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Patterns of diversity and endemism in palms on ultramafic rocks in New Caledonia

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Several factors can explain the high diversity and endemism of New Caledonian palms on ultramafic rocks. A geographical pattern can be recognized, with many species occurring on the extensive and continuous ultramafic outcrop of the southern part of New Caledonia, and other species endemic to isolated ultramafic mountaintops. In these cases, a substrate effect may be difficult to distinguish from the geographical effect, since a similar pattern of diversity and endemism occurs on schistose rocks, and seems to be linked to Pleistocene refugia. However, a morphological or physiological specialization in relation to the ultramafic substrate can be identified in several species. Adaptive radiation on ultramafic rocks occurs in the genus *Burretio kentia*, which includes several closely related species restricted to very small areas and growing on the most selective, hypermagnesian soils. One species, *Campecarpus fulcitus* (Brongn.) Wendl. ex Becc., is a stilt-rooted palm growing only in rocky peridotitic habitats. Another pattern is represented by species widespread on the island but restricted to ultramafic rocks. These species often have a wide ecological range (growing on very diverse soil types, both in rainforest and *maquis*, at different elevations) and are more likely to be competitively excluded from other substrates rather than really requiring ultramafic rocks for their growth. Palm diversity and endemism on ultramafic rocks is the result of several factors related to the history and ecology of the ultramafic environment as a whole and not only or not directly to the peculiar edaphic conditions.

Introduction

The influence of ultramafic rocks on species richness, floristic composition and endemism in New Caledonia has been discussed by Viot,¹ Jaffré² and Schmid³ and more specifically for 'maquis' vegetation by Morat *et al.*⁴ and for the rainforests by Jaffré *et al.*⁵ There are, however, few studies that discuss the role of ultramafic substrates in specific taxa from a phylogenetic perspective. The most significant study on this aspect is that of Setoguchi *et al.*⁶ on the Araucariaceae.

In this article, we discuss the distribution pattern of palms growing on ultramafic rocks. The New Caledonian palms comprise 37 species, all endemic to the island and belonging to 16 genera, of which 15 are also endemic.⁷⁻⁹ Palms are distributed throughout the main island but almost exclusively in rainforests (Fig. 1), with a peak of endemism and diversity in the south and northeast (Table 1).

These palms represent three evolutionary lineages. *Pritchardia* is a monotypic genus belonging to the ancient and unspecialized subfamily Corphoideae and is restricted to a single location on ultramafic rocks. In subfamily Arecoideae, tribe Areceae, there are two well diversified monophyletic groups,

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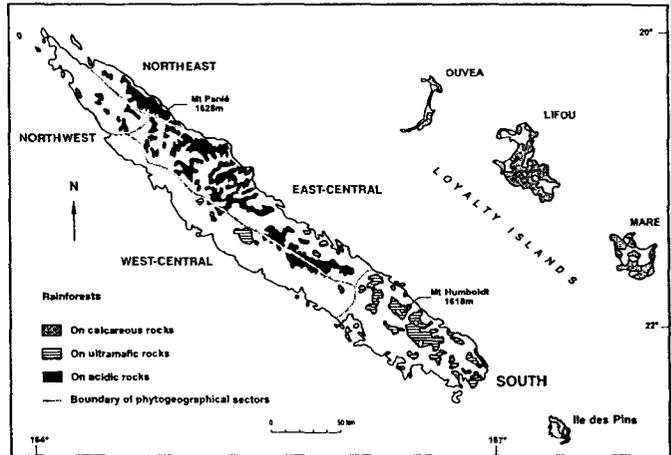


Fig. 1. Distribution of rainforests and phytoecographical units in New Caledonia.

one in subtribe Archontophoenicinae, including three genera and eight species and the other in the Iguanurinae, with 12 genera and 28 species.^{10,11} These arecoid palms are well represented on both ultramafic and schistose rocks. We base our study on a comparison between the distribution and phylogeny of the species (Figs 2 and 3).

Materials and methods

Phylogenetic data come from two cladistic analyses, of subtribes Archontophoenicinae¹⁰ and Iguanurinae,¹¹ based on morphological and anatomical characters. Distribution data for each species over its range were compiled by Pintaud *et al.*¹² and are presented here as Figs 2 and 3.

Results

The distribution of palms is strongly linked to the nature of the substrate. Fifteen species are restricted to ultramafic rocks, 13 to schists and one to coral limestone. Only eight species occur on both schistose and ultramafic rocks (Table 2).

