

Chorology of New Caledonian palms and possible evidence of Pleistocene rain forest refugia

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Abstract – The distribution of the 36 palm species of New Caledonia is studied in relation to several parameters: elevation, rainfall, geological substrate, phytogeographical sectors and vegetation types. The climate (thermal gradient and rainfall) appears to be the principal factor influencing the distribution of palms, the substrate effect being subordinate to the climatic pattern. Nearly all palm populations are included within the 1 500 mm isohyete. Maximum levels of species richness and endemism are located in four areas receiving more than 3 000 mm of annual rainfall. We interpret these areas as former Pleistocene refugia of lowland rain forest based on three lines of evidence: 1) all locally endemic lowland palm species and genera are restricted to these areas; 2) local endemics occur on east-facing slopes receiving the highest rainfall and most likely to have sustained rain forests during the driest periods; and 3) several pairs of sister species are disjunct between the southeastern and northeastern high rainfall areas. © 2001 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

palms / New Caledonia / chorology / ecology / Pleistocene / forest refugia / paleoendemism

Résumé – **Chorologie des palmiers de Nouvelle-Calédonie et mise en évidence possible de refuges de la forêt dense humide au Pléistocène.** La distribution des trente-six espèces de palmiers de Nouvelle-Calédonie est étudiée en fonction de l'altitude, des précipitations, du substrat géologique, des secteurs phytogéographiques de l'île et des types de végétation. Le climat est le principal facteur déterminant la distribution actuelle des palmiers, l'effet du substrat lui étant subordonné. Presque toutes les populations de palmiers sont incluses dans l'isohyète 1 500 mm et le maximum de richesse et d'endémisme se rencontre dans quatre zones recevant plus de 3 000 mm de pluie par an, que nous interprétons comme d'anciens refuges de la forêt dense humide de basse altitude durant les épisodes secs du Pléistocène. En effet, 1) tous les endémiques locaux de basse altitude sont cantonnés dans ces zones; 2) ces endémiques sont situés sur les façades est, les plus arrosées et ayant le plus probablement conservé des forêts denses durant les périodes sèches; 3) il existe plusieurs cas de distributions disjointes et limitées à ces zones. © 2001 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

palmyers / Nouvelle-Calédonie / chorologie / écologie / Pléistocène / refuges forestiers / paléo-endémisme

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Version abrégée

Depuis longtemps, la Nouvelle-Calédonie est reconnue comme étant une des régions où richesse floristique, diversité et endémisme sont parmi les plus élevés. La flore néo-calédonienne a été interprétée comme un exemple de flore du Crétacé supérieur se rapprochant de celle de l'Est de l'Australie. La persistance de nombreux taxons archaïques, éteints sur d'autres territoires, témoignent de la relative stabilité du climat de la Nouvelle-Calédonie depuis le Crétacé supérieur. Cependant, à ce jour, les effets des fluctuations climatiques du Pléistocène sur cette flore ont été peu étudiés. Dans cet article, à partir de l'exemple des palmiers, qui avec 37 espèces endémiques et 16 genres dont 15 endémiques et une distribution étroitement corrélée au substrat géologique reflètent de façon remarquable les caractéristiques de la flore néo-calédonienne, nous montrons que l'histoire climatique récente doit être prise en compte pour interpréter les modèles de la distribution actuelle des plantes sur l'île.

Les données concernant la distribution des palmiers ont été établies à partir des collections d'herbiers existants. La distribution des espèces a ensuite été superposée à la carte des secteurs phytogéographiques de l'archipel, à la carte géologique, à la carte de la végétation et à la carte des isohyètes. La distribution des palmiers en fonction de l'altitude est également représentée.

La distribution de chaque espèce de palmier par secteur, par type de substrat, par type de végétation et selon l'altitude est présentée en tableau. L'endémisme local est la règle. Les espèces largement répandues l'exception. Les secteurs les plus riches sont ceux du Nord-Est et du Sud. La diversité des palmiers est plus élevée à basse et moyenne altitude qu'aux altitudes supérieures ; la diversité maximale est concentrée autour de 400–600 m. La répartition des espèces est largement liée à la nature du substrat. Le nombre d'espèces inféodées à l'un des deux substrats (schistes et roches ultrabasiqes) est à peu près égal. Toutes les espèces poussent en forêt dense humide.

La distribution des palmiers en Nouvelle-Calédonie semble être due principalement au climat. Hormis *Kentiopsis oliviformis*, la distribution des palmiers est comprise à l'intérieur de l'isohyète 1 500 mm ; tous les sites où la richesse est supérieure à dix espèces et/ou l'endémisme supérieur ou égal à deux espèces sont circonscrits dans l'isohyète 3 000 mm. La chute rapide de la diversité au-dessus de 1 000 m est probablement liée aux basses températures, puisque la majorité des palmiers néo-calédoniens sont des espèces mégathermes. Les variations de la richesse spécifique et de l'endémisme de l'île sont aussi étroitement corrélées à la pluviométrie.

Cette étroite corrélation écologique est cohérente avec l'hypothèse selon laquelle les palmiers appartiennent au groupe originel des forêts tropicales humides de l'Est-Gondwana et par conséquent confinés dans cet environnement où ils se sont diversifiés.

Une autre hypothèse permettant d'expliquer ce patron de distribution est que l'isohyète 3 000 mm actuel correspondrait à l'isohyète 1 500 mm lors des épisodes de sécheresse maximale contemporains des périodes de glaciation. Nous considérons que l'isohyète actuelle de 3 000 mm correspond à celle de 1 500 mm lors du dernier maximum glaciaire, ce qui permet d'identifier quatre zones potentielles de refuges de forêt tropicale humide (*figure 2*) : le massif du Nord-Est avec un genre et cinq espèces endémiques, le massif des Lèvres (dont la flore est peu connue), le massif du Sud avec trois espèces endémiques et la plaine des Lacs avec un genre et deux espèces endémiques. En Nouvelle-Calédonie comme sur d'autres continents, les aires réduites de forêt tropicale humide sont remarquables par leur haute diversité et leur endémisme élevé.

