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Time and tempo of diversification in the flora of New Caledonia

Yohan Pillon

Department of Biology

University of Hawai‘i at Hilo

200 West Kawili Street

Hilo, HI, 96720

USA

ABSTRACT

New Caledonia is well-known for its rich and unique flora. Many studies have focused on the biogeographic origins of New Caledonian plants, but rates of speciation on the island have scarcely been investigated at all. Here we use dated phylogenies from selected published studies to evaluate the time and tempo of diversification in New Caledonia. The 12 plant lineages investigated all seem to have colonised the island less than 37 My ago, when New Caledonia re-emerged after a period of inundation. The timing of these arrivals is spread across the second half of the Cenozoic. Speciation rates are not particularly high and are negatively correlated with lineage age. The palms have the fastest speciation rates and also the most recent arrival times. The lineage ages of rainforest plants suggest that this ecosystem has been present for at least 6.9 My. The New Caledonian flora seems to represent a relatively old community which may have reached a dynamic equilibrium. Colonisation by new immigrants has been possible until relatively recently and diversity-dependent processes may still be affecting the diversification rates of the earlier colonisers. Further studies on the diversification of large plant clades with exhaustive sampling should help to clarify this.

Keywords: Biodiversity hotspots, island biogeography, Pacific, palms, serpentine, speciation rate, ultramafic soils

INTRODUCTION

New Caledonia is an archipelago in the south-west Pacific, well-known for its rich and distinctive flora. It is considered as one of the major biodiversity hotspots of the planet (Myers *et al.*, 2000) and has attracted major interest in biogeographical studies. The genus *Nothofagus* Blume (Nothofagaceae) exemplifies well the different phases of progress in phylogeographical studies, based first on cladograms built up from morphological data (Hill & Jordan, 1993), then on molecular data (Manos, 1997) and most recently using molecular clocks (Cook & Crisp, 2005).

New Caledonia is a continental island that drifted away from Australia in the late Mesozoic (ca. 80 My ago) and has been isolated since then (Pelletier, 2006). The island was then submerged under deep sea during the first half of the Cenozoic as shown by the deposit of Paleocene-lower Eocene pelagic limestone (Paris, 1981; Picard, 1999; Pelletier, 2006). Re-emersion of the island occurred about 37 My ago (Cluzel & Chiron, 1998) when the island was uplift and the ophiolitic nappe overthrust that is the origin of the ultramafic soils. These soils, including serpentinite in the strict sense, have several characteristics that are limiting to plant/ low fertility (low N, P, K); high Mg/Ca ration, high concentration of heavy metals (Co, Cr, Ni, etc.), low water-holding capacity and increased susceptibility to fire (Proctor, 2003). Although evidence for immersion of the island have been available for a long time, most biologist have favoured until recently the hypothesis of the persistence of the New Caledonian biota since its separation from Australia and throughout the Cenozoic. This conviction is increasingly challenged as biologists begin to take into account evidence from geological studies (some of which were published some time ago), that indicate that New Caledonia was submerged from the end of the Cretaceous to the mid-Cenozoic and emerged only ca. 37 My ago. The presence of nearby islands during the early Cenozoic that could have served as refuge cannot be excluded although evidence are lacking (Pelletier, 2006). The debate is still

running on the vicariant (Ladiges & Cantrill, 2007) or entirely long-distance dispersal (Grandcolas *et al.*, 2008) origins of the New Caledonian biota, but the latter concept is gaining increased support. Indeed, as more molecular clock analyses are becoming available, no study has provided firm evidence for a colonisation of any terrestrial organism prior to 37 My (reviewed in Grandcolas *et al.*, 2008; Cruaud *et al.*, 2012). It seems likely that biologists have been misled by the abundance of “early branching” plant lineages in New Caledonia and the erroneous assumption that they persist in their ancestral area (Crisp & Cook, 2005; Crisp, Trewick & Cook, 2011). A large number of plant lineages present in New Caledonia and once thought to be “archaic” (Winteraceae, Monimiaceae, Atherospermataceae, etc.) belongs to the Magnolianaes and more specifically Laurales. These clades have been shown to be over-represented in New Caledonia, possibly because of an exaptation (“pre-adaptation”) to ultramafic soils (Pillon *et al.*, 2010). Therefore their abundance may be better explained by ecological factors rather than biogeography, and the same may also be true for Conifers, which are exceptionally diverse on the island (de Laubenfels, 1996).

