10,11] and a better knowledge of the part played by 'stress' on the operation of biological diversity, a major theme in current research on the environment.

Overall diversity

The latest published synthesis on overall phanerogamic ultramafic flora of New Caledonia[12] (Table 1) shows that 1844 species of native phanerogams belonging to 440 genera (representing in each case over 60% of the native flora of New Caledonia) and to 119 of the 154 native families, occur on soils derived from ultramafic rocks. The rest of the Territory of New Caledonia with double the area has only about the same number of species. More than 90% (1671 species) of the flora of ultramafic substrata are endemic to the Territory and 69% (1153 species) are moreover confined to these substrata.

Table 1
Phanerogamic native flora of the ultramafic rocks of New Caledonia

	Species			Genera			Families		
	Total	Endemic		Total	Endemic		Total	Endemic	
		Number	%		Number	%		Number	%
Overall flora	1844	1671	90.6	440	91	20.7	119	4	3.4
Maquis flora	944	875	92.7	282	58	20.6	77	0	0
Rain forest	1156	1021	88.3	342	63	18.4	100	4	4

The floristic richness due to the presence of ultramafic rocks appears also on comparing the flora of the Isle of Pines and that of the Loyalty Islands. The former with both calcareous coral rocks and ultramafic rocks has nearly 500 native species for 134 km^2 while the latter, essentially raised coral, have fewer than 400 species for 1970 km^2.

It has been emphasized[2] that the geographic isolation of ultramafic mountains in the northwest of New Caledonia and the fragmented biotopes in the Southern Massif, which favour micro-endemism and vicariance phenomena, have contributed to the enrichment of the flora and that unfavourable conditions of mineral nutrition, in preventing invasion by aggressive introduced species, have contributed to preserve it.

Floristic diversity of the 'maquis miniers'

The 'maquis miniers'[2,4] include all the associations on ultramafic rocks (peridotites and serpentinites) belonging neither to rain forest nor to gallery forest. They are formed of sclerophyllous evergreen heliophilic shrubs in more or less continuous communities, or scattered in a thick herbaceous cover of Cyperaceae. They may locally be dominated by an open layer of *Araucaria* spp. or *Agathis ovata*. The 'maquis miniers' cover about 4500 km^2; their phanerogamic flora[4] (Table 1) contains 944 species in 282 genera and 77 families. Of these, 875 species (93%) and 58 genera (21%) are endemic to the territory. Maquis develops in very varied climatic and edaphic conditions. The shrubby maquis at low altitudes on the west coast have an average annual rainfall of less than 900 mm while those at high altitudes in the Southern Massif receive more than 4000 mm. The edaphic substrata vary from hypermagnesian brown soils and vertisols to ferralitic-ferritic soils[13] or oxidisols[14]. The former, rich in clay containing iron or magnesium, have a pH above 7 and a high exchange capacity saturated with magnesium. The latter, formed mainly of iron sesquioxides and lacking clay phyllites, have a low exchange capacity and an acid pH, sometimes below 4. From a phyto-edaphic viewpoint[15], the former belong to a dystrophic environment and the latter to an oligotrophic one. Between these two extremes there is a whole series of intermediate soils modified by erosion or in colluvium and variously enriched or impoverished in magnesium and in heavy metals (chromium, cobalt, manganese and nickel)[2].

Examination of the number of species (Table 2) of the plant associations recognized in the Massifs of Koniambo[16], Boulinda and the South[2] shows, except for hydromorphy, no simple relations between soil factors and number of species. Thus the associations richest in species occur on brown hypermagnesian soils on Koniambo and Boulinda but on desaturated ferralitic soils in the Southern Massif. It should however be noted that brown hypermagnesian soils are rare compared to desaturated ferralitic soils in the area studied on the Southern Massif. It may also be supposed that the poverty in species of certain plant associations is due more to dominance, occurring after fire, by gregarious species such as *Acacia spirorbis*, *Carpolepis laurifolia* or *Tristaniopsis guillainii*, than to the chemical nature of the substratum. It is also likely that the comparative richness of foothill associations passing into forest on ferralitic colluvium reflects the multiple stratal feature of the

Table 2
Number of species in various maquis associations on different soil types in the Grand Massif du Sud (S), in the Boulinda Massif (B) and in the Koniambo Massif (K), New Caledonia

Soils	Brown hyper-magnesian soil	Desaturated ferralitic soil	Colluvial ferralitic soil	Eroded ferralitic soil	Altitude
Well-drained soil				S:67	>1200 m
		S:62 D:82 K:46		S:67 B:63 K:129	600 m to 1200 m
	S:76 B:88 K:131	S:106 B:49 K:41	S:80 B:68	S:81	<600 m
Hydromorphic soil	S:14		S:30		<600 m
		S:45			

vegetation. These associations are rather local in the South and very limited on Boulinda.

Species numbers and the Shannon-Wiener diversity indices based on representative plots of 0.1 ha (Table 3) also show considerable variations in richness and floral diversity among the 'maquis miniers'. The highest values were obtained for a little-disturbed shrubby maquis passing into forest on brown hypermagnesian soil, the lowest for an open shrubby maquis dominated by a gregarious species. In general, diversity increases with the structural complexity of the association.