L'existence de refuges d'époque Pleistocène de la forêt dense humide et d'une expansion de cette végétation est également suggérée par les contrastes de richesse floristique entre les versants est et ouest de la chaîne orientale. La dissymétrie entre versants est particulièrement accusée en ce qui concerne les peuplements de palmiers comme le montrent les transects effectués à partir de la côte Est, traversant chacun un refuge supposé. Les versants orientaux sont plus riches avec des espèces endémiques, au contraire les versants occidentaux sont assez pauvres et ne comprennent que des espèces banales à vaste répartition et large amplitude écologique. Le modèle asymétrique de la répartition des espèces suggère que la forêt tropicale humide a disparu des versants ouest lors des périodes sèches du Pleistocène durant les quelles elle ne subsiste que sur les versants est.

En Nouvelle-Calédonie, le haut degré d'endémisme dans les zones supposées de refuges semble résulter de la persistance d'une vieille flore qui n'a pas pu se maintenir ailleurs comme cela a été évoqué pour d'autres forêts tropicales humides, notamment en Amazonie. Ainsi, le genre *Pritchardiopsis*, le seul caractérisé en Nouvelle-Calédonie par des feuilles palmées, y présente un caractère manifestement rélictuel du Gondwana et témoigne que le rôle des refuges fut avant tout un rôle de conservation. Les refuges supposés ont pu assurer jusqu'à nos jours la permanence de la forêt dense humide d'époque tertiaire comme le corrobore la distribution bipolaire de plusieurs couples d'espèces sœurs ayant un ancêtre commun direct tel que mis en évidence par l'analyse phylogénétique des palmiers de

Nouvelle-Calédonie. Les endémismes locaux de basse altitude sont effectivement concentrés dans les massifs du Sud et du Nord-Est. Les peuplements post-Pléistocène de ces forêts de basse altitude sont pauvres et constitués d'espèces à large distribution, tandis que les espèces plus récentes du Nord-Est et du Sud ont subi peu de modifications depuis le Tertiaire.

La répartition des palmiers en Nouvelle-Calédonie est également influencée par celle des sols, mais cette influence est souvent indissociable de celle du climat. En effet, l'endémisme édaphique local se superpose largement aux zones d'endémisme majeures du Nord-Est et du Sud que nous mettons en relation avec l'existence de refuges. Sur les treize espèces inféodées aux terrains schisteux, dix sont localement endémiques et parmi celles-ci neuf sont confinées dans le secteur Nord-Est entièrement schisteux. La forte pression exer-

cée par les sols dérivés de roches ultrabasiques ont provoqué d'étroites spécialisations morphologiques et/ou physiologiques.

En conclusion, l'évolution et la diversification des palmiers en Nouvelle-Calédonie est indiscutablement due à de multiples facteurs parmi lesquels les effets du substrat ont pu être importants. Toutefois, leur distribution semble principalement influencée par les variations climatiques du Pléistocène effaçant une grande partie des facteurs de distribution qui auraient pu témoigner de causes plus anciennes. Le faible dynamisme d'expansion des palmiers dans de nouveaux milieux forestiers favorables expliquerait en grande partie la distribution limitée des espèces dans ce que nous considérons comme étant des refuges du Pléistocène. Le paléo-endémisme serait donc le trait dominant de la flore de palmiers de Nouvelle-Calédonie.

1. Introduction

New Caledonia has long been recognized as a major area of diversity and endemism [1–6]. With nearly 3 500 vascular plant species, of which 80 % are endemic, a generic endemism of 15 % (nearly 100 endemic genera) and 5 endemic families [7], the flora of New Caledonia is extraordinarily rich and distinctive, especially considering the small size of the island (about 18 000 km²), and compared to neighbouring Melanesian archipelagos [8]. The unique nature of this flora has been related to the continental origin of New Caledonia (as opposed to the comparatively recent volcanic origin of the other Melanesian islands) and to its very long isolation in the southwestern Pacific, following separation from eastern Gondwana ca. 80 million years ago [9]. Raven and Axelrod [10] interpreted the flora of New Caledonia as a “surviving, modified sample of the Late Cretaceous flora of eastern Australia”. They emphasized, as previous authors, the high diversity and endemism of gymnosperms, the numerous primitive angiosperm families (such as Amborellaceae, Trimeniaceae, Winteraceae) and the rarity of advanced dicotyledons (Asteraceae, Scrophulariaceae, Verbenaceae are for example almost lacking). Modern phylogenetic studies reveal the basal position of many New Caledonian taxa in a number of lineages, and most noticeable being *Amborella*, which is sister to all other living angiosperms in several molecular analyses [11], giving added strength to a Gondwanian origin of a large part of this flora. The persistence of numerous archaic taxa now extinct elsewhere is largely attributable to the relative stability of the New Caledonian climate since the Late Cretaceous, as opposed to the desertification that has occurred in Australia since the Miocene [12] and the glaciations in New Zealand during Plio-Pleistocene [13]. Another fundamental aspect of the evolution of the New Caledonian biota is the overthrust of ultramafic rocks on most of the

island in Late Eocene–Early Oligocene (45–38 Ma). This probably led to extinctions initially, but ultramafic rocks seem also to have been involved in the conservation of some ancient taxa and clearly stimulated adaptive radiations in many groups [4, 14, 15]. However, while much emphasis has been put on Cretaceous and Tertiary events, little attention has been paid to date to the effects of Pleistocene (–2 000 000 years to –10 000 years) climatic fluctuations on the New Caledonian flora. In this article, we use the example of palms to show that the recent climatic history also needs to be taken into account when interpreting present plant distribution patterns on the island.

With 36 species (all endemic) in 16 genera (all but one endemic) and a distribution strongly linked to the geological substrate [16], palms reflect the most remarkable characteristics of the New Caledonian flora. As a result of several recent studies, they are also very well known taxonomically [17–19], and their distribution throughout most of the island has been accurately documented. Palms are therefore an ideal subject for chorological analysis on the main island, Grande Terre (the Loyalty islands, with only one palm species and an overall poor flora with little endemism are excluded from this study).

2. Materials and methods

Distribution data were obtained from existing herbarium collections. Those made before 1980 (more than 600) were listed and mapped by Moore and Uhl [17], and more recent collections (about 300, most of them made by us) were recorded at Paris (P), Kew (K), Nouméa (NOU) and Cornell (BH) herbaria.