Whether we consider the New Caledonia biota to date back to the split from Australia in the Cretaceous or to its re-emergence in the mid-Cenozoic, it is not known if the vegetation has been the same throughout. Furthermore, although the island has been inhabited by plants for a long time, it can still be a land of immigration, as dispersal over long distances can also occur within a continent (Galley *et al.*, 2007; Gehrke & Linder, 2009). For example, although Africa has been geologically stable for a long time, it is widely accepted that the Cape flora is relatively recent and probably developed after the establishment of a Mediterranean climate (Richardson *et al.*, 2001; Linder, 2005). The Cenozoic history of New Caledonia is still poorly understood. It is not clear for example how its mountain range has changed with time. New Caledonia was once entirely covered by ultramafic rocks (Pelletier, 2006) and it is not known at what rate this terrain may have weathered and fragmented. Because of the

abundance of these poorly fertile soils, New Caledonia may be considered as an old, climatically buffered, infertile landscape (OCBIL, Hopper, 2009) along with the Cape flora or the South-West Australia, however its climatic stability remains to be proven. There is some evidence that Quaternary climatic oscillations may have affected the New Caledonian flora (Pintaud, Jaffré & Puig, 2001; Pillon *et al.*, 2009), but this requires further studies. The main vegetations of New Caledonia include rainforest, sclerophyll forest, savanna (a secondary vegetation mostly dominated by *Melaleuca quinquenervia* (Cav.) S.T. Blake)) and maquis (Jaffré, 1993). The maquis is a typical scrubby vegetation found on ultramafic soils which may have been dependant on the onset of a climate favourable to a certain fire-regime (Jaffré, Rigault & Dagostini, 1998). It is not known how old each of these vegetation types are and their occurrence is highly tight to climate and geology.

If so-called “ancient” lineages may have received more attention in the study of New Caledonian biogeography, there may be something to learn from more recently diverged lineages which may actually be older than expected. First, they represent the largest proportion of the flora in terms of numbers of species and also as ecologically dominant species. Furthermore, the fact that they diversified in New Caledonia (vs. a monotypic group) implies that their crown diversification can be dated. The latter provides a more reliable minimum age for the origins of the New Caledonia biota. Thus, as New Caledonia is now widely acknowledged as a ‘museum of biodiversity’, we investigate here how old it is as a cradle of biodiversity. We selected here a taxonomically diverse set of studies that satisfy a number of criteria (described below) in order to develop relatively unambiguous evidence. This study aims not to be extensive in terms of its coverage of taxa, but to develop reasonably reliable estimates of the age of the vegetation and the tempo of diversification in the New Caledonian flora.

METHODS

A literature search was carried out to identify any studies on New Caledonian seed plant phylogenetics and was largely based upon the author's knowledge accumulated over years. Only the studies satisfying the following criteria were retained: 1) the group investigated must be the result of single colonization event and must contain more than one species; 2) to ensure that the most basal split in this clade is contained in the study, all (or almost all) the species of each clade must be included, or all the endemic genera it contains must be included and 3) estimates of the stem age and the crown age of the clade endemic to New Caledonia must be provided. If molecular clock studies may contain methodological problems and uncertainty that can greatly affect age estimation (Graur & Martin, 2004), the compilation of multiple studies should reduce the impact of such confounding factors.

The stem age (the age of the divergence between the endemic clade and its non-New Caledonian sister lineage, preferably continental) provides a conservative estimate of the earliest time of the group's arrival in New Caledonia (Figure 1). At the other extreme, the crown age provides a conservative estimate of the latest time of arrival of this group in New Caledonia, and also the latest date of the first diversification event. Thorough sampling of the clade is therefore important as the absence of some basal taxa could lead to a significant under-estimate of crown age. Because extinction may have erased intermediate nodes in the land of origin or in New Caledonia, it is not possible to determine when the dispersal/vicariant event took place between the stem-age and the crown-age, nor when the clade started to diversify in New Caledonia (Figure 1). Some attention must be paid to the sister-clade, which, especially in the case of an island endemic group (rather than continental, but see figure 1), may actually represent an ancient dispersal out of New Caledonia.

To develop an estimate of the mean diversification rate of each clade in New Caledonia, we use equation 4 from Magallón & Sanderson (2001) which utilises species

numbers and crown age. Although these are rather simplistic estimates, the aim of this study was to compare diversification rates in New Caledonia with those in other areas and this was done by applying the same calculation for all clades considered. We used mean or median age for speciation rate calculation as age range were not available for many studies, and we aimed at comparing speciation rate between groups rather than estimate precisely speciation rate for individual groups. We also included data (crown age and species number) from a number of radiations in New Zealand (reviewed in Linder, 2008) and recalculated mean diversification rate with the same equation to compare with New Caledonia as well as a few groups from the Mascarenes and from Hawai'i. We compared species richness, crown age and diversification rate between New Zealand and New Caledonian clade with a Mann-Whitney test. Correlation between species richness, crown age and diversification rate within New Caledonia were tested with a Spearman rank test.

NEW CALEDONIAN LINEAGES INCLUDED

Arecoid Palms

The palm flora of New Caledonia comprises several lineages within Arecoideae, that are all trees and that are mainly found in rainforests (Pintaud *et al.*, 2001). We follow here the classification of Pintaud & Baker (2008) and use the dated tree of Papadopoulos *et al.* (2011). The endemic genera *Clinosperma* Becc.-*Cyphokentia* Brongn. (6 species) form a monophyletic group that diverged from its sister group from Australia and New Guinea 6.1 My ago and has a crown age of 3.3 My. The endemic genera *Burretiokentia* Pic.Serm.-*Cyphophoenix* H.Wendl. ex Hook.f. (9 species) diverged from their widely-distributed, mostly Oceanic sister-group 4.5 My ago and have a crown age of 2.6 My. The endemic genera *Chambeyronia* Vieill. and *Kentiopsis* Brongn. (6 species) diverged from their sister group (mostly from Australia and New Guinea) 5.1 My ago and have a crown age of 2.0 My.