Table 3
Plant species diversity in maquis based on the number of stems in 0.1 ha plots

Locality	Vegetation	Soil	Total number species	Woody species	H′[a]
Boulinda	Shrubby open maquis dominated by *Tristaniopsis guillainii*	Ferralitic	35	30	3.43
Plaine des Lacs	Shrubby open maquis with *Neocalliptropsis pancheri*	Ferralitic	66	58	4.18
Tontouta	Shrubby open maquis with *Gymnostoma chamaecyparis*	Brown hyper-magnesian soil	64	57	4.68
Tontouta	Shrubby closed maquis passing into low forest	Brown hyper-magnesian soil	118	108	5.39

[a] H′ = Shannon-Wiener diversity index (see Table 6)

The overall diversity of the 'maquis miniers' in New Caledonia is due mainly, in spite of some species-rich associations, to varied environmental conditions allowing the co-habitation of species with different requirements and tolerances. The variation in diversity between communities also depends on repeated anthropogenic perturbations which reduce structural complexity.

Diversity of forests on ultramafic rocks

The forests on ultramafic rocks (Table 1) have, according to the latest synthesis[17], brought up to date with the latest revisions of the *Flore de la Nouvelle-Calédonie*, a total of 1156 phanerogamic species in 342 genera and 100 families. There are 1021 species (88.3%), 63 genera (18.4%), and 4 families endemic to the Territory. The forest flora thus seems overall richer than that of the maquis. It should also be emphasized that the extent of the forested area is only a quarter of that of the maquis and that both pteridophytes and bryophytes, obviously more common in forest than in maquis, were omitted from the surveys. Without an exhaustive study of the ultramafic forest soils of New Caledonia it is difficult to have a precise idea of their variety.

A comparative study of the flora of two contiguous forests on ultramafic rocks, one on alluvium, the other on eroded ferralitic soil[18] (Table 4), showed the forest on slopes to be richer, (except for trees with diameters above 30 cm) than that on alluvium. The former had 209 species on 0.25 ha and 309 on 2.79 ha; the latter 138 on 0.25 ha and 219 on 2.68 ha. In each case, the number of species on about 0.25 ha with dbh > 10 cm is less than that given for forests on ultramafic rocks in Sabah[19] (Table 5). From this study the Shannon-Wiener and Simpson diversity indices have been calculated for the two types of forest on the basis of individuals and of area occupied at breast height (1.3 m) (Table 6). These data could provide a baseline for comparative studies; they deserve to be extended to analyse the diversity of different forests and to follow it in relation to environmental factors.

Table 4
Number of species in 5 plots of 2500 m^2 in a forest on alluvium and in a forest on rocky slopes

	dbh (cm)								
	Total	⩾2	⩾5	⩾10	⩾20	⩾30	⩾40	⩾50	⩾60
<u>Forest on alluvium</u>									
Average	138	100	81	58	31	19	11	6	4
Range	124–150	91–108	75–92	54–63	29–38	17–21	8–13	3–8	2–5
<u>Forest on slopes</u>									
Average	209	153	116	69	32	15	8	4	1.5
Range	199–227	140–175	109–129	63–72	24–40	12–17	6–10	3–6	1–3

Table 5
Number of species (diameter ⩾ 10 cm) in forests on ultramafic rocks in New Caledonia (on 0.25 ha plots) and in Sabah (on 0.24 ha plots)

	New Caledonia[18]		Sabah[19]	
	Forest on alluvium	Forest on slope	Forest at 610 m	Forest at 700 m
Average	58	69		
Range	54–63	63–72	91	91

Table 6
Number of species and floristic diversity (H′: Shannon-Wiener; D: Simpson) in a forest on alluvium (A) and in one on rocky slopes (S). Underlined indices are based on numbers of stems; indices in parentheses are based on areas occupied at breast height (1.3 m)

Diameters (cm)		⩾2	⩾5	⩾10
Plot size (ha)		0.1	0.25	0.25
Number of species	A	87	81	58
	S	136	116	69
$H' = -\sum_{1}^{n} p_i \log_2 p_i$	A	<u>5.23</u> (4.81)	<u>5.16</u> (5.02)	<u>5.14</u> (4.74)
	S	<u>6.46</u> (5.18)	<u>5.76</u> (5.22)	<u>5.14</u> (4.79)
$D = 1 - \sum_{1}^{n} p_i^2$	A	<u>0.056</u> (0.058)	<u>0.054</u> (0.041)	<u>0.039</u> (0.056)
	S	<u>0.049</u> (0.049)	<u>0.031</u> (0.045)	<u>0.045</u> (0.058)

The study undertaken in New Caledonia shows that for two forests at the same altitude the more ill-balanced soil from the mineral viewpoint shows the lowest floristic diversity. This is however the more specialized as shown by the most unusual occurrence together of five 'hypernickelophore' species[18] defined as species accumulating nickel to concentrations above 10,000 $\mu g\ g^{-1}$ dry matter[20].

Conclusion

The general diversity of the ultramafic flora of New Caledonia also appears in each major vegetation type. Nevertheless, forest is floristically richer than maquis. For the latter, variations in plant diversity depend certainly on edaphic conditions but also very widely on human activities which by their nature and frequency disturb the structure and the floral composition of the plant associations.

The floristic diversity of the vegetation on ultramafic rocks in New Caledonia arises from several causes and phenomena, among them:

- The floristic richness of the archipelago, linked to historical and biogeographical conditions during the development of the flora.
- The fragmentation and the isolation of ultramafic outcrops and biotopes.
- The diversity of plant associations linked to major variations in environmental conditions, notably edaphic conditions arising from different types of soil development.
- The floristic richness of certain associations, and particularly those in forest, or maquis passing into forest, which have structures more complex than that of the open maquis.
- The ability of ultramafic soils to preserve the rich indigenous flora from competition with aggressive introduced species.

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