Species distributions were then superimposed on a series of maps depicting the phytogeographical sectors of New Caledonia [20], the geology [21], the vegetation [22] and the rainfall isolines [23]. The relevant parts of the first three

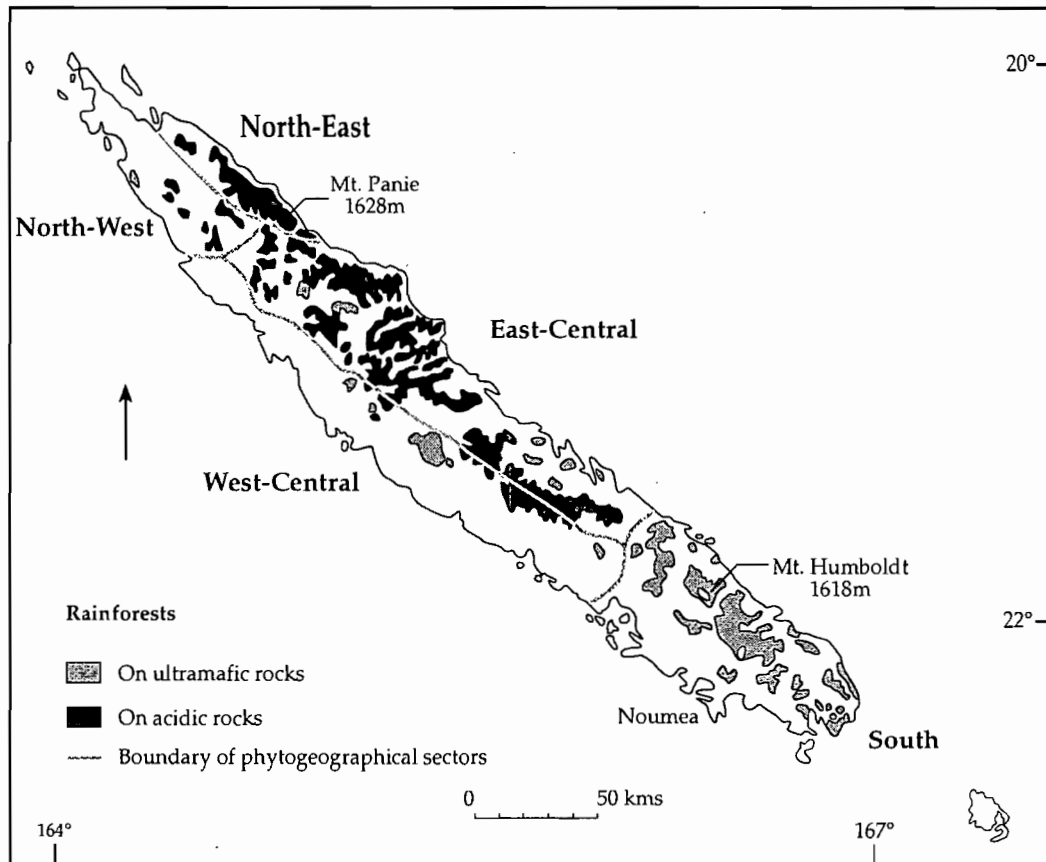


Figure 1. Rain forests, substrates and phytogeographical sectors in New Caledonia

maps are combined on figure 1. Figure 2 shows the isocontours, with major areas of palm richness and endemism highlighted. Species distribution as a function of elevation is also recorded in figure 3. In addition, the distribution of palm species was precisely studied along three transects crossing the eastern mountain range (table IV, figure 2, and figure 4).

3. Results

The distribution of each palm species with respect to the phytogeographical sectors, elevation, types of substrate and vegetation is summarized in table I.

More than half of the species (20) are restricted to a single phytogeographical sector and 11 of them are known from an area not exceeding 50 km². Only five species are distributed in four of the five sectors (no species occurs in all of them). Local endemism is thus the rule, and widespread species the exception. The richest sectors are those of the Northeast (11 genera and 17 species, with 9 species endemic to this sector) and of the South (10 genera and 19 species, 8 endemic) (table II).

Palm diversity is higher at low and medium elevations than at higher elevations: 28 species occur between 10 and 700 m (12 of which do not occur higher up), while 23

species are recorded between 700 m and 1 600 m (among them, only 8 do not occur at lower elevations, the others having a wide altitudinal range). Species diversity drops abruptly above 1 000 m elevation, and only 4 species grow on the top of the mountains (1 400–1 600 m), all of them belonging to the genus *Basselinia*. Maximum diversity is concentrated in areas around 400–600 and 900–1 000 m (figure 3).

The distribution of species is also strongly linked to the nature of the substrate. Only eight out of 36 species grow on both ultramafic and schistose rocks. On the other hand, the number of species restricted to one or the other substrate is similar (table III).

All the palm species grow in rain forest and only five also occur, but marginally, in *maquis minier* (an open, heath-like sclerophyllous, mostly fire-induced vegetation derived from rain forests on ultramafic rocks). One species, *Kentiopsis oliviformis*, also occurs in some semi-humid forests along the west coast. Apart from a few isolated populations receiving about 1 200–1 400 mm of annual rainfall (*Basselinia pancheri*, *K. oliviformis*), all New Caledonian palms are included within the 1 500 mm isoline. Moreover, all areas where the palm richness exceeds 10 species (with often several local endemics) are included within the 3 000 mm isoline (figure 2).