The endemic genus *Basselinia* s.l. (*Basselinia* Vieill. and *Alloschmidia* H.E. Moore) was not included because of doubt on its monophyly. In the analysis of Papadopulos (2011), *Basselinia* s.l. is not recovered as monophyletic as *Hedyscepe* H.Wendl. & Drude (Lord Howe Island) is nested within it. This study includes a single species of *Basselinia* s.s., which itself may not be monophyletic (Baker et al. unpublished in Pintaud & Baker, 2008). Therefore there is no reliable estimate of the crown age of *Basselinia* in a broad or a narrow sense, but its stem age is likely not older than 5.3 My, that is the age of the divergence between the clade formed by *Basselinia* s.l. and *Hedyscepe* from its sister group. Similarly, the following two genera were excluded: *Actinokentia* Dammer (a single species was included in the phylogenetic analysis of Papadopulos *et al.*, 2011) and *Cyphosperma* H.Wendl. ex Hook.f. (a non-endemic genus with a single endemic species).

Kermadecia-Sleumerodendron (Proteaceae)

The genera *Kermadecia* Brongn. & Griseb. and *Sleumerodendron* Viot are two endemic genera of large rainforest trees containing together 5 species (Viot, 1967). *Sleumerodendron* is the sister group of *Kermadecia* + *Turrillia* A.C.Sm. (Mast et al., 2008), the latter genus, endemic to Vanuatu and Fiji, most likely represents a secondary dispersal event from New Caledonia to these two archipelagos. The divergence between the clade containing these three genera and their sister group, the genus *Euplassa* Salisb. from South America is dated to 11.4 My (8.1-15.6, Mast *et al.*, 2008), the age of the crown clade is estimated at 9.8 My (4.9-11.4). Diversification for this clade was calculated only for the New Caledonian species and the dispersal to Vanuatu-Fiji was ignored in this calculation.

Dracophyllum (Ericaceae)

In New Caledonia, the genus *Dracophyllum* Labill. contains 9 endemic species (Wagstaff *et al.*, 2010) of shrubs or sometimes small trees. It is present mostly in maquis on ultramafic soils (Virot, 1975). In an analysis containing all New Caledonian species, Wagstaff *et al.* (2010) date the divergence of the New Caledonian clade from its Australian sister group to 6.7 My (4.0-9.7 My, Bayesian estimate) and the crown age to 5.2 My (2.6-7.2).

Pycnandra (Sapotaceae)

The genus *Pycnandra* Benth. is currently recognised as the largest endemic genus of the New Caledonian flora (Morat *et al.*, 2012) with 57 species of trees and shrubs of diverse ecology. In an analysis containing all but eight taxa, Swenson *et al.* (2008) found a basal split within the genus between the two clades BDCE and FGH. In an analysis of Chrysophylloideae, Bartish *et al.* (2011) included members of the Swenson *et al.* clades, D, G and H, thus allowing a reliable estimate of crown age: 23.6 My (18.3-29.7). The divergence between *Pycnandra* and its sister group *Niemeyera prunifera* F.Muell. from Australia is dated to 35.8 My (no deviation provided).

Metrosideros (Myrtaceae)

The genus *Metrosideros* Banks ex Gaertn. (Myrtaceae) is a genus of shrubs and trees with 18 species in New Caledonia (Dawson, 1992), found mostly in high-elevation maquis and forest. All New Caledonian species have been included in molecular phylogenetic analysis (Wright *et al.*, 2000), and a dating of the phylogeny is provided in Papadopulos *et al.* (supplementary data, 2011) that include both subgenera *Mearnsia* and *Metrosideros*. The clade A contains *M. punctata* J.W.Dawson, *M. humboldtiana* Guillaumin, *M. nitida* Brongn. & Gris, *M. engleriana* Schltr., *M. microphylla* (Schltr.) J.W.Dawson, *M. tetrasticha* Guillaumin and *M. cherrieri* J.W.Dawson (7 species) diverged from its sister group *M.*

