The Impact of Forest Disturbance on the Palms of New Caledonia

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1. Seedlings of *Kentiopsis pyriformis* germinate on red colluvium rich in iron oxide. This material originates from the erosion of ultrabasic rocks (peridotite) on nearby slopes. *Kentiopsis pyriformis* is one of the first plant species to establish itself on these unstable, newly deposited soils.



As natural vegetation is being transformed by human activities, survival of many species depends on their ability to persist and reproduce in anthropogenic vegetation. Deforestation is the major effect of human intervention in the tropics, causing endangerment of many species strictly associated with primary forest. Other forest species on the contrary, including various palms, can take advantage of these changes and become more abundant than they are in undisturbed habitat, eventually becoming dominant or invasive in some secondary vegetation types (Mitja & Farraz 2001).

New Caledonian palms provide an interesting illustration of this phenomenon. The island's palm flora includes 37 species in our present taxonomic understanding (Hodel & Pintaud 1998), although this number will rise to 39–40 with forthcoming taxonomic treatments. All species are endemic to New Caledonia and grow primarily in forests. Moreover, the vast majority of species have very small distribution ranges, which make them especially vulnerable to habitat destruction.

Alteration of natural habitats has indeed been extensive in New Caledonia. Primary forests have been greatly reduced and highly fragmented all over the island, due to mining activities, logging and land conversion for agriculture. Despite this, only six species are considered endangered or critically endangered, according to IUCN Categories (Pintaud et al. 1999 and Table 1). Among these species, four are threatened by habitat destruction.

So how do palm species respond to habitat changes? At least 16 species have ecological adaptations which make them able to survive in disturbed vegetation, and sometimes to thrive more successfully in such environments than in primary forest.

Response of palms to primary forest disturbance

Even under natural conditions, the tropical rainforest of New Caledonia is a very dynamic and changing ecosystem. Landslides are frequent along the rapidly eroding steep slopes of the mountains that cover most of the island, and cyclones can cause widespread damage to the forests. Some species are specialized in surviving such damage, especially through a biological phenomenon called mast seeding (i.e., considerable variation from year to year in seed output in perennial plants). In some cases, most of the plants flower at the same time and subsequently die, after dispersing huge quantities of seeds. This is typically the case of the endemic bamboo genus Greslania, which is common in forests on ultrabasic rocks and in secondary vegetation. In the case of the monocarpic pioneer tree Cerberiopsis candelabrum (Apocynaceae), cyclones promote massive flowering. Millions of winged seeds

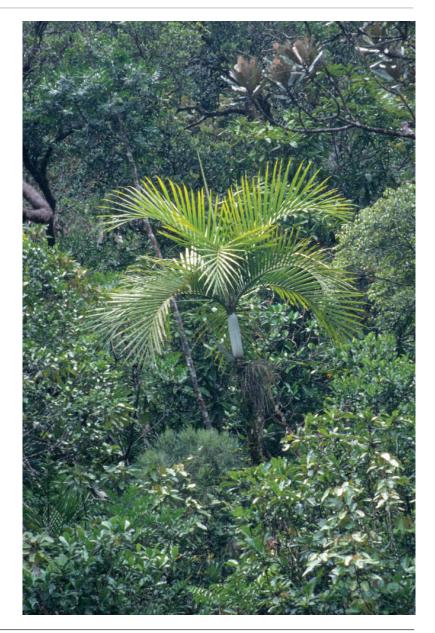
2 (left). The rare *Kentiopsis piersoniorum* requires local events of forest disturbance to establish new stands but will not tolerate a strong alteration of its habitat. 3 (right). A dense stand of *Cyphokentia macrostachya* forms a monospecific canopy in a former gap produced by logging activities four decades earlier in the Rivière Bleue Provincial Park.



are thereafter wind-dispersed and germinate quickly in open areas, where they begin to regenerate the forest. Southern beeches (*Nothofagus* spp.) also undergo mast seeding and constitute patches of mono-dominant forests, which are presumably established similarly, although there is no direct evidence of it due to slow growth of these species (Read et al. 1995).

Some palms that tend to form pure stands, such as *Kentiopsis* species (Pintaud & Hodel 1998), also have distinctive fruiting patterns. Each year these palms produce over a short period (one month) large quantities of small, bright red fruits, which are actively dispersed

by birds. Seeds germinate within a few days after dispersal, especially on barren soil (Fig. 1), and probably contribute to restoring monodominant stands in more or less open, or disturbed areas. As for *Nothofagus*, this must, however, take so much time that it is difficult to demonstrate. Despite their ability to grow in naturally disturbed sites, *Kentiopsis* species are rare and endangered. In fact, they do not tolerate any human alteration of their environment and are threatened by habitat loss. It seems that they need vast areas of natural forest, only infrequently and very locally disturbed, in order to maintain their population dynamics (Fig. 2).