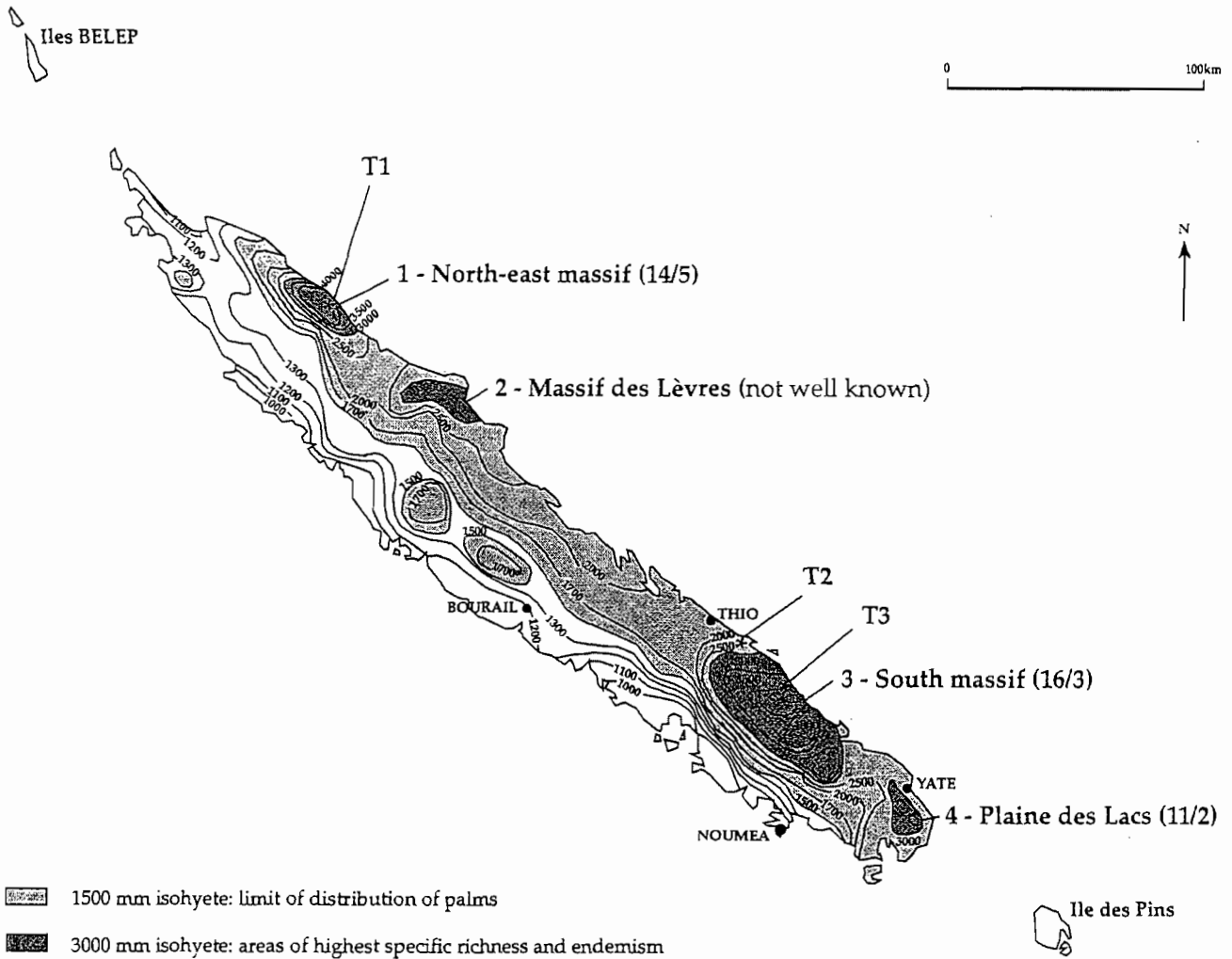


Figure 2. Isolines (yearly average for 1956–1975-period of record), principal hypothesized Pleistocene rain forest refuge areas (1 to 4) with number of palm species/number of endemic species; T1, T2, T3: transects studied. Isolines from Atlas de Nouvelle Calédonie, Orstom, Paris. 1981.

4. Discussion

The distribution of palms in New Caledonia appears to be determined primarily by the climate.

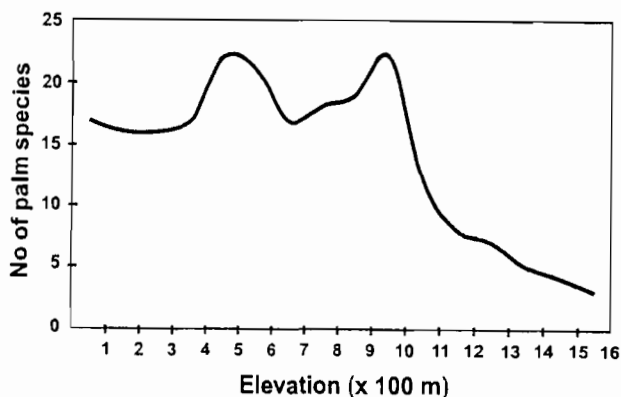


Figure 3. Variation of species richness of the New Caledonian palm flora as a function of elevation.

The rapid decrease of diversity above 1 000 m elevation (figure 3) is most probably linked to the decrease in temperature, most New Caledonia palms being evidently megatherm species. The 1 000-m level corresponds roughly to the elevation from which absolute minimal temperatures reach 0 °C. Lower temperatures (to –1 or –2 °C) are rare even near the summits, given the modest height of mountains (to 1 628 m elevation) and nearly permanent high humidity.

The bimodal distribution of species diversity below 1 000 m of elevation, with two prominent peaks at 400–600 m and 900–1 000 m (figure 3) requires more detailed explanation. These peaks correspond to zones where the altitudinal ranges of two ecological groups of species overlap. Lowland palms occur mostly up to 500–600 m of elevation, whereas many upland species begin to appear at elevations 400 m of (this is particularly striking on the east side of Mont Panié, figure 4); the strictly montane species appear mostly at 900 m elevation while many wide ranging species with a lowland tendency do not extend above 1 000 m. In addition, most

Table 1. Distribution and ecology of New Caledonian palms.

Sector: phytogeographical sector(s) of occurrence: S: South; C: Centre (east- and west-central combined); NE: northeast; NW: northwest. Elev.: altitudinal range of the species. Subst.: geological substrates: B: basalts; S: schists; U: ultramafic rocks. Veg.: type of vegetation: RF: rain forest; MF: mesic forest; M: maquis. No. loc.: number of localities (= area of less than 50 km²) of recorded occurrence.