Within the Archontophoenicinae, three species are restricted to ultramafic rocks, four to schistose rocks and only one is present on both substrates. The genus *Actinokentia* is confined to ultramafic rocks, with one species, *A. divaricata* (Brong & Gris) Vieill., widespread in the southern and central parts of the island, and another, *A. huerlimannii* H. Moore, with very local distribution in the south. The genus *Chambeyronia* contains one species apparently indifferent to the substrate and one restricted to schistose rocks in the northeast. The genus *Kentia* includes

Table 1. Distribution of palms within the phytoecographical sectors (see Fig. 1).

Sectors	Genera	Endemic genera	Species	Endemic species	
Northeast	11	4	17	9	
Northwest	2	0	2	0	
Central-west	8	0	16	2	4
Central-east	7	0	16	0	
South	10	2	19	8	
				Total centre:	Total centre:
				18	4

Table 2. Distribution of palm species on the three main substrate types.

Substrate	Genera	Species
Ultramafic rocks only	3	15
Schists only	4	13
Limestone only	0	1
Both ultramafic rocks and schists	8	8

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four species, with only one growing on ultramafic rocks (Fig. 2).

Within the Iguanurinae, the species are almost equally distributed on both substrates, except in *Basselinia* section *Basselinia* (numbers 18–21 in Fig. 3) and in *Burretiokentia* (numbers 29–33), two groups clearly more diversified on ultramafic rocks.

The only coryphoid palm, *Pritchardiopsis jeanneneysi* Becc., has a single locality on ultramafic rocks in the south (Fig. 2).

Discussion

The mere documentation of the number of species restricted to each type of substrate and growing on several (Table 2), gives little information about how the species distributions are linked to substrate. Indeed, there are two major centres of diversity and endemism in New Caledonia – one in the northeast and the other in the south. The northeastern part is entirely schistose and the southern part is completely covered with peridotites, so the 17 species endemic to these sectors (half of the palm flora) are obviously restricted to a single type of substrate. This bipolar distribution is most probably related to climatic fluctuations during the Pleistocene, since lowland rainforest is likely to have persisted only in the northeast and south during the dry period.^{11,13} Montane forest refugia may also have existed in the central part of the island, accounting for local endemism on either ultramafic or schistose rocks.

This geographical pattern is illustrated by the closely related monotypic genera *Veillonina* and *Campecarpus* (Fig. 4), the former being restricted to the northeast on schist and the latter to the south on ultramafic rocks. However, *Campecarpus fulcitus* (Brong. & Gris) Wendl. ex Becc. is restricted to a particular type of habitat – rocky, unstable peridotitic slopes – where it is able to become established and grow by means of its long stilt roots. These roots hold the trunk above the rocks and reach the soil in crevices and cracks between the boulders (Fig. 5). The distribution of this species is therefore determined by both geographical (historical) and ecological factors.

Another distribution pattern is represented by species widespread

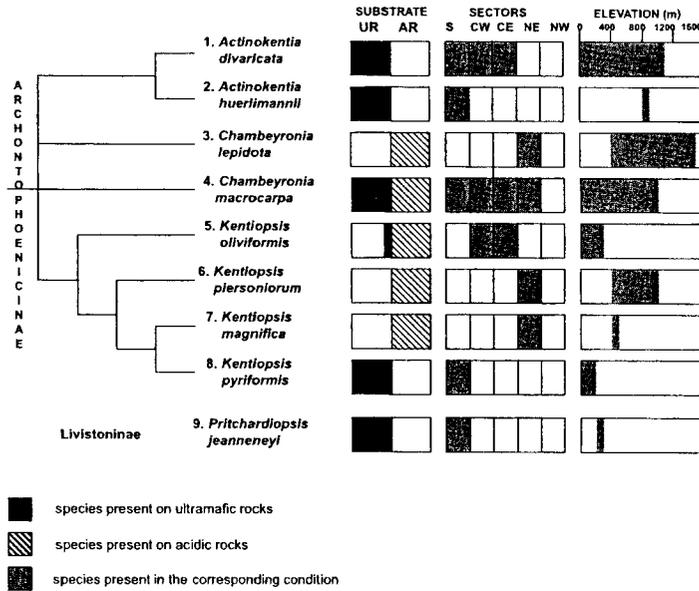


Fig. 2. Phylogeny and ecological range of the New Caledonian Archontophoenicinae (and Livistoninae). Substrate: UR, growing on ultramafic rocks; AR, growing on acidic rocks; sectors: see Fig. 1; blank, species absent.