ochrantha A.C.Sm. (Fiji) + *M. boninensis* (Hayata ex Koidz.) Tuyama (Bonin islands) 16.6 My ago, and the age of the crown is 13.7 My. Meanwhile, *Metrosideros whitakeri* J.W.Dawson, *M. dolichandra* Schltr. ex Guillaumin, *M. porphyrea* Schltr., *M. longipetiolata* J.W.Dawson and *M. brevistylis* J.W. Dawson (5 species) form clade B, which diverged from its sister group clade D (New Zealand) 21.7 My ago and the crown is dated to 11.5 My. *Metrosideros paniensis* J.W. Dawson, *M. operculata* Labill., *M. cacuminum* J.W.Dawson, *M. rotundifolia* J.W.Dawson and *M. patens* J.W.Dawson (clade C, 5 species) diverged from the New Zealand sister clade 29.9 My year ago and the crown age is date to 8.4 My. The last New Caledonian species, *Metrosideros oreomyrtus* Däniker is phylogenetically isolated and is therefore not very informative by itself. An alternative scenario may be that all New Caledonian *Metrosideros* descend from a single colonizer, and that multiple events of dispersal to other Pacific islands obscured its biogeographical history. If we considered the smallest clade including all New Caledonian *Metrosideros*, its crown age is 37.1 My and its stem-age 42.2 My. In statistical analyses on diversification rate, *Metrosideros* was considered as three distinct clades (three colonization events) as similar results were obtained if a single colonisation event was considered.

Nothofagus (Nothofagaceae)

The genus *Nothofagus* is represented in New Caledonia by a clade of five endemic species of rainforest, which have all been included in a phylogenetic analysis (Sauquet *et al.*, 2012). The crown age of this clade is estimated to 16.5 My (6.7-27.5, figure 2 of Sauquet *et al.*, 2012) and the divergence from the New Guinea sister group is estimated to 25.4 My (13.7-39.1).

Araucaria (Araucariaceae)

The genus *Araucaria* Juss. is represented in New Caledonia by 13 species of emergent trees in rainforest, maquis and coastal formations (de Laubenfels, 1972). The divergence between the New Caledonian *Araucaria* and their sister group *A. heterophylla* (Salisb.) Franco, endemic to Norfolk Island is dated to 14.4 My (26.6-6 My, Biffin, Hill & Lowe, 2010). AFLP (Amplified Fragment Length Polymorphism) data (Gaudeul *et al.*, 2012) suggests that within the New Caledonian clade the coastal group containing *A. columnaris*, *A. luxurians* and *A. nemorosa* is sister to the rest (including *A. rulei*). The divergence between *A. columnaris* Hook. and *A. rulei* F.Muell. is dated to 4.8 My (2.4-10.8) and corresponds therefore to the crown age of New Caledonian *Araucaria*. It is possible that *A. heterophylla* represent a case of dispersal from New Caledonia, and the stem-age of New Caledonian *Araucaria* would then be the divergence between the clade formed by the New Caledonian *Araucaria* and *A. heterophylla*, and *A. cunninghamii* (Australia, New Guinea) which is dated to 21.6 My (10.8-38.4).

Dacrydium (Podocarpaceae)

The genus *Dacrydium* Lamb. is represented in New Caledonia by a clade of four endemic species of shrubs and trees, growing in rainforest, maquis or on the banks of rivers and lakes (de Laubenfels, 1972). All four species have been included in a phylogenetic analysis (Keppel *et al.*, 2011) and the crown age is estimated to 5.5 My (no range provided). The divergence from its Fijian sister group is estimated to 9.6 My (2.9-18.9). It is possible that the two Fijian species are the result of a dispersal event from New Caledonia, and the actual stem-age of the New Caledonian *Dacrydium* may actually be the age of the divergence between the New Caledonian-Fijian clade and its South-East Asia sister group: 15.4 My (7.1-27.9).

Non-New Caledonian lineages

To compare speciation rate, we used all of the eight New Zealand lineages analysed in the study by Linder (2008), plus a clade of New Zealand *Metrosideros* (see below). We also used as a comparison the two largest plant radiations of the Hawaiian archipelago: the Hawaiian Lobeliads (126 species, crown-age of 13.2 My, Givnish *et al.*, 2009) and the Hawaiian *Cyrtandra* J.R.Forst. & G.Forst. (53 species, crown age of 4.4 My Clark, Wagner & Roalson, 2009). To compare diversification rate of closely related clade in and out of New Caledonia of closely related we also included the Hawaiian *Metrosideros* that have a crown age estimated at 4.7 My (Percy *et al.*, 2008). We also considered a group of *Metrosideros* Banks ex Gaertn. from New Zealand (clade D), including *M. parkinsonii* Buchanan, *M. fulgens* Sol. ex Gaertn., *M. perforata* (J.R.Forst. & G.Forst.) Druce, *M. carminea* W.R.B.Oliv., *M. diffusa* (G.Forst.) Sm. and *M. colensoi* Hook. f., of which the crown clade is dated to 25.2 My (Papadopulos *et al.*, 2011). Finally we added a clade of Arecoid palms endemic to the Mascarenes: *Acanthophoenix* H. Wendl.-*Tectiphiala* H.E.Moore (4 species) of which the crown clade is dated to 1.7 My (Papadopulos *et al.*, 2011).