Genre et espèce	Sector	Elev. (m)	Subst.	Veg.	N. loc.
<i>Actinokentia divaricata</i> (Brongn.) Dammer	S, C	10–1 100	U	RF	>4
<i>Actinokentia huerlimannii</i> H.E. Moore	S	850–900	U	RF, M	2
<i>Alloschmidia glabrata</i> (Becc.) H.E. Moore	N-E	10–1 200	S	RF	>4
<i>Basselinia deplanchei</i> (Brongn. & Gris) Vieil.	S, C	400–1 500	U	RF, M	>4
<i>Basselinia favieri</i> H. E. Moore	N-E	300–500	S	RF	1
<i>Basselinia gracilis</i> (Brongn. & Gris) Vieil.	S, C, N-E	10–1 600	S, U	RF	>4
<i>Basselinia humboldtiana</i> (Brongn.) H.E. Moore	S, C	800–1 000	U	RF	4
<i>Basselinia iterata</i> H. E. Moore	N-E	900–1 000	S	RF	1
<i>Basselinia pancheri</i> (Brongn. & Gris) Vieil.	S, C, N-W	10–1 100	U	RF, M	>4
<i>Basselinia porphyrea</i> H.E. Moore	S	700–1 000	U	RF, M	2
<i>Basselinia sordida</i> H.E. Moore	S, C	900–1 500	U	RF	>4
<i>Basselinia tomentosa</i> Becc.	C	900–1 100	S	RF	2
<i>Basselinia velutina</i> Becc.	S, C, N-E	400–1 600	S, U	RF	>4
<i>Basselinia vestita</i> H.E. Moore	C	900–1 000	U	RF	1
<i>Brongniartikentia lanuginosa</i> H.E. Moore	N-E	700–1 300	S	RF	>4
<i>Brongniartikentia vaginata</i> (Brongn.) Becc.	S	10–1 000	U	RF, M	>4
<i>Burretiokentia dumasii</i> Pintaud & Hodel	C	600	U	RF	1
<i>Burretiokentia grandiflora</i> Pintaud & Hodel	S	250–1 000	U	RF	1
<i>Burretiokentia hapala</i> H. E. Moore	N-W, N-E	20–500	S	RF	3
<i>Burretiokentia koghiensis</i> Pintaud & Hodel	S	450–550	U	RF	1
<i>Burretiokentia vieillardii</i> (Brongn. & Gris) Pichi-Sermoli	S, C, N-E	400–1 300	S, U	RF	>4
<i>Campecarpus fulcitus</i> (Brongn.) H. Wendl. ex Becc.	S	10–1 000	U	RF	>4
<i>Chambeyronia lepidota</i> H.E. Moore	C, N-E	400–1 400	S	RF	>4
<i>Chambeyronia macrocarpa</i> (Brongn.) Vieil. ex Becc.	S, C, N-E	10–1 000	S, U	RF	>4
<i>Clinosperma bracteale</i> (Brongn.) Becc.	S, C	10–1 100	S, U	RF	>4
<i>Cyphokentia macrostachya</i> Brongn.	S, C	10–800	S, U	RF	>4
<i>Cyphophoenix elegans</i> (Brongn. & Gris) H. Wendl. ex Sal.	N-E	50–550	S	RF	1
<i>Cyphosperma balansae</i> (Brongn.) H. Wendl. ex Salomon	C, N-E	10–1 000	S, U	RF	>4
<i>Kentiopsis magnifica</i> (H. E. Moore) Pintaud & Hodel	N-E	400–550	S	RF	1
<i>Kentiopsis oliviformis</i> (Brongn. & Gris) Brong.	C	10–300	S, B, U	MF	4
<i>Kentiopsis piersoniorum</i> Pintaud & Hodel	N-E	400–1 000	S	RF	1
<i>Kentiopsis pyriformis</i> Pintaud & Hodel	S	10–200	U	RF	2
<i>Lavoixia macrocarpa</i> H.E. Moore	N-E	500–550	S	RF	1
<i>Moratia cerifea</i> H.E. Moore	C, N-E	10–600	S	RF	>4
<i>Pritchardiopsis jeanneneyi</i> Becc.	S	250	U	RF	1
<i>Veillonina alba</i> H. E. Moore	N-E	10–600	S	RF	>4

species displaying a restricted altitudinal range (including many local endemics) are also concentrated in these two zones. Consequently, at a local scale, the richest palm communities are usually encountered at these elevations (for example, 10 species including three endemics are sympatric at 500 m elevation on Mont Panié, figure 4).

Variation in species richness and endemism within the island is also strongly linked to the pattern of rainfall (figure 2). The restriction of nearly all palms to the areas contained within the 1 500 mm isoline is related to their almost exclusive occurrence in rain forests, which are delimited by this isoline [22]. This narrow ecological range of New Caledonian palms is consistent with the hypothesis that they belong to groups which originated in East-Gondwanian rain forests in the late Cretaceous, and subsequently remained confined in this environment where they have diversified [17, 24, 25].

The fact that the areas of highest rainfall (more than 3 000 mm annually) correspond to those with the highest palm diversity could also be explained by a simple corre-

lation between rainfall and species richness. Gentry [26] showed in neotropical forests that rainfall and floristic diversity are positively correlated up to 3 000–4 000 mm of annual rainfall, a level at which floristic diversity tends to reach a maximum. However, although virtually nothing is known about the auto-ecology of New Caledonian palms, it is unlikely that the many locally endemic palms which are also concentrated in these high rainfall areas actually require 3 000 to 6 000 mm of annual rainfall to survive. The other palm species occurring in these areas but not restricted to them grow throughout the range of the rain forests, i.e. above 1 500 mm of annual rainfall.

An alternative hypothesis which could explain this pattern of endemism is, that the present day 3 000 mm isoline corresponds to the 1 500 mm isoline during the dry periods of the Pleistocene concomitant to glaciations. Rain forests would therefore have been restricted during these periods to the present day areas of highest diversity and endemism. The palynological record in the Plaine des Lacs, near Yaté, one of the areas (No. 4) included within