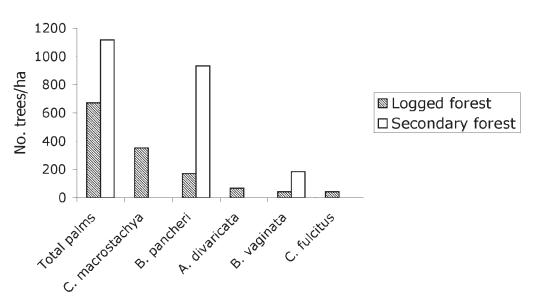


4. In undisturbed forest, *Cyphokentia macrostachya* occurs as isolated, scattered individuals (Rivière Bleue, 250 m elevation). Table 1. Conservation status and occurrence of New Caledonian palm species in primary and secondary vegetation types. IUCN conservation status: LRlc = low risk, least concern; LRcd = low risk, conservation dependant; Vu = vulnerable, E = endangered, CR = critically endangered.

Palm species	Conservation status	Primary forest	Secondary forest	Maquis
Actinokentia divaricata	LRlc	+	+	
Actinokentia huerlimannii	Vu	+	+	+
Alloschmidia glabrata	LRlc	+		
Basselinia deplanchei	LRlc	+	+	+
Basselinia favieri	LRcd	+		
Basselinia gracilis	LRlc	+	+	
Basselinia humboldtiana	LRcd	+	+	
Basselinia iterata	Vu	+		
Basselinia pancheri	LRlc	+	+	+
Basselinia porphyrea	LRcd	+	+	+
Basselinia sordida	LRlc	+		
Basselinia tomentosa	Vu	+		
Basselinia velutina	LRlc	+		
Basselinia vestita	CR	+	+	
Brongniartikentia lanuginosa	LRlc	+		
Brongniartikentia vaginata	LRlc	+	+	+
Burretiokentia dumasii	LRcd	+		
Burretiokentia grandiflora	LRcd	+		
Burretiokentia hapala	Vu	+		
Burretiokentia koghiensis	Vu	+		
Burretiokentia vieillardii	LRlc	+		
Campecarpus fulcitus	LRlc	+		
Chambeyronia lepidota	LRlc	+		
Chambeyronia macrocarpa	LRlc	+		
Clinosperma bracteale	LRlc	+	+	
Cyphokentia macrostachya	LRlc	+		
Cyphophoenix elegans	Vu	+	+	+
Cyphophoenix nucele	CR	+		
Cyphosperma balansae	LRlc	+		
Kentiopsis magnifica	Vu	+		
Kentiopsis oliviformis	E	+		
Kentiopsis piersoniorum	LRcd	+		
Kentiopsis pyriformis	CR	+		
Lavoixia macrocarpa	CR	+		
Moratia cerifera	LRlc	+		
Pritchardiopsis jeanneneyi	CR	+		
Veillonia alba	LRlc	+		
Total Vu: 7	7; E: 1; CR: 5	37	11	6

Rainforest species, which develop in the understory or lower canopy at low to moderate densities, appear more prepared to survive larger-scale disturbance than the tall gregarious *Kentiopsis* species. Many of these species have a long establishment phase consisting of

increasing leaf size without producing an aerial trunk (Tomlinson 1990). This phase can go on under low light conditions, while trunk development requires a significant increase in light intensity (Kahn & de Granville 1992). Typically, populations of these palms comprise



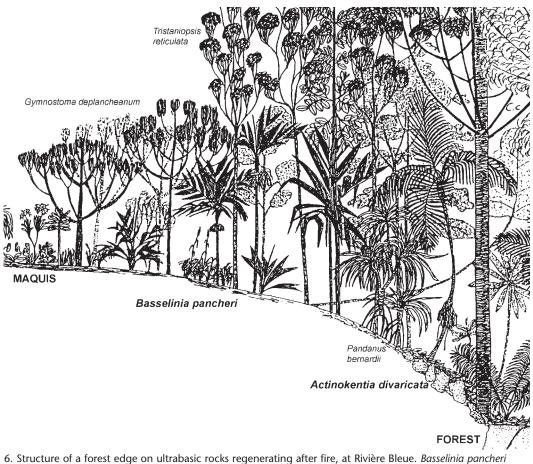
Density of palms > 5 cm dbh

a large proportion of juveniles in establishment phase, many of them waiting for appropriate growth conditions, a few in the stage of rapid growth, and adult trees showing only slow growth. An anthropogenic disturbance such as selective tree logging, producing many gaps in the canopy, will therefore promote a rapid growth of the trunk in a great number of juvenile plants, allowing them quickly to reach the adult size, before closure of the canopy. This will result in unusually high densities of adult palms, persisting decades after the restoration of the canopy.