DISCUSSION

Timing of colonisation

For all clade included in this study, colonization seems to have happen around 37 My (emergence of New Caledonia) or after (table 1, figure 2). The oldest stem age are found in *Pycnandra* (35.8 My), *Nothofagus* (25.4 My, 13.7-39.1) and *Araucaria* (21.6 My, 10.8-38.2), if we considered that *Araucaria heterophylla* (Norfolk) dispersed from New Caledonia. If New Caledonian *Metrosideros* are treated as a single clade, their stem age is 42.2 My (crown age is 37.1 My), the oldest monophyletic clade within New Caledonia (clade C) has a stem age of 29.9 My. All other stem-age are considerably younger. This suggest that the

colonization of these plants is more recent than the separation of New Caledonia from Australia and simultaneous or posterior to the re-emersion of the island ca. 37 My ago (Cluzel & Chiron, 1998). So far, therefore, all evidence is consistent with colonisation of New Caledonia by long-distance dispersal over water, as well as with a post-emersion origin of the flora, in agreement with the observations reviewed by Grandcolas *et al.*(2008) and Cruaud *et al.*(2012). This data does not provide evidence for survival of these clade on putative islands around New Caledonia during early Cenozoic, but do not allow to rule allow out this hypothesis. The colonisation of the plant lineages is concomitant with the overall cooling of the climate in the Oligocene and Miocene (figure 2, Zachos *et al.*, 2001), although the colonisation is not markedly simultaneous across lineages. Events of colonisation of New Caledonia are spread across the second half the Cenozoic, suggesting that the island was still able to be invaded by new migrants long after the arrival of the first lineages. Because of the limited number of observations and the coarse estimation of the time of colonisation (large intervals between stem and crown ages), it is not possible to determine if there has been a particular time when more colonisation events occurred or when any simultaneous onset of diversification was triggered. Only the ages observed for *Pycnandra* and possibly *Metrosideros* are congruent with an immediate colonisation of New Caledonia after emergence. An early arrival of *Metrosideros* would be consistent with its high dispersal capacity and its ability to grow on barren soils including young lava flow (Drake, 1992). Interestingly, when considering the two conifer group included in this study, both *Araucaria* (4.8 My) and *Dacrydium* (5.5 My) have a younger crown age than the average Angiosperms lineages studied (9.7 My). This is consistent with the conclusions of Nagalingum *et al.* (2011) and Crisp & Cook (2011) that extant Gymnosperms are not living fossils and therefore cannot be used as evidence for the persistence over a long period of time of the New Caledonian flora.

Synchronous arrivals of palm clade

A striking observation is the almost simultaneous independent colonisation of New Caledonia by the Arecoïd palms lineages, where the short time separating the stem-age and crown-age allows quite precise estimation of the time of arrival of these lineages. A somewhat similar pattern is observed in *Metrosideros* but not so clearly. This may be explained by the appearance of key-innovations in the common ancestor of these palms, possibly high dispersal capacity or features that allow them to outcompete other plants occupying the same niche. The relative youth, and the similar ages of the different lineages of the New Caledonia Arecoïd palms, which comprise all palms of the archipelagos except *Cocos nucifera* L. and *Saribus jeanneneyi* (Becc.) C.D.Bacon & W.J.Baker is striking. Palms from various clades have shown clear abilities to colonise distant islands (Mascarenes, Hawai'i, Lord Howe Island) and it can be accepted that they were among the earliest colonizers. It is possible that the New Caledonian environment was either not suitable for palms before relatively recently, or that the current Arecoïd palms have displaced a cortege of palms previously present, of which *Saribus* could be a survivor.

Age of New Caledonian ecosystems

The crown age of *Pycnandra*, 23.6 My (18.3-29.7) may be used to provide a conservative estimate of the latest arrival time of the first plants in New Caledonia. There are too few lineages included in the present study to reasonably date the different vegetations of New Caledonia. However the crown age of groups restricted to a given ecosystem can be considered to provide a conservative minimum age for the presence of these ecosystems. Considering the lineages restricted to rainforest, the crown age of *Nothofagus* is estimated to 16.5 My (6.9-27.5) , the crown age of *Kermadecia-Sleumerodendron* to 9.8 My (4.9-11.4),

and all Arecoïd palm lineages in New Caledonia are younger than this, the oldest having a crown age of 3.3 My. Therefore, in a conservative approach, it seems likely that rainforest has been present on New Caledonia for at least 6.9 My, but probably more. None of the lineages investigated here is restricted to maquis, although *Dracophyllum* is present mostly in this ecosystem. Its crown age is 5.2 My (2.6-7.2) and this could be considered a minimum age for this ecosystem. Data would be desirable for clades restricted to maquis such as *Dubouzetia* Pancher ex Brongn. & Griseb., *Greslania* Balansa or *Thiollierea* Montrouz.