Mont Panié (1628 m) - eastern slope

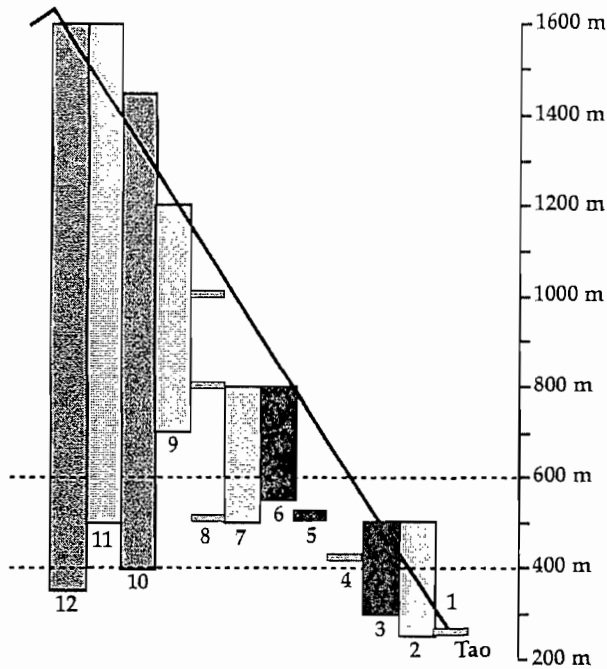


Figure 4. Distribution of palm species along the eastern slope of Mont Panié, from 200 m elevation (forest margin) to the summit (1 628 m). The richest zone is delimited by the dotted lines. Each bar represents the altitudinal range of a species (pale or dark grey: not endemic, black: endemic to Mont Panié); 1: *Cyphosperma balansae*; 2: *Veillonina alba*; 3: *Basselinia favieri*; 4: *Chambeyronia macrocarpa*; 5: *Lavoixia macrocarpa*; 6: *Kentiopsis piersoniorum*; 7: *Moratia cerifera*; 8: *Burretiokentia vieillardii*; 9: *Brongniartikentia lanuginosa*; 10: *Chambeyronia lepidota*; 11: *Basselinia velutina*; 12: *Basselinia gracilis*.

the present day 3 000 mm isoline (figure 2) indicates the continuous presence of a rain forest environment (including associated secondary facies caused by recurrent natural fires) since at least 40 000 BP [27], while the last glacial

Table II. Distribution of genera and species of palms within the phytogeographical sectors of New Caledonia.

Sectors	No. genera	Endemic genera	No. species	Endemic species
Northeast	11	4	17	9
Northwest	2	0	2	0
West-central	8	0	16	2
East-central	7	0	16	0
W-C + E-C	9	0	18	4
South	10	2	19	8

Table III. Distribution of palms according to substrate type.

	No. genera	No. species
on ultramafic rocks only	3	15
on schists only	4	13
on both substrates	8	8

Table IV. Results of inventory of palm species along three Transects (T1–3) crossing the eastern mountain range.

T1		T2		T3	
W	E	W	E	W	E
7 (0)	13 (3)	3 (0)	11 (1)	6 (0)	7 (1)

W: western slope; E: eastern slope; first figure: number of palm species, second figure, in parentheses: number of species endemic to this locality.

T1: Mont Panié (W-Ht Coulna 20°38' S, 164°44' E, 400 m -top 1 628 m - E-Tao 20°34' S, 164°47' E, 200 m);

T2: W-Saille (21°41' S, 166°14' E, 400 m) - ridge 1 200 m - E-Neuméni (21°40' S, 166°16' E, 500 m);

T3: W-Dent de Saint Vincent 21°52' S, 166°14' E, 400 m - top 1 618 m - E-Nékando (21°52' S, 166°27' E, 600 m).

maximum (LGM) occurred at 18 000 BP [28]. Moreover, there is evidence of decreased rainfall in New Caledonia during periods of glaciations. Latham [29] suggested from soil data that a rainfall decrease of 30 % compared to present occurred between 26 000 and 18 000 BP. Podwojewski [30] correlated gypsum accumulation to a dry period between 120 000 and 18 000 BP, with a short interruption between 85 000 and 80 000 BP. Wind erosion on the west coast, resulting in terrigen sand accumulation on seashores indicates that some areas protected from trade winds had a semi-arid climate during this period [21]. Data from Australasia indicate a generally drier climate than present during the last glaciation, due to cooler sea-surface temperatures, cooler trade-winds, and larger areas of exposed lands with a lowering of ca. 150–200 m of the sea level at the LGM [28].

A model of reduced modern precipitation pattern has been previously developed by van der Hammen and Absy [31] to infer the geographical position of possible LGM rain forest refugia in Amazonia. These authors also took the 1 500 mm isoline as a limit of the rain forest extension. They concluded that a reduction of 40 % of the present rainfall meets the available palynological data for the glacial Amazon and is therefore most likely to explain the distribution of Amazonian rain forests at the LGM.

Following this methodology, if we consider the present day 3 000 mm isoline as a marker of the 1 500 mm LGM isoline in New Caledonia, we can identify four main possible refuge areas for the lowland rain forests (figure 2):

- The northeastern mountain range around Mont Panié (one endemic genus, *Lavoixia*, and 5 endemic species,
- The Massif des Lèvres (not well known floristically but with at least two species, *Chambeyronia lepidota* and *Moratia cerifera* only recorded from areas 1 and 2),
- The southern massif (three endemic species),
- The Plaine des Lacs (one endemic genus, *Pritchardiopsis* and two endemic species).

Evidence of Pleistocene refugia and of Holocene expansion of the rain forest also comes from floristic contrasts between the eastern and western slopes of the eastern

mountain ranges, which run along the east coast. In absence of human disturbance, the rain forest completely covers both sides of these mountains and reach the summits. The eastern slopes receive higher rainfall due to orographic precipitation associated with the East–West trade winds, but it is likely that rainfall on the west side of these eastern mountains (over 1 500 mm) is not a constraint to the development of most rain forest taxa. The westward rainfall decrease induces a dramatic change in vegetation only on the west side of the main central mountain range or of isolated western mountains where lower elevations (under 300–500 m) are occupied by mesic or dry forests. However, even on the eastern mountain ranges covered by rain forests, plant communities are often very asymmetrical between the eastern and western slopes, as it is illustrated by the distribution of palms along three transects crossing two of the putative refugia (figures 2 and 4 and table IV). Palm communities on the eastern slopes are very rich (up to 13 species on Mont Panié) and include locally endemic species (three on Mont Panié), while those on the western slopes are comparatively poor (3 to 7 species) and include only widespread species. The contrast is most spectacular between the two slopes of the Forêt de Saille (T2), with three species on the western slope and 11 species on the eastern slope. Structurally, this rain forest is rather similar on both slopes, and even larger trees develop on the floristically poorer, western side, with the dominance of *Agathis lanceolata* (Araucariaceae).