In fact selective logging has affected most of the New Caledonian rainforest at low to medium elevation. Some large tree species providing excellent woods have been extensively logged, especially kaoris (Agathis spp., Araucariaceae) and houp (Montrouziera cauliflora, Guttiferae), modifying substantially the forest structure. In the rare but spectacular remnants of lowland pristine forests, Agathis trees (A. lanceolata on ultrabasic rocks and A. moorei on schists) are so abundant that they tend to form a 40–45 meters-tall canopy above the 25 m tall angiosperm species. On ultrabasic rocks, narrowly columnar araucarias (A. subulata) reaching 60 m tall emerge from the canopy. Logging of these conifers basically suppresses the upper forest layer. Montrouziera cauliflora is a gigantic emergent and scattered tree producing a magnificent and extremely durable red wood. Logs abandoned in the forest of Mont Koghi above Nouméa after WWII are still in perfect shape. Removing these enormous trees produces large gaps in the forest and leads to local disappearance of the species, prompted by its very slow and difficult regeneration.

Such human interventions produce an important light increase in the forest understory, of which subcanopy palms with a long establishment phase benefit considerably, increasing rapidly their density. A few decades after selective logging, the forest will look pristine to an observer unaware of these processes, while the forest has in fact been considerably modified in its structure and to some extent, floristic composition. With more than 2000 individuals of *Cyphokentia* macrostachya of all sizes per ha. (Pintaud 1999), some forests in southern New Caledonia will look spectacular to the palm enthusiast (Fig. 3). This, however, is clearly an anthropogenic effect, C. macrostachya being much more scattered in primary forest (Fig. 4). Other species commonly forming dense populations as a consequence of selective logging include Burretiokentia vieillardii and B. hapala, Cyphosperma balansae and Chambeyronia macrocarpa.

^{5.} Composition of palms communities in adjacent selectively logged forest and secondary forest at Rivière Bleue. Total palm density is higher in secondary forest, but species diversity is much lower than in selectively logged forest.



6. Structure of a forest edge on ultrabasic rocks regenerating after fire, at Rivière Bleue. *Basselinia pancheri* develops abundantly in the *Gymnostoma deplancheanum* scrub on the forest edge and in the adjacent myrtaceous (with *Tristaniopsis reticulata*) low secondary forest. *Actinokentia divaricata* appears farther inside the forest, among well-grown secondary forest species such as *Cerberiopsis candelabrum* (*C. c.*) and *Pandanus bernardii*. No primary forest palm is found within these early successional stages of the forest (Drawing by J.-C. Pintaud).

Palms in secondary forest

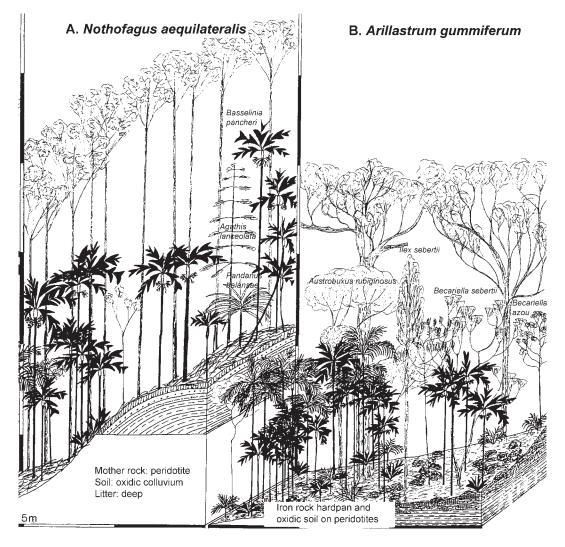
In the previous paragraph, I dealt with alterations of the primary forest which do not disrupt the biological and ecological cycles of the ecosystem. Secondary forests, on the contrary regenerate after complete destruction of the original forest, and have a much simpler structure and poorer floristic composition. These forests will eventually return to primary forest, but after a very long time. In New Caledonia, eleven palm species occur in secondary forest (Table 1), and some of them in much higher densities than in primary or moderately disturbed forest. The most frequent and widespread cause of primary forest destruction and therefore secondary succession in New Caledonia is fire. Early mining activities and traditional agricultural practices produced extensive fires, but natural fires have also been important for a long time (Hope & Pask 1998).