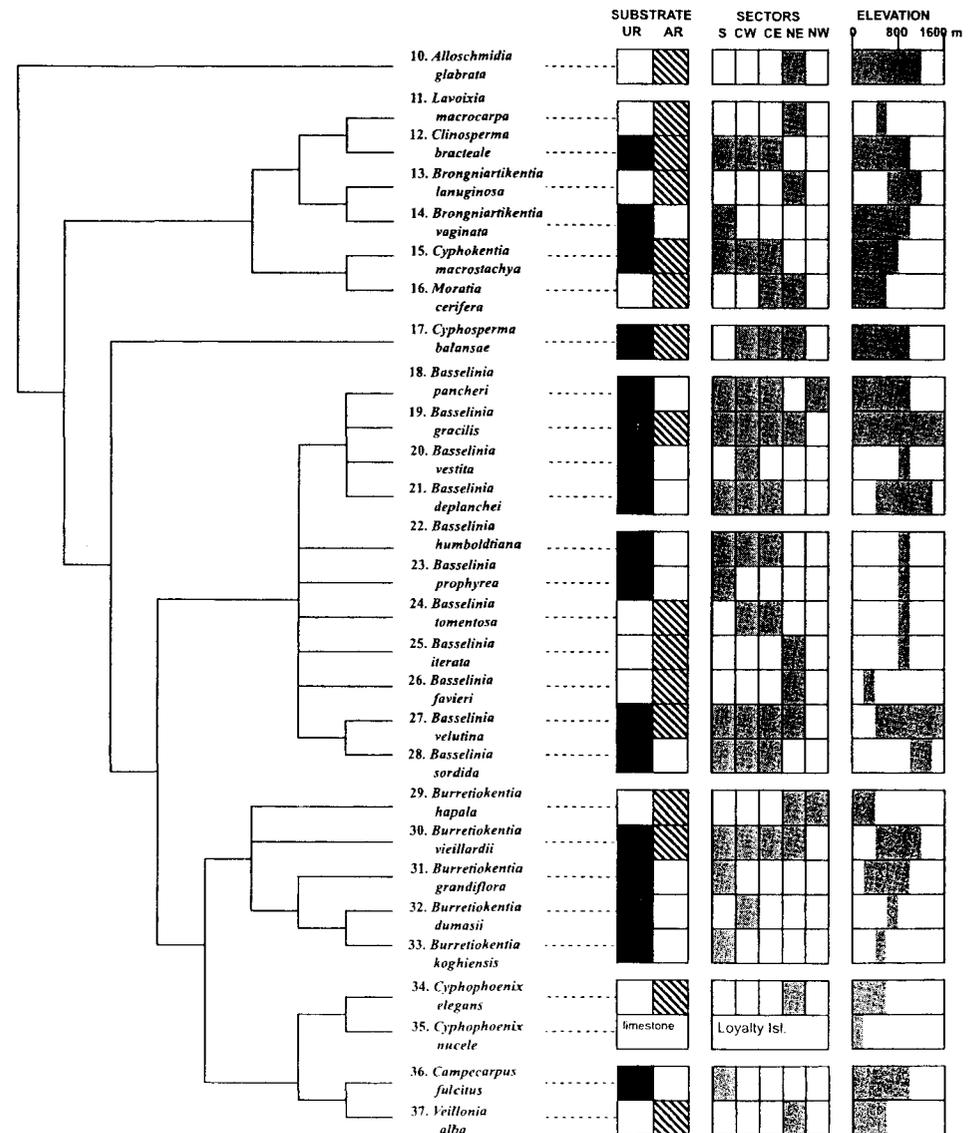


Fig. 3. Phylogeny and ecological range of the New Caledonian Iguanurinae. Legend as in Fig. 2.