This asymmetrical pattern of species distribution suggests that the rain forest has disappeared on the western slopes during the driest periods of the Pleistocene and was then restricted to the eastern slopes. If the spread of the rain forest on the western slopes was recent (Holocene), one would indeed expect to find mostly widespread species with efficient dispersal systems there. In contrast, the less dynamic species would remain confined to the eastern areas where rain forests occurred continuously.

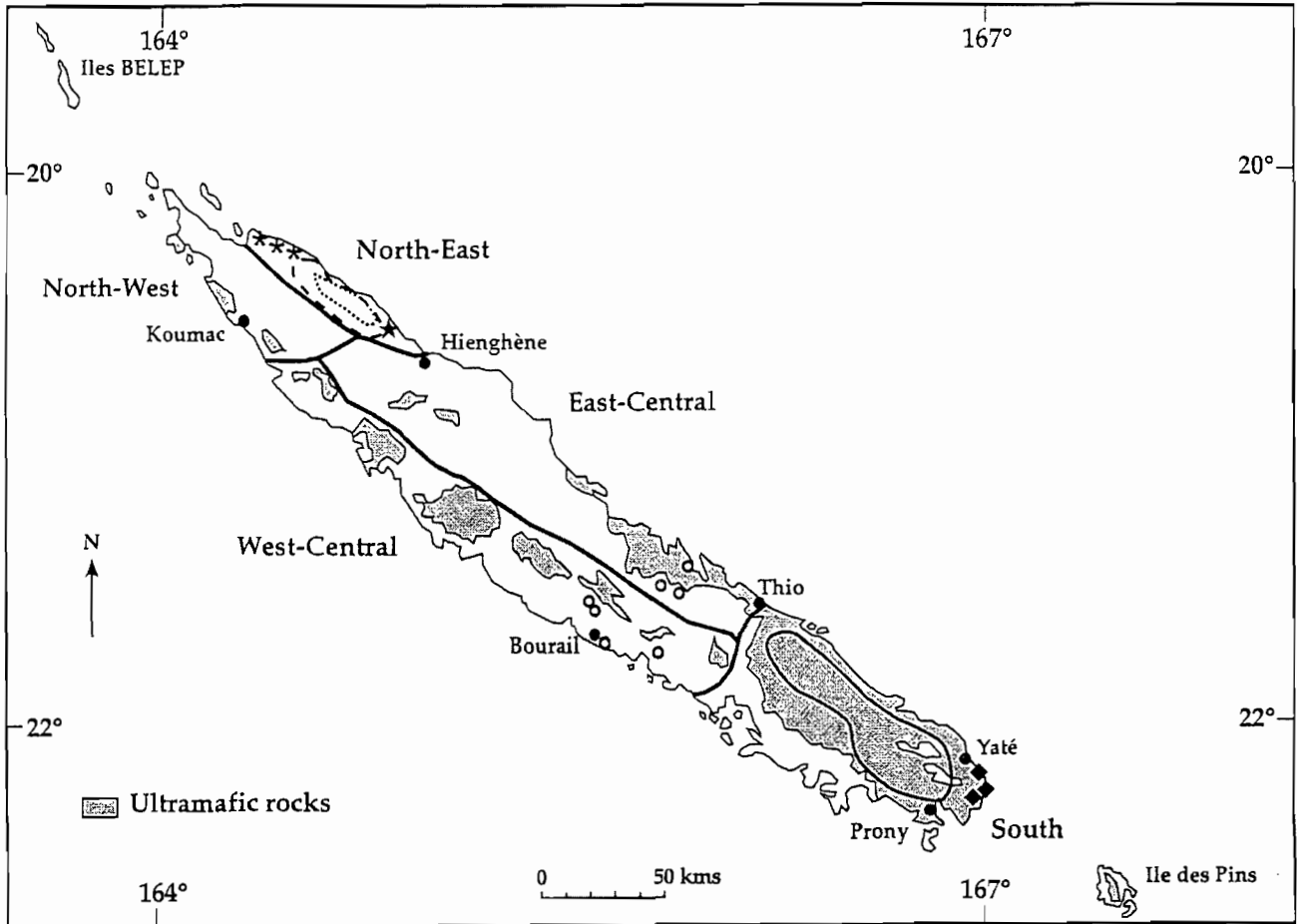
In his theory of refugia, Haffer [32] suggested that the contraction of forests during dry periods leads to extinctions, while the species persisting in such forest refugia are either conserved without modification, or evolve through allopatric speciation, due to the fragmentation of the initial biota. Bennett [33] suggested that the time scale of Pleistocene climatic fluctuations (a few tens of thousands of years) did not allow long-lived species with long generation time such as trees to evolve significantly during a dry period. If this is correct, then it is unlikely that the local endemism of New Caledonia palms (at the specific and generic level) in putative refuge zones can be explained by Pleistocene allopatric speciation. Hooghiemstra and van der Hammen [34] also interpreted mega-diversity of tropical rain forests as “a legacy from the Tertiary rather than as a product of the Quaternary climatic fluctuations”. In New Caledonia, the high level of endemism in the inferred refuge areas is also likely to be due to the conservation of an older flora extinct elsewhere on the island. This seems to be particularly true for the two locally endemic monotypic palm genera, *Pritchardiopsis* and *Lavoixia*. Both are large-

fruited palms, lacking mean of dispersal (the heavy fruits drop below adults and germinate there), and are each known from a single small population. *Pritchardiopsis*, the only New Caledonian palm with palmate leaves, has its closest relatives in Australia and seems to be a Gondwanian relict. *Lavoixia* hardly regenerates in its undisturbed natural habitat, and is at the verge of extinction.

Another line of evidence in support of rain forest refugia is the bipolar distribution of various pairs of sister taxa, as shown by the phylogenetic analysis of New Caledonian palms [35–37]. Within each pair, one species is located in the northeast massif and the other in the south massif. This is the case with *Campecarpus fulcitus*/*Veillonia alba*, *Brongniartikentia vaginata*/*B. lanuginosa* and *Kentiopsis magnifica*/*K. pyriformis*, as shown on figure 5. These sister, but highly differentiated, taxa (even considered as distinct genera in the case of *Campecarpus fulcitus* and *Veillonia alba*) are unlikely to have arisen through Pleistocene allopatric speciation and more probably originated from the Tertiary.