Surveys in the Rivière Bleue Provincial Park, in southern New Caledonia, showed marked differences in adjacent palm communities in selectively logged forest and secondary forest regenerating after burning. In selectively logged forest, there were five species, the most abundant being Cyphokentia macrostachya and Basselinia pancheri on colluvium, Campecarpus fulcitus and Actinokentia divaricata on eroded rocky soil, while the rarest species was *Brongniartikentia vaginata*, with no more than 10 adult trees per ha. On the contrary, in secondary forest, there were only two species, Basselinia pancheri and Brongniartikentia *vaginata*, both at much higher densities than in the selectively logged forest (Fig. 5). In both forest types, palms are the most abundant trees at the family level, representing 9–10 % of all stems > 2 cm dbh, followed by Guttiferae (8%) and Cunoniaceae (7%) in secondary forest,

and Lauraceae (8 %) in primary forest (Pintaud 1999).

Secondary forests harboring dense palm populations are mostly restricted to ultrabasic rocks. Typically, the regeneration of the forest on ultrabasic rocks begin with a scrub developing on bare oxidic soil or iron-rock hardpan were *Gymnostoma* species (Casuarinaceae), especially *G. deplancheanum* and *G. glaucescens*, develop and eventually form a mono-dominant low forest. These trees produce an abundant litter and have a root symbiosis with a micro-organism (*Frankia*), allowing them to assimilate atmospheric nitrogen and fertilize the soil, as do legume plants with other symbionts (*Rhizobium*). These improved ecological conditions allow in turn the development of a more diverse forest flora, including the first palms, especially *Basselinia pancheri*. As the forest continues to grow, other palms appear, such as *Actinokentia divaricata*, *Brongniartikentia vaginata* and *Clinosperma bracteale* (Fig. 6.). Palms restricted to the primary forest, such as *Cyphokentia macrostachya*, *Campecarpus fulcitus*, *Burretiokentia vieillardii* and *Chambeyronia macrocarpa* will only begin to appear in a much later stage of the succession.

7. Architecture of mono-dominant forests and associated palm communities at Rivière Bleue. *Nothofagus* forests (A) have a very simple architecture with basically a smooth canopy made of southern beeches of same size and presumably age, and a subcanopy layer composed mostly of *Basselinia pancheri*. *Arillastrum* (Myrtaceae) forests (B), have a much more irregular and open canopy, allowing the development of a diversified and heterogeneous subcanopy layer, where *Basselinia pancheri* and *Brongniartikentia vaginata* are abundant (Drawing by J.-C. Pintaud).



(-). All species present are characteristic of secondary vegetation (see Table 1).	aracteristic of secondary	vegetation (see Table 1).		
Secondary forest type:	Monodominant	Mixed	Monodominant	Monodominant
Main floristic trait:	Nothofagus	Guttiferae-	Nothofagus	Gymnostoma
	aequilateralis	Cunoniaceae	aequilateralis	glaucescens
Location:	Rivière Bleue Park	Rivière Bleue Park	Pic Grand Kaori	Nodela
Elevation:	150 m	150 m	200 m	600 m
Palm species:				
Actinokentia divaricata	+	ı	+	+++
Basselinia pancheri	+++	+++	+++	+++
Basselinia gracilis		ı	+++	+++
B. pancheri \times gracilis		ı	++	+
Brongniartikentia vaginata	+	++	I	
Clinosperma bracteale	I	ı	I	+
Total number of species	3	2	3 + 1 hybrid	4 + 1 hybrid
Number of species in				
adjacent primary forest	5-7	5-7	4	7

There are several other interesting features of secondary forests on ultrabasic rocks. Secondary forest types are surprisingly varied on this substrate. They can be divided into two main types: mixed and mono-dominant. Mixed secondary forests have a canopy composed of many different species, while mono-dominant ones have an upper layer composed of a single species. The causes determining the forest types are not very clear.