Diversification rate

Diversification rates were relatively modest, ranging from 0.080 in clade B of *Metrosideros* (or 0.059 if *Metrosideros* is considered as a single clade) to 0.58 in *Burretiokentia-Cyphophoenix*, what is much lower than that observed in rapid plant radiation (Valente, Savolainen & Vargas, 2010). On average, speciation rates were lower than in New Zealand (0.236 vs. 0.516). However no significant difference was found between the two archipelagos regarding species-richness ($p=0.15$, Mann-Whitney test), crown age ($p=0.3$) and diversification rates ($p=0.17$). New Caledonian palms have a similar diversification rate to the Mascarenes endemic clade *Acanthophoenix-Tectiphiala*. New Caledonian *Metrosideros* have a higher diversification rate than the New Zealand ones, but lower than the Hawaiian ones.

Across the New Caledonian clades we found no significant correlations between species number and crown age ($p=0.69$, Spearman rank test), a nearly significant positive correlation between species number and diversification rate ($p=0.056$), and a significant negative correlation between diversification rate and crown age ($p=0.00079$). Therefore, species-richness within a clade does not seem to be explained by greater age or may be not by higher diversification rate. The fact that the youngest clades are the ones that diversify fastest and the absence of correlations between species richness and clade age suggests a slowing

down of diversification in the older clade, i.e. perhaps the occurrence of density-dependant diversification (Rabosky & Lovette, 2008; Rabosky, 2009). A slowing down in diversification rate has indeed been observed in *Pycnandra* and also in several New Caledonian animal lineages (Espeland & Murienne, 2011).

New Caledonia, an old community

Diversification rate in New Caledonia seems to be relatively low. It is possible the flora reached saturation some time ago and that the new species are only replacing species as they go extinct. Gillespie and Baldwin (2010) considered that the oldest Hawaiian islands particularly Kaua'i (4.7 My) may already have reached equilibrium, whereas in the youngest islands, Hawai'i and possibly Maui, the species number is still growing. It is also possible that the considerable isolation of this archipelago strongly limits the number of colonisers, and so these may have had more opportunity to diversify. Although the New Caledonia vegetation has existed for at least 23 My (crown-age of *Pycnandra*) and equilibrium may have been reached shortly after this, colonisation seems to have been possible for a long time after this, e.g. the youngest clade of this study (*Burretiokentia-Cyphophoenix*) arrived no earlier than 4.5 My (stem age). Compared to other oceanic islands, often of volcanic origin, New Caledonia may have a relatively old flora, allowing equilibrium to have been reached (MacArthur & Wilson, 1967). As time passed, extinction created phylogenetically isolated taxa but new species still appeared and others invaded the system. The continuous arrival of new taxa that compete with previous settlers could explain why there are no dramatic examples of adaptive radiation today in New Caledonian plants compared to those in other islands, whether these either never existed or they suffered extinction through competition. The apparent faster diversification rates in New Zealand may be explained by its relatively recent orogenesis and

the origin of the alpine biome which could have triggered a recent burst of diversification (Linder, 2008).

Compared to other areas that underwent intense diversification, the ten largest genera of the New Caledonia flora encompass 18.9% of the species compare to 29.1% in south-west Australia (Hopper & Gioia, 2004), 21.4% in the Cape Floristic Region (Goldblatt & Manning, 2002) and 32.3% in Hawai'i (Wagner, Herbst & Sohmer, 1999). Even of those genera may not form a monophyletic clade in each of these areas (but likely so in Hawa'i, Baldwin & Wagner, 2010), they are probably composed of one main radiation and this comparison gives an idea of the diversification opportunity of a small collection of closely related plant clades that exploit their environment in a similar. So, in the floras of Hawa'i, south-west Australia and the Cape, some large radiations seem to represent a much greater proportion of the flora. It is possible that some rapidly-diversifying clades tend to take over a community on settlement but, as time passes, more immigrants arrive and diversify and this gradually decreases the representation of the earlier fast-diversifying clades. This may be a manifestation of the density-dependant diversification effect that becomes stronger as the community approaches equilibrium. The flora of Hawai'i is still young because of the recent volcanic origins of these islands. Meanwhile, the floras of Cape Province and of south-west Australia underwent turnover as their climates became drier in the Cenozoic (Hopper & Gioia, 2004; Dupont *et al.*, 2011). Explosive radiation is expected by the neutral theory as a new community arises or if some dramatic change (e.g. climate) cause large-scale extinction (Hubbell, 2001). It is possible that New Caledonia has reached a greater degree of maturity than the three flora mentioned above. This may not be a matter simply of community age, it may take more time for a large community such as those of the Cape Flora or of south-west Australia to reach equilibrium, and the stability of the physical environment of a community is also difficult to determine over long periods.