The genus *Kentiopsis* (figure 5) offers some insight for understanding the origin of these bipolar distributions. It comprises two locally endemic species in the northeast (*K. magnifica* and *K. piersoniorum*), one in the southeast (*K. pyriformis*), and one with scattered populations in the central part of the island (*K. oliviformis*). All four species grow at low to middle elevation (10–700 m). *Kentiopsis oliviformis* grows mostly in transitional forests between the dry and wet forests (rainfall ca. 1 200 mm per year) while the other species, all locally endemic, are confined to high rainfall areas. *Kentiopsis oliviformis* probably owes its survival at low elevation in central New Caledonia to its adaptation to a drier climate. No other palm species occurs in transitional forests. As shown on figure 2, there is no high rainfall area (more than 3 000 mm per year) in central New Caledonia. It is therefore likely that a large part of the lowland rain forest flora disappeared from the central sectors during the dry periods of the Pleistocene. This flora may have persisted only in the south and northeast massifs during these periods, thus explaining the bipolar distribution of groups which did not expand during the Holocene.

All locally endemic lowland rain forest palm species are currently restricted to the south and northeast massifs (table I), and all lowland rain forest palm species occurring in the centre are widespread and probably followed the Holocene expansion of the rain forest. Jaffré and Veillon [38] suggested that the floristically rather poor rain forests of central New Caledonia are indeed young, while the richest rain forests of the south and northeast have been undisturbed since Tertiary times. Typically, rain forests of central New Caledonia below 500 m elevation hold palm communities composed primarily of *Burretiokentia vieillardii* or/and *Chambeyronia macrocarpa* and *Basselinia gracilis*, with additionally either *Basselinia velutina*, *Clinosperma bracteale*, *Cyphokentia macrostachya* or *Cyphosperma balansae*, depending on the locality. These species are found on both ultramafic and schistose sub-



- * *Kentiopsis magnifica*
- ★ *Kentiopsis piersoniorum*
- *Kentiopsis oliviformis*
- ◆ *Kentiopsis pyriformis*
- *Brongniartikentia vaginata*
Campecarpus fulcitus
- *Veillonia alba*
- *Brongniartikentia lanuginosa*

Figure 5. Distribution of some palm species in New Caledonia.

strates and are the most widespread, and probably the most efficiently dispersed as well. Dispersal of palms is almost entirely carried out by frugivorous birds [39, 40]. The most active bird in this respect is the *notou* (*Ducula goliath*), a giant pigeon which is the only species able to ingest the largest palm fruits, those of *Chambeyronia macrocarpa*. This common palm is an important part of the

bird's diet, a fact which may account for its very wide distribution. The parakeet *Cyanoramphus novaezelandiae* subsp. *saisseti* eats small palm fruits such as those of *Basselinia*, *Brongniartikentia* and *Cyphokentia*. These forest birds are also New Caledonian endemics and are mostly involved in short distance dispersal within the rain forest [41].

At higher elevation, the Quaternary vegetational history of the central sectors can be different, because refugia may have existed there due to the increase of rainfall with elevation. The only two locally endemic species of these sectors, *Basselinia tomentosa* and *B. vestita* are confined to montane habitats. *Basselinia vestita* could however be a neoendemic on an isolated ultramafic mountain top (Me Ori), since it is closely related to and partly introgressed with two widespread species occurring in parapatry (*B. gracilis* and *B. pancheri*). *Basselinia tomentosa* is known from two small localities 20 km apart, which may represent the remains of a wider range. Several other species (*Cyphokentia macrostachya*, *Cyphosperma balansae*, *Basselinia sordida*, *B. velutina*) also have disjunct populations but covering a wide range in central New Caledonia, at middle to high elevation, which could be relictual as well. Likewise, two species which have their main populations in area No. 1 in the northeast, *Chambeyronia lepidota* and *Moratia cerifera*, also have isolated populations in area No. 2 in the Centre–East. This seems to indicate a former continuous range along the eastern mountains, which linked areas No. 1 and No. 2 together, prior to the Pleistocene.

It is clear that the distribution of palms in New Caledonia is also influenced by substrate variations, but this is partly correlated with climatic effects, and sometimes hardly separable from them. Indeed, local edaphic endemism is largely superimposed on the four areas of major diversity and endemism recognized above. This is especially true on schistose substrates, where nine of 13 species restricted to this type of substrate are confined to the areas No. 1 or 1+2 combined, which are entirely schistose. This correlation is not so evident on ultramafics, since only five of 15 species restricted to this substrate are endemic to the ultramafic areas No. 3 and 4.

Among the 12 species sufficiently widespread to be potentially dispersed on both ultramafic and schistose rocks, seven do occur on both substrates, five are restricted to ultramafic rocks, and none to schistose rocks. More-

over, the strong selective pressure exerted by soils derived from ultramafic rocks (which are very poor in essential nutrients and rich in phytotoxic heavy metals) have led to highly specialized morphological and/or physiological adaptations in several palm species restricted these substrates [36, 37], a phenomenon which has been well documented for the entire flora of the ultramafic outcrops [14, 23].

Based on these considerations, we suggest that closely related species which occur on different substrates, and are now geographically very distant from one another (e.g. one in the south on ultramafic rocks and the second in the northeast on schists), may have differentiated prior to fragmentation of the once continuous forest, at a time when the ancestor of the sister species was able to disperse on both substrates. Thus, Tertiary edaphic vicariance may be an explanation to these sister species pairs, while Quaternary disjunct distribution would not have been involved in the speciation process, as suggested above.

5. Conclusion

The evolution and diversification of palms in New Caledonia is undoubtedly due to multiple factors, among which the effect of substrate must have been important. However, the present distribution of species may have been so strongly influenced by Pleistocene climatic fluctuations that Tertiary distribution patterns, potentially informative for understanding causes of speciation, have been blurred. Since populations of most of these palms do not expand rapidly into new suitable forest habitats, they remain mainly in what we consider being Pleistocene refugia. Paleoendemism therefore seems to be the dominant trait of this palm flora.

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