Table 2 (continued)				
MONTANE SECONDARY FOREST				
Secondary forest type:	Monodominant	Monodominant	Monodominant	Mixed
Main floristic trait:	Nothofagus	Nothofagus	Nothofagus	Araucaria
	codonandra	balansae	baumanniae	mont. Araliaceae
Location:	Mont des Sources	Menazi	Mont Mou	Me Ori
Elevation:	950 m	1000 m	1050 m	900 m
Palm species:				
Actinokentia divaricata	+	+	I	ı
Basselinia pancheri	I	+	ı	+
Basselinia gracilis	I	I	I	+++
Basselinia vestita	ı	I	ı	+
B. gracilis \times vestita	1	1	1	+++
Brongniartikentia vaginata	+	ı	ı	ı
Basselinia deplanchei	+++	++	+	ı
Basselinia humboldtiana	++	+++	ı	++
Basselinia porphyrea	++	I	1	ı
Clinosperma bracteale	1	I	I	++
Total number of species	5	4	1	5 + 1 hybrid
Number of species in				
adjacent primary forest	7	4	0	5

For example, regeneration after a fire on a forest edge can lead to either mixed secondary forests (with a predominance of Araliaceae, Guttiferae, Cunoniaceae or Myrtaceae) or mono-dominant *Gymnostoma* forests.

Moreover, very commonly we can observe a mosaic of mixed-canopy primary forest and patches of mono-dominant forests composed either of *Nothofagus* spp., *Arillastrum gummiferum* (Myrtaceae), *Balanops pancheri*



8. A hybrid between Basselinia vestita and B. *gracilis* on the top of Me Ori. The plant is reminiscent of B. gracilis but has the greyish tomentum on the underneath of leaflets characteristic of B. vestita. As hybrids already outnumber pure individuals of B. vestita, this species endemic to the summit of Me Ori is likely to disappear within the genepool of the more abundant and widespread B. gracilis and B. pancheri.

(Balanopaceae), Cerberiopsis candelabrum (Apocynaceae), Cocconerion minus (Euphorbiaceae) Agathis ovata (Araucariaceae) and some other species. Ecologists assume that all these mono-dominant forest patches are of secondary origin, establishing through some kind of disturbance. In the case of rapidly growing species, such as Cerberiopsis or Cocconerion, this can be demonstrated, but in many other instances, the causes promoting the establishment of stands are unknown. This is especially true for Nothofagus stands, which can be very large and are common and widespread on ultrabasic rocks. Interestingly, all mono-dominant forest types contain palm communities very similar to those of typical mixed secondary forest, thus indicating their probable secondary origin (Table 2 and Fig. 7).

Another curious characteristic of secondary forests on ultrabasic rocks is that their palm species richness increases with elevation, while it is the opposite in primary forest (Pintaud et al. 2001). Consequently, secondary forests are much poorer in palm species than adjacent primary forest at low elevation (Table 2a and Fig. 5) but they are often equally rich or richer at higher elevation (Table 2b). This is due to the fact that primary forest above 900–1000 elevation is lower, more open and structurally more similar to secondary forests, but with a more diverse flora of dicotyledonous trees and conifers.

Palm communities in secondary forests are not only modified with respect to primary forests in species composition and density of individuals, but are also deeply affected at the level of plant biology and population genetics. Light increase in the understory of secondary forest promotes growth and flowering of palms, and higher densities of individuals in some species facilitate cross pollination, as all species except Pritchardiopsis are strongly protandrous and thus allogamous. In the complex of closely related and often sympatric species of Basselinia section Basselinia, such processes will promote interspecific hybridization. As a matter of fact, hybridization in this group has been repeatedly observed in various secondary forests, but never in primary forest. We have seen that density of Basselinia pancheri can be more than five times higher in secondary than in primary forest (Fig. 5). In several secondary forests where B. pancheri grows with B. gracilis, interspecific hybrids have been observed. Basselinia pancheri is solitary and has bilobed fruits, while B. gracilis is caespitose with rounded fruits. Among these typical plants, are also found individuals which are caespitose but with bilobed fruit. Similarly, a putative hybrid between Basselinia pancheri and Basselinia deplanchei occurring on Mont Nekando, has the fruits of the first parent and the habit of the second. It was initially described as a separate genus (*Nephrocarpus* schlechteri) and latter reduced in synonymy of Basselinia pancheri. On Me Ori, a dome-shaped mountain of central-western New Caledonia reaching 1000 m elevation, there are three sympatric species of Basselinia section Basselinia: B. gracilis, B. pancheri and B. vestita, the last endemic to Me Ori. In the secondary forest, apparently pure individuals of *B. vestita* are very scarce, while hybrids of this species with *B. gracilis* and *B. pancheri* are very common. Some plants even show a mixture of characters from the three species. Such phenomena can have various implications. For one part, it locally increases the genetic and morphological diversity, producing a wide range of intermediate forms between the parent species and also completely new characters as a result of genetic recombination. This may promote the evolutionary dynamics of the species complex. However, it is at the same time a threat to the integrity of each individual species, and may lead to extinction through genetic dilution in the case of the very locally endemic Basselinia vestita. Extensive burning on Me Ori and surrounding areas has limited the extension of Basselinia *vestita* to the very top of the mountain and at