Towards the study of large radiation in New Caledonia

This study suffers from the inclusion of several clades that have only a small number of species. One can expect that larger clades may also be older ones and also ones that diversify fastest. *Pycnandra* (57 species), the largest endemic genus included in this study, although probably the oldest coloniser in the groups investigated, does not have the highest diversification rate. At this stage, this is the largest endemic clade whose monophyly has been tested and confirmed with molecular phylogenetics. Further attention to the extensive New Caledonian radiations is therefore required. However there do not seem to be many larger radiations than *Pycnandra*. There are very few occurrences of endemic genera forming monophyletic clades outside the palms, and none of these is species rich. Only three genera have more species than *Pycnandra* in New Caledonia: *Phyllanthus* L. (108 endemic species), *Psychotria* L. (ca. 80 species, all endemic) and *Syzygium* Gaertn. (69 endemic species). New Caledonian *Syzygium* are not monophyletic and are composed of several independent clades (Biffin *et al.*, 2006), which may not exceed *Pycnandra* in size. This seems to be relatively common in the large New Caledonia genera, as the same pattern has been observed in *Planchonella* Tiegh. (Swenson, Munzinger & Bartish, 2007), *Diospyros* L. (Duangjai *et al.*, 2009) and probably *Pittosporum* Banks ex Gaertn. (Chandler *et al.*, 2007). Some genera such as *Eugenia* L., *Tapeinosperma* Hook.f., *Myrsine* L. or *Elaeocarpus* L. require further investigation. As for *Psychotria*, multiple colonisations are likely, although most species may belong to a single monophyletic clade of ca. 75 species (L. Barrabé, pers. comm.). *Phyllanthus* also colonised New Caledonia on multiple occasions (Kathriarachchi *et al.*, 2006), and it is not clear yet if there is one predominant radiation on the island within that genus. Therefore, there seem to be very few, if any, instances of large, explosive radiation within the New Caledonia flora.

CONCLUSION

As new studies on New Caledonian plants continue to be published, none have yet provided firm evidence for the persistence of vegetation throughout the Cenozoic but, instead, are congruent with a colonisation postdating the re-emersion of the island in the mid-Cenozoic. The occurrence of relict lineages seems to be misleading. The only firm evidence for the persistence of some lineages since the Cretaceous could come from fossils or a radiation in which the crown age pre-dates the re-emersion of the island (Crisp *et al.*, 2011). Plant lineages seem to have been able to colonise New Caledonia throughout the second half the Cenozoic and, so far, there is no evidence that there has been a particular time when colonisation has been more frequent or when diversification of multiple clades started simultaneously. Diversification rate seems to have been relatively slow and there is no correlation between clade age and species-richness. This suggests that density-dependent processes dominate. The New Caledonian flora may thus be a community that has reached equilibrium, albeit still dynamic. Further studies on large plant radiations may shed some light on the ecological parameters that triggered speciation, the trend of diversification rate over time, the importance of climatic oscillations or the principal mode of speciation (sympatric vs. allopatric).

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Figure 1. Inferring time of colonisation and onset of diversification from dated phylogeny. For illustration, we choose a simple case of colonisation of New Caledonia from an Australian lineage. The left-hand diagram illustrates what is probably the most common pattern, where the time of dispersal and first diversification event cannot be determined without fossils, but a maximum age is given to both by the observed stem age and a minimum age by the observed crown age. The middle and right-hand diagrams indicate alternative but less-likely scenarios, which may not be entirely disregarded.

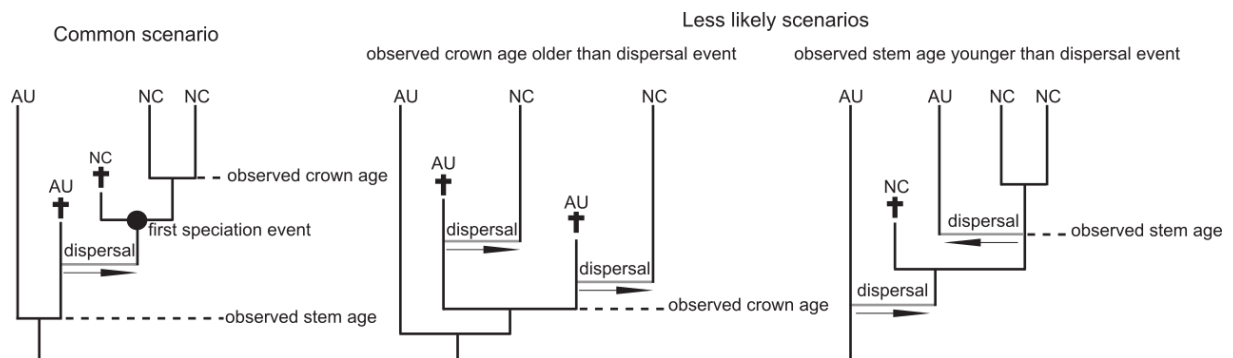


Figure 2. Estimated intervals of arrivals and first events of diversification of nine selected New Caledonian endemic clades, as delimited by observed stem and crown ages. Grey bars indicate standard errors where available. $\delta^{18}\text{O}$ is inversely proportional to global temperature (modified from Zachos *et al.*, 2001). Dispersal and onset of diversification of all clades considered are after the emersion of New Caledonia and contemporary with a global atmospheric cooling. There is no striking synchronicity across all nine clades.