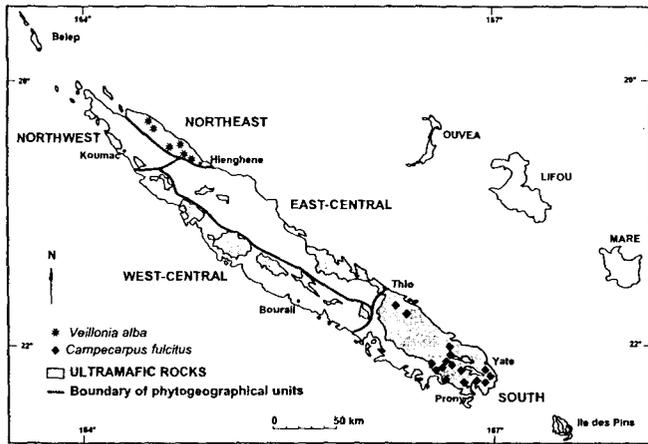
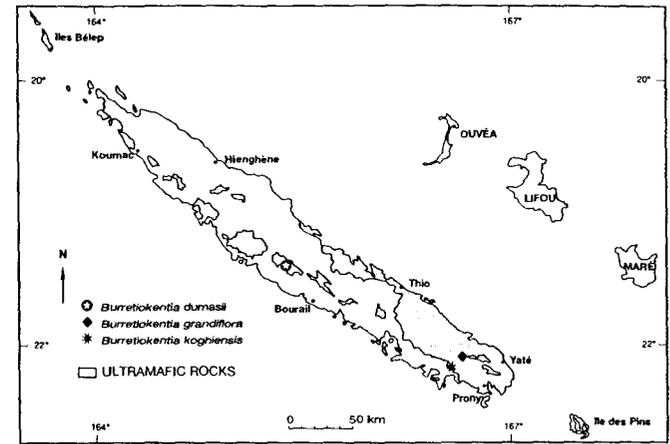
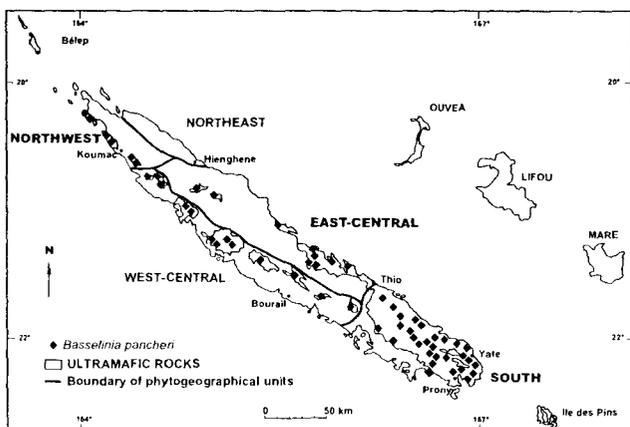
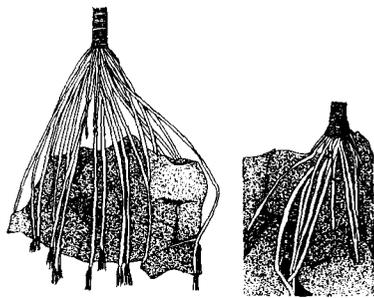


Fig. 4. Example of bipolar distribution of sister taxa, *Campecarpus fulcitus* on ultramafic rocks in the south and *Veillonnia alba* on schist in the northeast (see Fig. 3, numbers 36–37).

on the island (and therefore potentially dispersed on various substrates), but restricted to ultramafic rocks. This is illustrated by two genera essentially diversified on ultramafic rocks, *Actinokentia* (Fig. 2) and *Basselina*, especially in the section *Basselina* (Fig. 3, numbers 18–21). *Actinokentia* has two species, which grow only on ultramafic rocks. One is very localized in the southern sector and the other, *Actinokentia divaricata*, is very common and widespread in the southern and central parts of the island. In section *Basselina*, one species is ubiquitous (*B. gracilis* (Brong. & Gris) Vieill.), one is restricted to an ultramafic mountain-top in the central region (*B. vestita* H. Moore), and two are widespread but restricted to ultramafic rocks — *B. deplanchei* (Brongn. & Gris) Vieill. has almost the same distribution as *Actinokentia divaricata* and *B. pancheri* (Brong. & Gris) Vieill. is found throughout the island on most ultramafic outcrops (Fig. 6). These three species not only share the same distri-



bution pattern, but also ecological similarities: they are pioneer species, abundant in secondary forest, with a broad ecological range on ultramafic rocks. It is likely that these species are absent from other substrates because they are competitively excluded from them rather than because of mineral nutrition.

A different pattern of diversity is represented by *Burretiokentia*, a genus of five species (Fig. 3, numbers 29–33), four of which grow on ultramafic rocks. Three of these species (*B. grandiflora* Pintaud & Hodel, *B. dumasii* Pintaud & Hodel and *B. koghiensis* Pintaud & Hodel) form a monophyletic group, are very localized (Fig. 7), and restricted to brown hypermagnesian soils derived from serpentine. It is likely that this clade represents an adaptive radiation on this peculiar, very distinctive type of soil, where nickel hyperaccumulators are also found.

It appears therefore that soils derived from ultramafic rocks induce some specializations and radiations, but some endemism on this substrate is also partly due to factors unrelated to the edaphic conditions.

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