9. The Col d'Amos range in far north New Caledonia has been almost entirely deforested since pre-European times. Captain Cook found this desolate landscape reminiscent to the Scottish (Caledonian) countryside and therefore named the island New Caledonia. Crowns of *Moratia cerifera* emerge from a gully where a fragment of forest persists. In the foreground is a *maquis* vegetation on schistose rocks with *Dracophyllum verticillatum* (Ericaceae).



the same time promoted the expansion of *Basselinia gracilis* and *B. pancheri*. Hybrids with *B. vestita* have been observed up to the summit of Me Ori (Fig. 8), which means that this species no longer exists as a pure population. In a previous study (Pintaud et al. 1999), I did not give much attention to this problem and assessed the conservation status of *B. vestita* as vulnerable. Here I consider it to be critically endangered due to the hybridization process (Table 1).

On schistose rocks, the situation is very different. Only two palm species occur in secondary forest. One of them, *Basselinia gracilis*, is the species having the largest geographical distribution and broadest ecological range in New Caledonia; therefore

it is not surprising to find it in secondary forest. The other species, Cyphophoenix elegans, has on the contrary a limited distribution. It is associated with Kentiopsis magnifica and Moratia cerifera (Fig. 9) in remnants of the primary forest in far northern New Caledonia, and develops in adjacent secondary forest and Melaleuca maquis regenerating after fire. Absence of palms in most secondary forests on schistose rocks is probably due to competition with fast growing pioneer Cunoniaceae and Myrtaceae species. Secondary vegetation has a much slower growth on ultrabasic rocks (and also on the very windy schistose ridges of northern New Caledonia where Cyphophoenix elegans thrives), allowing establishment of the slow growing palm species.



10. Brilliantly coloured crownshafts of *Basselina deplanchei* are a common sight in secondary forest and *maquis* on ultrabasic rocks. Haute Neuménie, 900 m elevation.

Palms in *maquis* vegetation

The maquis is an open, low vegetation composed of sedges, ferns and sclerophyllous shrubs. It is essentially developed on, and characteristic of ultrabasic rocks, although it can be found occasionally on schistose rocks (Fig. 9). It is mostly of secondary origin, replacing the forest after fires, but it also occurs naturally under severe conditions (on sharp rocky or windswept ridges or on iron rock hardpan for example). Nowadays, the maquis covers 80 % of all ultrabasic outcrops, while only 15 % of the area is occupied by rainforest and 5% by swamps. The soils on which develop the maguis of the ultrabasic outcrops are very poor, with high content in toxic heavy metals and very low content of organic matter.

Nine out of ten plant species developing in this very peculiar habitat are endemic to New Caledonia (in total 1019 endemic species out of 1142 reported from maquis by Jaffré et al. 1994). Among them, only six species are palms, and three belong to the genus Basselinia (Table 1). The maguis is the preferential habitat of two palm species, Basselinia porphyrea and Basselinia deplanchei. Both species occur only marginally in primary forest. They have very hard and thick leaves and are especially attractive, although very slow growing (Front Cover). Basselinia deplanchei is a very polymorphic species, with either pinnate or bifid leaves, and generally colorful crownshafts (Fig. 10). These species represent an adaptation to very harsh conditions, uncommon among New Caledonian palms. Basselinia porphyrea has a very limited distribution, while B. deplanchei is widespread and has probably expanded through the extensive maquis on ultrabasic rocks of anthropogenic origin. On Cyphophoenix rocks, schistose elegans occasionally occurs in maquis in the form of dwarf individuals with very thick leaves, similar in habit to Basselinia porphyrea.

Therefore, disturbed vegetation on ultrabasic rocks, with its structural and floristic diversity, contributes significantly to conserve the endemic New Caledonian flora, and especially the palms, as nearly one-third of them not only survive but sometimes develop exuberantly in such habitats.

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