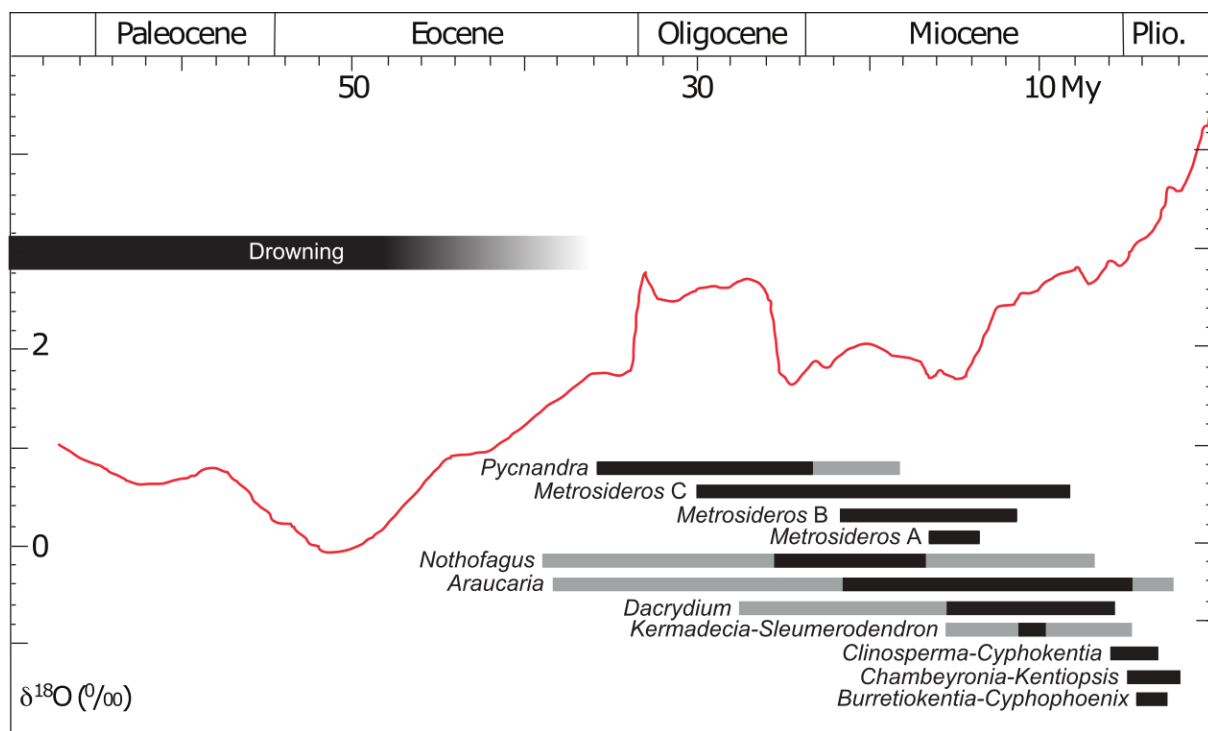


Table 1. Speciation rates for various clades of New Caledonian plants and a comparison with other regions. Alternative stem-age are given in parenthesis for *Araucaria* and *Dacrydium* (see methods). See text for references for species numbers, crown and stem ages, and for complete age range.

Clade	Species number	Stem age (My)	Crown age (My)	Diversification rate
New Caledonia				
<i>Clinosperma-Cyphokentia</i>	6	6.1	3.3	0.33
<i>Burretiokentia-Cyphophoenix</i>	9	4.5	2.6	0.58
<i>Chambeyronia-Kentiopsis</i>	6	5.1	2	0.55
<i>Kermadecia-Sleumerodendron</i>	5	11.4	9.8	0.093
<i>Dracophyllum</i>	9	6.7	5.2	0.29
<i>Pycnandra</i>	57	35.8	23.6	0.14
<i>Metrosideros</i> A	7	16.6	13.7	0.091
<i>Metrosideros</i> B	5	21.7	11.5	0.080
<i>Metrosideros</i> C	5	29.9	8.4	0.11
<i>Metrosideros</i> (one clade)	18	42.2	37.1	0.059
<i>Nothofagus</i>	5	25.4	16.5	0.056
<i>Araucaria</i>	13	14.4 (21.6)	4.8	0.39
<i>Dacrydium</i>	4	9.6 (15.4)	5.5	0.13
New Zealand				
<i>Abrotonella</i>	20		4.2	0.55
<i>Chionochloa</i>	22		5	0.48
<i>Forsteria</i>	7		6	0.21
<i>Gentianella</i>	30		2.05	1.32
<i>Hebe</i>	100		3.9	1.00
<i>Myosotis</i>	34		8.35	0.34
<i>Pachycladon</i>	8		2.25	0.62
<i>Scleranthus</i>	3		4.45	0.091
<i>Metrosideros</i> D	5		25.2	0.036
Hawai'i				
Lobeliads	126		13.2	0.31
<i>Cyrtandra</i>	53		5.2	0.63

<i>Metrosideros</i> Hawai'i	5	4.7	0.19
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Mascarenes

<i>Acanthophoenix-Tectiphiala</i>	4	1.7	0.41
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